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Insect Behavior

2ⁿᵈ Edition

Springer

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Second Edition

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Cover design: Boekhorst Design BV

Cover photo credit: The male Eastern Tiger Swallowtail, *Papilio glaucus*, shown here is one of the
most recognizable butterflies in North America; females of this species are dimorphic, appearing in both
yellow and black forms. Like many other butterflies, swallowtails are attracted to the aromatic flower
clusters of *Lantana* for nectar, but do not lay eggs on its somewhat toxic foliage. The authors took this
photograph in their garden.

Printed on acid-free paper

Preface to the Second Edition

This book is for all who are interested in the biological sciences. Like the course that originally inspired it, the text is designed for use at senior undergraduate level for college and university students, so we trust that it will find readership among those who have had some basic introduction to entomology and animal behavior. However, we also hope it will prove useful to newcomers who may be approaching behavioral study from other perspectives.

This is our second edition, born anew after thirty years. Much has changed during that time, especially in the breadth and depth of a field that (like us) was fairly young back in 1978. New technologies are allowing scientists to shape—and answer—questions in ways that once could not even have been envisioned. Insect behavior research now has wings, and is poised to take off. However, at this juncture, we all must also take care not lose an awareness of our roots. Thus, as writers introducing this exciting field of study to the next generation of scientists and insect enthusiasts, we have tried to strike a balance between new ideas and old, and between modern developments and historical insights.

Our objectives in writing this edition remain the same as they have always been. The first of these has been to help readers understand how a number of major behavioral systems function. Thus, this is not an encyclopedia, but an introduction to fundamental concepts and processes as seen from a comparative evolutionary viewpoint. We have not documented numerous strings of examples merely for 'completeness of coverage' but instead have tried to give a flavor of the diversity of ways in which insects approach similar life tasks. Because the Internet and excellent search engines have made access to information sources easy and nearly instantaneous, we have not burdened readers with a cumbersome citations in the text; searching on key terms, aided when necessary by references associated with figure credits at the book's end, will provide entry into additional literature for those interested in further pursuing subjects we can but introduce.

Our second objective has been to help readers gain insights into accessible ways in which behavioral research can be conducted. Whenever possible, we have included discussions of important experiments and investigations, rather than presenting a rhetoric of conclusions. Selected principles are interwoven with case studies of specific situations, presenting actual examples in a manner compatible with the dynamic, open-ended field and laboratory experiences in which they have arisen.

Like any writers of a general textbook, we recognize a deep obligation to many others—to those of whose work we write, to other authors whose ideas we use, to our own teachers who have shaped our perspectives and interests, and to our students, friends and colleagues with their many stimulating and invaluable suggestions and criticisms.

We also thank the many scientists and journal editors who have freely granted permission for the use of published material. Many colleagues have generously provided us with photographs, which are acknowledged in the credits list; special thanks are due to Douglas W. Whitman for contributing numerous new images and to Robert E. Silberglied and Carl W. Rettenmeyer, both now deceased, whose photographic talent continues to enhance this edition. We also are especially grateful to Joan W. Krispyn and Paul H. Matthews for numerous original drawings.

Athens, Georgia   Robert W. Matthews
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The History and Scope of Insect Behavior

1.1 Introduction

An overview of the insect world reveals two paradoxical characteristics: great diversity and equally great constancy. On the one hand, there are over one million named insect species, with estimates ranging up to three million. How can such a great diversity be explained? Study of this basic question has become the domain of evolutionary biology. On the other hand, each kind of organism tends to reoccur in virtually the same form with the same basic features for generation after generation. Why do they tend to show such constancy, such resistance to change? The study of this question, in turn, is largely the domain of genetics. Together, these two great branches of biology—evolution and genetics—form a powerful tool for the investigation of nearly every aspect of life. This introductory chapter deals briefly with their application to the study of behavior and then turns to an overview of behavior as a field of study to provide a perspective for the chapters that follow.

1.1.1 What Is Insect Behavior?

A flashing firefly flits through the evening shadows. In a tree, a caterpillar pauses in its feeding, stiffens, and sways back and forth. Behind a stone, a cricket chirps, while nearby ants scurry along in precise single file.

Behavior can be simply defined as what animals do. More precisely, it is the ways in which an organism adjusts to and interacts with its total environment. As such, insect behavior encompasses the relationships an insect has with members of its own species, with members of other species, and with the physical environment. A species must behave in the 'right' ways in order to survive, and its members must survive (at least long enough to successfully reproduce) if it to be evolutionarily successful.

Admittedly, the term 'behavior' covers a very wide range of activities, and it can be helpful to recognize some subcategories. General locomotion, grooming, and feeding, for example, are essentially individual matters. These *maintenance* activities keep an insect in good shape but usually have little influence on others

of its kind. On the other hand, a broad range of *communication* activities are concerned with conveying information to, and influencing the activities of others. Often such actions are conspicuous and stereotyped, and not surprisingly they have been a favorite study material for behaviorists. The firefly's flash and the cricket's chirp may have the same function, to gain a mate. The caterpillar in essence sends the predator world the message that it is not food. The ants share their message that travel along this particular trail is apt to be rewarding. But while the firefly, cricket, and ants are communicating with their own kind, the caterpillar obviously is not. Thus, insect communication signals come in two broad, somewhat overlapping categories; even when the method of signaling is the same, the results of intraspecific and interspecific communication are quite different.

This division is broadly reflected in the book's organization. The first chapters concern behavior of the individual insect—how it moves, orients, disperses, and feeds, including the role of the nervous and endocrine systems in integrating behavioral responses. The chapters on communication in a sense form the core of the book and logically relate to defensive, reproductive, and social behaviors, all of which are mediated by communicative codes.

The question 'what is insect behavior?' also can be answered another way. Insect behavior is, of course, a discipline nested within the larger field of animal behavior study. For many thousands of years, humans and their ancestors have keenly observed animal habits and characteristics for entirely practical reasons, ranging from the need to hunt game animals to the desirability of avoiding biting insects and encouraging useful ones. Early Greek and Roman scholars such as Aristotle and Pliny often wrote at some length about the natural world, including its insect inhabitants. However, the rigorous scientific study of animal behavior only began in the latter part of the nineteenth century, with the convergence of three major developments—publication of the theory of evolution by natural selection, development of a systematic comparative method, and studies in genetics and inheritance. In the 1930s, Darwinian natural selection was combined with Mendelian inheritance to form what is called 'the modern evolutionary synthesis', an explanation of ways in which natural selection and genes interconnect (see Section 1.2.2).

Over time, from these beginnings, different major research areas arose within the general field of animal behavior. One approach concentrated on the mechanisms controlling behavior; this became the fields of comparative animal psychology and physiology. A second approach concentrated on the functional significance and evolution of behavioral traits, especially in natural settings; this became the field of ethology. Somewhat later, a third area of study concentrated upon the biological relationships between an organism and its environment, especially from an ecological and evolutionary viewpoint; this became the field of behavioral ecology. Most recently, significant technological genetic advances have been enabling and supporting the emergence of behavioral genetics and behavioral genomics as new research concentrations.

In this way, four great disciplines have contributed to the study of behavior—physiology (particularly neurophysiology), ecology, ethology, and psychology. There are no distinct boundaries, yet each has had its own developmental history

and tradition of established methods and brings its own viewpoint to the subject. Somewhat facetiously, they once were distinguished from one another by behavioral scientist Kenneth Roeder as follows: The ethologist, attempting to leave the animal as unrestricted as possible in order to study its 'normal' behavior, tolerates any necessary discomforts while enclosing himself in a blind. The psychologist, attempting to reduce external variables, places the blind around the animal, thereby making it uncomfortable. The physiologist, attempting to learn what makes the animal behave, removes it from the blind and probes directly into its nervous and motor systems. The behavioral ecologist, we might add, spends his time studying how the blind itself affects the animal's behavior. Finally, the behavioral geneticist snips off tiny samples of the animal and takes them behind the blind for a closer look.

As will become evident in the examples in this book, in recent years these approaches have increasingly melded back toward a single discipline that contains elements of all of these approaches. This does not mean that these fields have lost their distinct character; in this chapter we'll touch on what that means for behavioral insights. However, it does mean that no matter what they may call themselves and what direction they may approach a problem from, insect behaviorists today pursue quite comparable goals and rely upon shared theoretical frameworks.

1.1.2 Insect Behavior's Biological Context

Insects make up a significant proportion of the world's biota (Fig. 1.1). The approximately 920,000 species that have been described represent almost 85% of all known animal species; many more have yet to be been given scientific names.

Insects belong to the phylum Arthropoda, a very large assemblage of animals with jointed legs and a hard outer skeleton. One major group in this phylum, the Chelicerata, have sickle-shaped jaws and lack antennae; they include the Arachnida (spiders, mites, scorpions, etc.) and two smaller marine groups. The other major group, the Mandibulata, possess antennae and have mandibles (mouthparts) that work against each other. Besides the insects (including the entognathous hexapods), other major groups in the Mandibulata are the crustaceans (a predominantly aquatic group), the centipedes, the millipedes, and two smaller classes, Symphyla and Paurapoda. Of all the land arthropods, insects are by far the most abundant, followed by mites and spiders.

The class Insecta is divided into a number of orders. The exact lines along which these divisions should be made remain a matter of dispute, but in general, ordinal divisions reflect the present understanding of the evolutionary history of the class (Fig. 1.2). More than one-third of the named species of insects are beetles, the Coleoptera. The next largest orders, in descending numbers, are Lepidoptera (butterflies, moths, and skippers), Hymenoptera (wasps and bees, and Diptera (flies). Together, these four orders include more than 80% of the named species of insects.

Broadly speaking, four important stages are distinguished. First was the appearance of primitively wingless insects (including the three orders of entognathous

PERCENTAGES OF DESCRIBED SPECIES
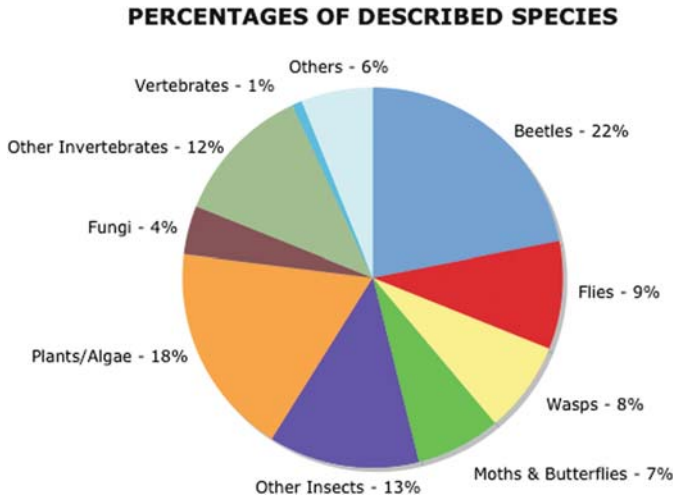
Fig. 1.1   Tallying the numbers. Insects comprise a major proportion of the world's biota, and beetles make up a major proportion of the Insecta

hexapods) probably in the late Silurian Period. Bristletails and silverfish are living representatives of these earliest insect forms. Second was the development of wings, hypothesized to have occurred during the late Devonian or early Carboniferous. These early winged insects had a wing-hinging mechanism that did not permit the wings to fold, so they had to be held out from the body. The Ephemeroptera (mayflies) and the Odonata (dragonflies and damselflies) are surviving remnants of these ancient groups.

The third stage, the Neoptera, developed a different wing flexion mechanism, that had evolved by the late Carboniferous. Now able to fold their wings down tightly over their abdomens, insects could more easily run and hide from predators and move into a wide variety of previously inaccessible niches. Among contemporary insects, roughly 97% have flexing wings, and this mechanism is one reason for the dominance of insects today.

The fourth important stage was the development of complete metamorphosis (holometaboly), which also seems to have arisen by the late Carboniferous. The earliest insects remained essentially similar in their wingless body form throughout their entire lives. More advanced groups developed the simple metamorphosis exhibited by insects such as grasshoppers today, where immature stages resemble miniature adults but wings are lacking (although external wing buds are plainly visible) until the last molt, when the insect becomes sexually mature. The most highly advanced groups, however, evolved the complete metamorphosis illustrated by the familiar life cycle of a butterfly. The immature stages, the larvae, bear no resemblance to adults, and wing buds are developed internally, becoming visible only when the larva transforms into the pupal stage, from which the winged adult emerges.
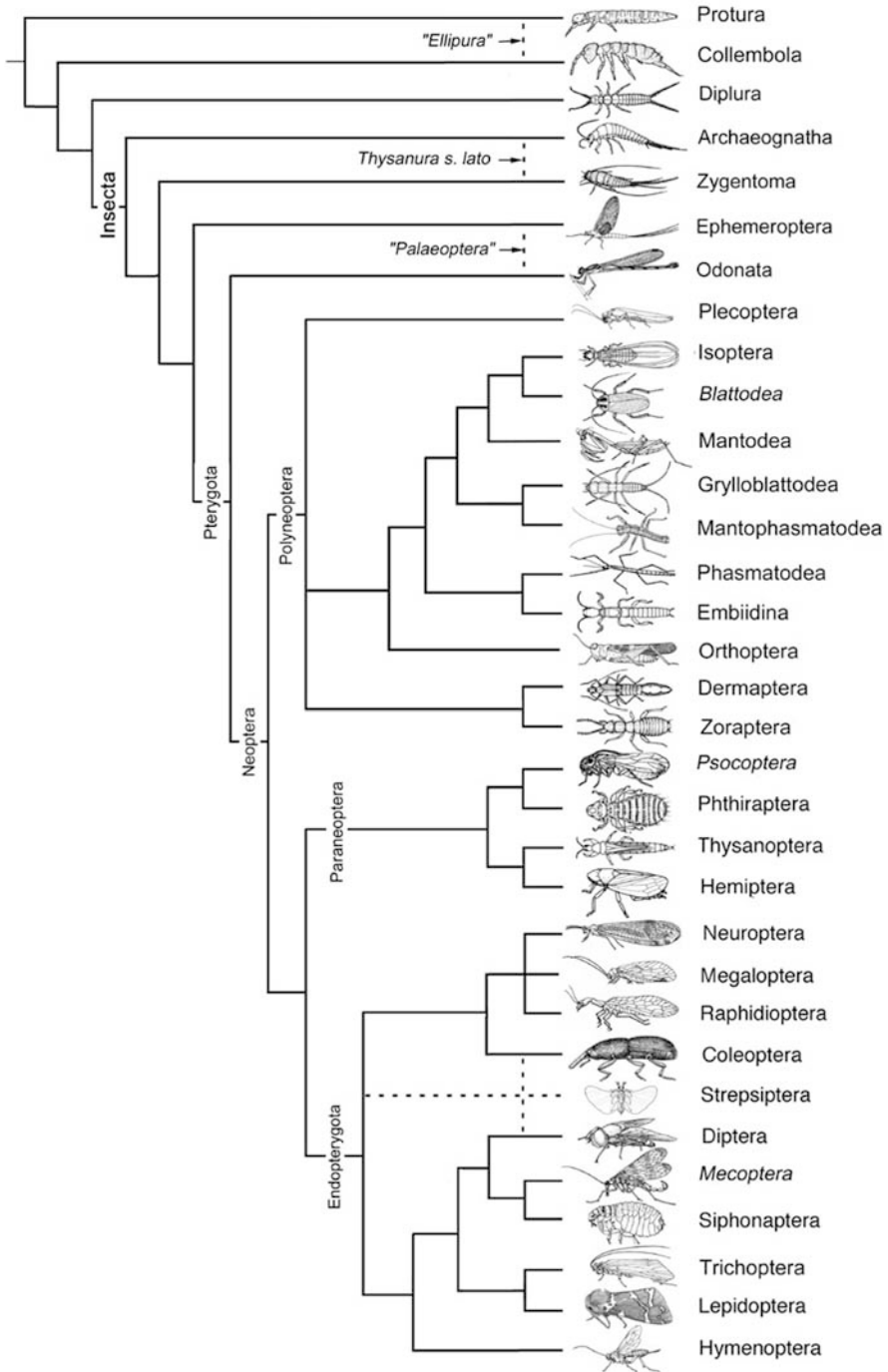
Fig. 1.2 Looking for connections. Probable evolutionary relationships among the living insect orders

1.1.3 Historical Foundations

The earliest observers of animal behavior were almost certainly driven by the need for animals as a source of food, clothing and raw materials for tools, but curiosity about the natural world has been part of the human experience since earliest times, and ancient perceptions were often surprisingly astute. As ubiquitous as they are, insects have been common elements in human folklore, superstitious tales, and mythology from earliest times. These stories serve a variety of purposes, from reenacting significant events such as the creation of the earth to instilling moral lessons or providing instructions for living one's life in a particular way, to simply entertaining the listeners. However, often they were an attempt to explain natural phenomena in a way that made sense to nonscientific minds. Explanations for commonly observed insect behavior often still take the form of folk tales and rhymes, such as the story from the Tahltan of British Colombia in which a beetle larva and a mosquito lived together. The envious larva asked the mosquito where it was able to find food so regularly, and not wanting to divulge its secret, the mosquito replied that it sucked its meals out of trees. The larva began boring into wood looking for food, an activity that continues to this day.

The many volumes of observations about animals compiled by scholars such as Aristotle (384–322 B.C.E.) and Pliny (C.E. 23–79) show that animal natural history has been a matter of extensive interest for some time. Some of these observations were quite astute. For example, a famous gold pendant from the Minoan culture some 2000 years B.C.E. very accurately depicts the essentials of the life cycle of a common social wasp (Fig. 1.3) and reveals a rather sophisticated understanding of these insects.

However, in other cases observations were misconstrued by incomplete knowledge about what was occurring or biased by beliefs based on religion or philosophy. As a case in point, consider *spontaneous generation*, the idea that living things could arise from non-living sources (Fig. 1.4). One of the most persistent of such misconstrued beliefs, it held sway for two millennia. Aristotle is credited with synthesizing this theory, compiling and expanding the work of earlier natural philosophers and various ancient explanations of the appearance of organisms; his examples included the generation of maggots from rotting meat, mice from dirty hay, birds from trees, and lice from sweat.

In the days before microscopes and careful scientific investigations, the ideas seemed quite reasonable to most people, but how could spontaneous generation be reconciled with Christian beliefs? Pope Innocent V in the thirteenth century had declared that belief in spontaneous generation went against Church teachings, since all life was created in the first days of Creation chronicled in Genesis. Saint Thomas Aquinas concluded that spontaneous generation of insects was the work of the Devil. The Greek tradition prevailed in the scientific community.

As the seventeenth century turned to the eighteenth, experiments and natural history observations began to rebut the prevailing opinions. Studies of insects led the way. One of the first experiments in the modern sense (with the use of controls) was the classic study of Francesco Redi (1668) who showed that maggots did not

Fig. 1.3   Depicting nature. An ancient pendant, considered one of the most outstanding examples of early Minoan goldworking, shows two paper wasps, *Polistes*. Their legs embrace a granulated disc thought to represent the paper nest; a droplet of food or wood pulp is held in their jaws. The cage-like fixture atop the heads may be an attempt by the artist to depict the vigorous antennal beating characteristic of all encounters between individuals on a nest. The opposition of the abdominal tips may have been intended to suggest mating, but is biologically inaccurate; more probably it reflects the heraldic symmetry common in Minoan art. Most classics texts incorrectly refer to the insects as bees, sometimes with elaborate explanations about the symbolism inherent in the 'honey droplet' between their jaws

arise spontaneously from rotten meat. Maria Sibylla Merian (Fig. 1.5) took the bold step of actually studying butterflies and moths throughout their entire life cycles, taking detailed notes and making careful illustrations. However, when Merian published her lavishly illustrated works, the scientific community largely ignored them although both Linnaeus and Fabricius's subsequent insect descriptions were apparently influenced by her work. The invention of the microscope in the 1600s might have resolved the matter of spontaneous generation but in fact it only served to enhance the belief by revealing a whole new world of microorganisms that appeared to arise spontaneously. The controversy around spontaneous generation continued until it was ultimately settled by the experiments of Louis Pasteur in the nineteenth century. Finally, well into the twentieth century, the work of Maria Merian was rediscovered and recognized. Her portrait has been printed on German postage stamps and was on the 500 DM note before Germany converted to the euro; in addition, many schools (and a modern research vessel) have been named after her.

The first 'major player' to introduce elements of scientific discipline to insect study was Rene Antoine Ferchault de Reaumur. Reaumur was a widely trained scientist who made major contributions to areas as disparate as geometry, metallurgy, and meteorology, but many consider his greatest work to have been in

Fig. 1.4 Explaining insect life. A sixteenth-century woodcut supposedly shows honey bees being generated spontaneously from a dead animal. Some medieval texts contained detailed directions for creating insects from substances as varied as dead animals, logs, and dirt

entomology. Published between 1734 and 1742, his six large volumes of *Memoirs pour Servir a l'Histoire des Insectes* applied precise observation, detailed experimentation, and accurate recording to phenomena as varied as social life, parasitic habits, and leaf-mining.

The historical development of the scientific field of animal behavior (and insect behavior as a sub-discipline within it) accelerated from about 1750 onward. At this time, all of European society was becoming 'scientific', and each important expedition began to include at least one professional naturalist. As a result so many exotic plant and animal specimens were being brought back to Europe from around the world that chaos loomed for the naturalists who were trying to identify, classify, and communicate what they gathered. Linnaeus' method of classification was gaining increasing exposure and acceptance as a way to organize all these data. When the tenth edition (1758–1759) of his *Systema Naturae* was chosen as the starting point for zoological nomenclature, it marked a major milestone in biology.

Thus, by the time the 1700s drew to a close, three kinds of entomological texts were prevalent. First, there were beautifully colored illustrative works such as those of Maria Merian. Second were descriptive classificatory works, such as Linneaus' *Systema Naturae* with its system of binomial nomenclature. Third were detailed works such as those of Reaumur's *Memoirs*, detailing specific aspects of insects such as their development, physiology, or internal anatomy.

Fig. 1.5   Illustrating the truth. Rejecting spontaneous generation, Maria Merian accurately unraveled the mysteries of metamorphosis in many Lepidoptera in the late 1600s, and published her findings in beautifully illustrated detail. (*left*, a portrait by her son-in-law, Georg Gsell; *right*, her drawing of the silkworm life cycle.)

However, for the next half-century it would still be a time when general observation predominated over specialization. Enthusiasm and subjectivity often affected the accuracy of behavioral observations, and interpretations were often slanted to embrace a particular philosophical creed. Most scientists still subscribed to Aristotle's Scala Naturae, a theory that all living beings could be classified on an ideal pyramid. The simplest animals occupied the base, and complexity rose progressively to the top, which was occupied by human beings. Animal species were generally thought to be eternal and immutable, created with a specific purpose (by which most people meant 'created by God to serve mankind'). It seemed like the most logical, and perhaps only possible, explanation for the incredible variety of living things and their surprising adaptations to their environment.

1.1.4 The Watershed Years

During the latter half of the 1800s, three conceptual advances occurred that were so revolutionary they deserve independent mention: evolution by natural selection (Section 1.2.1), the discovery of the genetic bases of biology (Section 1.2.2) and the development of a comparative approach to biological study (Section 1.2.3).

Keeping those developments aside to consider separately, consider for a moment the scientific mileau into which those three developments emerged. It has been said

that upon seeing an animal, the first question of both layman and scientist alike is always, 'What is it?' During the 1800s, a major driving force in science was the need simply to identify, name and classify the diversity that was present. The problem was particularly acute for places that were less well studied than the Old World that most scientists called home. With a system of binomial nomenclature having been established only relatively recently, and an entire world beckoning, the adventure of collecting and classifying organisms called out to many natural historians.

One who answered that call was John Lawrence LeConte. Like many scientists of his day, LeConte had the money and connections to indulge his passion. A few months after he was born in New York City, his mother died; raised by his father, a well-known naturalist, LeConte trained as a medical doctor. He never officially worked as an entomologist—the field was still too new for that. During the American Civil War he worked as a surgeon with the California volunteers, reaching the rank of lieutenant colonel. In 1878 he became the chief clerk (assistant director) of the United States Mint in Philadelphia, and retained that position until his death. Throughout his life, he traveled abroad extensively, explored the Colorado River, and accompanied the teams that built the Honduras Interoceanic Railway and Kansas Pacific Railroad.

Over the course of his life, LeConte almost single-handedly put American entomology on the map. He published his first scientific work in 1844, while he was still in medical school. Everywhere he went, he sent back insect specimens, sometimes by the tens of thousands. In all, he was responsible for naming and describing approximately half of the insect taxa known in the United States during his lifetime, including some 5,000 species of beetles. (Not surprisingly, he is often described as 'the father of American beetle study'.) Le Conte was probably the best known entomologist of his century, but it was a time of rapid growth and expansion in the sciences, and LeConte was part of an entire roster of insect afficionados whose names are still familiar to working scientists today. His influence was considerable, for LeConte was also very active in the scientific societies of his time; in addition to serving as vice-president of the American Philosophical Society and president of the American Association for the Advancement of Science, he was a founder of the American Entomological Society, and a charter member of the National Academy of Sciences.

Meanwhile, in France, the late nineteenth century had introduced the works of Jean-Henri Fabré. Born a pauper, his education and opportunities were limited. He was an avid naturalist, not a scientist; a moody and morose soul, his personal life reads like a tragic drama. However, the publication of his romantically titled *Souvenirs Entomologiques*, a set of ten volumes describing in detail the lives of insects in his own backyard, popularized insect behavior in writings that achieved the heights of literary excellence. (In both 1904 and 1911, he was nominated for a Nobel prize in literature.) Modern scientific advances have rendered much of his work obsolete, and for a time the scientific community had difficulty accepting him, particularly because he vigorously rejected the theory of evolution and was absolutely convinced of the 'fixity of instinct'. However, Fabré was one of the greatest popularizers of entomology the world has ever known, and his work served to

establish standards of observational patience and accuracy that subsequent workers were to continue. In addition, in the process of countering his ideas, his critics frequently made valuable contributions of their own, particularly in helping to focus on the variability of behavior and emphasizing the necessity for a firm taxonomic foundation for behavioral studies.

In emphasizing the growth of entomology as a field of study within zoology, it is important also to acknowledge that the study of insects has a unique twist because insects and humans have always had an uneasy relationship. In the struggle for human survival and well-being, insects have also been relentless pests, competitors for food and fiber, and threats to human health and comfort. When human agriculture arose, a mere 10,000 years ago, primitive hunter-gatherers entered into a new partnership with plants that intensified this antagonism. There are records of the Sumerians using sulfur compounds as insecticides over 4,500 years ago; the Rig Veda, which is about 4,000 years old, also mentions the use of poisonous plants for pest control. Ancient Chinese and Egyptian cultures are known to have used chemical pest controls. With the industrialization and mechanization of agriculture in the eighteenth and nineteenth century, chemical pest control became widespread, a development that accelerated with the twentieth century discovery of several synthetic insecticides, such as DDT.

Thus from the beginning, there has been a basic duality in entomology's aims, and it continues to this day. One branch of the field studies insects for the basic love of them; the other, with a desire to control or kill at least a certain subset of them. The former is often called 'basic' entomology; the latter, 'applied' or 'economic' entomology. Economic entomology involves the study of insects that are of benefit or those that cause harm to humans, domestic animals, and crops, often with intent of either eliminating, reducing or augmenting their numbers. Insects that cause losses are termed as pests; those that cause indirect damage by spreading diseases, vectors. Those termed 'beneficials' include insects valued for food products such as honey, for substances such as lac or pigments, for pollination, or as natural enemies for pest control.

Because control efforts offered immediately obvious benefits (at least theoretically and often as a practical outcome), economic entomology was a great driving force behind the establishment of insect study as a separate field. Across the United States, one state after another appointed state entomologists, beginning in 1854 with the appointment of Asa Fitch as the first professional Entomologist of the New York State Agricultural Society. The field grew even more rapidly in the late nineteenth and into the twentieth century, with the appearance of an influential body of reports written by Charles Valentine Riley and the establishment of the US Department of Agriculture.

Concurrently, similar government-sponsored growth in entomology occurred through military service, setting the stage for a new field of medical entomology. One of its early successes occurred when Walter Reed, a United States Army major, was appointed president of a board 'to study infectious diseases in Cuba paying particular attention to yellow fever' (Fig. 1.6). (Although Reed received much of the credit in history books, Reed himself correctly credited the Cuban doctor Carlos

Juan Finlay with identifying *Aedes* mosquitoes as the yellow fever vector and thus determining how yellow fever could be controlled.) Not long afterward, Carlos Chagas observed the peculiar infestation of rural houses in Brazil with *Triatoma*, demonstrated that it was the vector of *Trypanosoma cruzi*, and proved experimentally that it could be transmitted to marmoset monkeys that were bitten by the infected bug. His description of the new disease was to become a classic in medicine and brought him domestic and international distinction.

Fig. 1.6   Discovering a killer's cause. Yellow fever was one of the most dreaded diseases in port cities of the Americas. Poorly understood and feared as cancer is today, and known to have its origins in the Caribbean region, the disease was thought to spread directly and through contaminated clothing and bedding. When yellow fever became a problem for the Army during the Spanish American War, felling thousands of soldiers in Cuba, Major Walter Reed, M.D. (*left*) headed a team that proved that yellow fever is transmitted only by *Aedes* mosquitoes (*center*), confirming a theory first set forth in 1881 by Cuban doctor/scientist Carlos Finlay (*right*). The insight gave impetus to the new fields of epidemiology and biomedicine, and allowed the United States to build the Panama Canal, something that had confounded the French attempts only 30 years earlier

The 'basic' side of entomology also grew rapidly during this time. In 1901, the first widely used textbook, A. D. Imms' *General Textbook of Entomology* was published; going through numerous editions, for close to a century it remained one of the most widely used of all insect texts. At Columbia University, Thomas Hunt Morgan became one the first to conduct genetic research with the fruit fly *Drosophila melanogaster*, a development that would ultimately underpin the field of behavioral genetics.

In a similar way, all of animal behavior study was growing and subdividing into a multidisciplinary subject. The nineteenth century was a time when the nature of scientific enquiry was changing in ways that would have major impact on the field of insect behavior. In addition to general natural history studies, an increasing number of specialized disciplines began to characterize the natural sciences. Psychologists, anthropologists, ecologists, geneticists, and many others who contribute to the study of animal behavior can trace early common roots back to this period. It was during this time, born in the principles of evolution delineated by Charles Darwin and nurtured by this convergence of entomology and more objective scientific analysis, that modern insect behavior arose. However, as a field of study it went on to show its

greatest development after the turn of the century, with the emergence of the largely European school of ethology.

1.1.5 The Rise of Ethology

The word *ethology* has a long pedigree. Based on the Greek *ethos*, which has a variety of meanings, the term has been applied to everything from stage actors who portray human characters to people who study ethics. However, as it is used today, ethology means the study of the behavior of animals in their natural habitat. The term was first popularized in English by the American myrmecologist William Morton Wheeler in 1902, but it was hardly a new idea. Over 3,000 years ago, King Solomon recommended the study of insects in their natural habitat with those famous words in Proverbs 6.6: 'Go to the ant, thou sluggard; consider her ways, and be wise.'

In the early years of the twentieth century, two different major conceptual approaches to animal behavior study split off from one another. For most of the twentieth century, the discipline of comparative psychology developed most strongly in North America, whereas ethology was stronger in Europe. This led to different emphases, different philosophical underpinnings, and different experimental approaches. Comparative psychology came to pay particular attention to the psychological nature of human beings in comparison with other animals. A practical focus on laboratory studies made a logical base for experimental studies on human and animal brain function, learning, and motivation. Well-known studies include those of Ivan Pavlov on conditioning in dogs, Harry Harlow on the effects of social deprivation in monkeys, and those of various researchers on language abilities in apes.

In the 1920s and 1930s, when most behavioral research was laboratory based emphasizing the role of learning and hormones in the modification of behavior, two Europeans, Konrad Lorenz and Nikolaas ('Niko') Tinbergen, began publishing intensive and extensive natural behavior studies that quickly caught the attention of scientists and the general public. As their carefully detailed work unfolded, so did the foundations of ethological theory. As in most cases, their scientific work owed a debt to others. In a sense, Charles Darwin might be called the first modern ethologist; his book, *The Expression of the Emotions in Man and Animals*, continues to influence ethologists today. Some scholars would acknowledge Darwin's protégé George Romanes (see Section 1.2.3) as another 'father' to the field, despite his odd methods. Other clear leaders were Oskar Heinroth and Julian Huxley, who both concentrated on behaviors they called instinctive, or natural. Their focus was upon building an objective cumulative base of data about behavior. Thus, their first step in studying the behavior of any new species was to construct an *ethogram*, a kind of glossary describing each type of natural behavior shown by the animal and the frequency of that behavior's occurrence.

Later chapters in this book will return to the ideas of Lorenz and Tinbergen; for now it enough to realize that their research rested on a different practical and

philosophical foundation. Whereas the comparative psychologists focused on laboratory work in order to have more control over environmental parameters and over knowledge of an animal's history, these European behaviorists emphasized the study of animals in their natural environment, so that behaviors could be more easily placed in context and their evolutionary relationships could be more easily discerned. They also typically focused on a behavioral process rather than a particular animal group, and they often studied one type of behavior (such as aggression or sociality) in a number of unrelated animals. In this they also differed from comparative psychologists, who despite the name of their discipline, focused their efforts almost exclusively on the white rat.

The work of Lorenz and Tinbergen set in motion a whole new approach to behavior study. First, it provided hints of a general order and logic in the behavior of animals. Second, it demonstrated that certain behavior patterns are just as characteristic of species as certain morphological features are. Third, because it regarded behavior as part of every organism's equipment for survival and the product of adaptive evolution, its focus was the objective study of whole patterns of animal behavior under natural conditions. Thus, it emphasized the functions and evolutionary history of behavior patterns. Behavior, they said, always has a cause, and it always has one or more functions.

Through the efforts of Lorenz, Tinbergen, and their colleagues, ethology developed robustly in continental Europe in the years before World War II. After the war, Tinbergen moved to Great Britain, and ethology became much stronger in the United Kingdom. It was a time of increasing transcontinental study, and at this time ethology also began to take hold in North America. Similar travel in the other direction carried comparative psychology to Europe. As the years have passed, there has been an increasing realization that both approaches have their strengths and limitations, although it took a while before this was grudgingly acknowledged on both sides of the Atlantic.

Lorenz, Tinbergen and their early followers dealt mostly with birds, and included insects (and fish) only in passing. However, as the field has developed, it has come to encompass all animals and even human beings. Modern ethology combines laboratory and field science. It has strong ties to other disciplines such as neuroanatomy, ecology, and evolution. Since the 1970s, the field has subdivided once again, this time into comparative ethology and social ethology. The latter concentrates on the behavior of social groups and the social structure within them; jointly with evolutionary psychology, it lays claim to the study of sociobiology.

The appearance of insect behavior as a separate sub-discipline is a relatively recent phenomenon, but it shares a conceptual base with the entire field of ethology. Like all of behavioral research, insect behavior is still relatively young, however, and as such it lacks the strong theoretical framework that has come to typify more mature sciences such as chemistry. Additionally, since insects comprise over three fourths of all animals, insect behavior is a potpourri of knowledge and ignorance. Insects provide some of the most outstanding and best-developed examples of behavioral phenomena, notably in the areas of communication, courtship, mimicry, and the

development of sociality. But at the same time, even according to very liberal estimates, fragmentary behavioral data (host records, food plants, etc.) are recorded for no more than 5% of the described insect species; the number of species subjected to intensive investigation is far smaller yet.

1.2 Conceptual Frameworks

The rigorous study of animal behavior, and insect behavior as a subfield within it, began with three major developments in the last half of the 1800s: publication of the theory of evolution by natural selection, studies in genetics and inheritance, and development of a systematic comparative method. To understand the conceptual frameworks that underlie biological study in general and insect behavior study in particular, let us briefly consider each of these developments in turn.

1.2.1 Evolution by Natural Selection

Few people have never heard of the theory of evolution by natural selection and Charles Darwin's book, *The Origin of Species*. Darwin formulated his idea of natural selection in 1838 and was still developing his theory in 1858 when Alfred Russell Wallace sent him a similar theory that he had independently developed from his own data set. The works of both men were presented to the Linnean Society of London in separate papers.

Though these publications set a major paradigm shift in motion throughout the entire scientific community, their theory of evolution did not develop in a vacuum. It drew its ideas from the contributions and suggestions of many other people, from the selective breeding experiments of English farmers to the ideas of Thomas Malthus about human competition for survival and the fossil observations by geologist Sir Charles Lyell that suggested a process of continuous change in living material through time.

Jean-Baptiste Lamark, not Charles Darwin, actually was the first prominent biologist to set forth a complex theory of evolution. His theory proposed two major new ideas. One was that animal organs and behavior were not fixed; they could change according to the way they were used, and these changes could be transmitted from one generation to the next. The second idea was that every living organism, human beings included, tends to reach a greater level of perfection over time. Darwin was fully aware of these theories at the time of his journey on the H.M.S. Beagle, and he was deeply influenced by them. As an interesting historical side-note, whereas much debate ensued in England over Darwin's publication, it was a non-event in France. In the eyes of the French, Darwin was just attempting to reformulate theories already put forward by two of their own scientists, Lamarck and Etienne Geoffroy

Saint-Hilaire, a prominent colleague of Jean-Baptiste who expanded and defended Lamarck's evolutionary theories.

In a sense, one could say that the theory of evolution by natural selection gained its immediate prominence because it arrived at a point in history that provided a 'perfect storm' for its acceptance. As such, it set the stage for modern biological science and remains the foundation of every behavioral explanation couched in ultimate analysis terms. However, because the theory is often misunderstood, it is worth briefly reviewing what the theory is and is not.

Evolution refers to the natural or artificially induced process by which new and different organisms develop as a result of changes in genetic material. Although Darwin and Wallace did not have the benefit of modern genetic knowledge, they astutely recognized that evolutionary change is inevitable if just three conditions are met. First there must variation; some members of a species must differ in some of their characteristics. Second, the variation must be due to heredity; parents must be able to pass some of their distinct characteristics on to their offspring. Third, there must be differences in reproductive success; thanks to their distinctive characteristics, some individuals must have more surviving offspring than others in their population. When (as almost always happens) there is hereditary variation within a species and some variants consistently reproduce more successfully than others, eventually the increased numbers of living descendents of the more successful types will change the makeup of the species. Over many generations, *adaptations* (trait differences that make an animal better able to survive and reproduce) occur through a combination of successive, mostly small, random changes in traits and natural selection of the better-suited variants. Evolution occurs when these heritable differences become more common or rare in a population. Because the process that causes the change is natural, Darwin called it *natural selection*.

Evolution is a powerful explanatory and predictive idea set that directs research by constantly raising new questions. In the years since Darwin and Wallace first presented its tenets, evolution has become the central organizing principle of modern biology, providing a unifying explanation for the diversity of life on Earth. It is unfortunate that Darwin's choice of words in calling his ideas a 'theory' has caused problems for some non-scientists. When a layperson uses the word theory, he or she often means an idea or belief about something that is arrived at through speculation or conjecture—basically, a guess unsupported by evidence. However, theory means something entirely different in a scientific context. When a scientist uses the word, he or she means the body of rules, ideas, principles, and techniques that applies to a particular subject. In essence a scientific theory is a set of facts, propositions, or principles analyzed in their relation to one another and used to explain observed phenomena. Thus, a scientist may speak not only of the theory of evolution but of Einstein's theory of general relativity or Newton's theory of gravitational attraction.

Nowadays, the fact that organisms evolve is uncontested in the scientific literature and the modern evolutionary synthesis is widely accepted by scientists. However, evolution remains a contentious concept for some segments of society. As Darwin himself recognized, the most controversial aspect of evolutionary biology is its implications for human origins.

1.2.2 Genetics and Behavior

Nowadays even most schoolchildren know that a great deal of the variation among individuals in a species is due to differences in their genes (DNA segments that encode the information needed to make various proteins). Because genes can be copied and transmitted to offspring, parents can pass on the information needed to carry on these relevant distinctive characteristics; genetic variation within a species occurs when a gene exists in two or more forms, or alleles. Thus, it is sometimes difficult to remember that only about 150 years ago, when Darwin, Wallace, Lamarck, and others were developing their theories, scientists knew so little about the nature of heredity that they could not account for how various characters might be passed down from generation to generation.

In 1865 Gregor Mendel found that traits were inherited in a predictable manner, but at the time his work went largely unnoticed, and Darwin and Wallace were unaware of it. Then, in the early 1900s, Hugo de Vries and others rediscovered Mendel's work. Although the rediscovery provided the impetus for scientists to better understand how natural variation arises, disagreements over the rate of evolution predicted by early geneticists and biometricians led to a rift between the Mendelian and Darwinian models of evolution. In the early years of the twentieth century, a combination of specialization and poor communication among biologists resulted in much confusion and difficulty.

The rift did not begin to heal until the 1920s and 1930s, when evolutionary biologists such as J.B.S. Haldane, Sewall Wright, and Ronald Fisher established the foundations for the field of population genetics. In the 1940s, Oswald Avery and colleagues identified DNA as the genetic material, and in 1953 James Watson and Francis Crick published its structure, demonstrating the physical basis for inheritance. In 1956, Margaret Bastock published the first demonstration that a single gene could change a behavior pattern.

Beginning in the 1930s and 1940s, a number of leading biologists worked together to reconcile their various fields resulting in a more comprehensive view of evolution that combined natural selection and Mendelian inheritance called *the modern evolutionary synthesis.* It drew together ideas from several branches of biology that had become separated and provided compelling evidence that field-based population studies were crucial to evolutionary theory.

Today, genetics and molecular biology have become core parts of evolutionary biology. A newer field, genomics, has also developed. While the terms genetics and genomics are sometimes used interchangeably, genetics usually refers to the study of individual genes, whereas genomics refers to the study of the compete set of genes in an organism. The latter field of study is moving rapidly to sequence insect genomes.

It is now also clear that evolution is driven by not just one but two major mechanisms. The first is natural selection, the process just outlined, acting on the existing genetic variation in a population. The second is genetic drift, an independent process that produces random changes in the frequency of traits in a population due to chance rather than selection or gene flow.

Natural selection and genetic drift can only work on what is available, and for this reason it is important to recognize that the traits and alleles that are present in a population can vary over time. Various catastrophes, expansions into new habitats (causing a founder effect), or events that divide a population can lead to a population bottleneck, in which the number of breeding individuals in a population shrinks temporarily and therefore the population loses genetic variation. On the other hand, new traits can also arise, either from mutations in genes or from the transfer of genes between populations and between species. Mutations are the ultimate source of variation, but in species that reproduce sexually, new combinations of existing alleles are also produced by genetic recombination (by exchange of chromosome sections during meiosis). Gene flow is the exchange of genes between populations, usually of the same species. For example, some grasshoppers migrate widely before breeding; this migration brings previously isolated populations together and facilitates gene flow within the species, slowing the process of speciation that might have occurred had the populations remained segregated. Migration not only provides an opportunity for mixing; it also may add or remove genetic material from the gene pool of a population.

Genetic drift is random change in the frequency of alleles, caused by the random sampling of a generation's genes during reproduction. It results from the role probability plays in whether a given trait will be passed on as individuals survive and reproduce. Genetic drift is analogous to the way that flipping a coin over and over may give a proportion of 'heads' and 'tails' that differs from the equal numbers one would expect. Because the relative importance of natural selection and genetic drift in a population varies depending on the strength of the selection and the effective population size (the number of individuals capable of breeding), the size of a population can greatly affect its evolution. Natural selection usually predominates in large populations, while genetic drift dominates in small populations. For example, a population greatly reduced by a bottleneck will often show increased genetic drift. The dominance of genetic drift in small populations can even lead to the fixation of slightly deleterious mutations.

The changes produced in any one generation by selection, drift, mutation, and gene flow are small, but these differences tend to accumulate with each subsequent generation and over time they can cause substantial changes in the organisms. Consider a hypothetical case in which all of the beetles of one species living in the trees on an isolated mountaintop represent a population. A single gene in this population exists as two alleles that account for variations in the physical appearance (phenotype) of the organisms, in this case brown or green body color. A gene pool is the complete set of alleles in a single population, so each allele occurs a certain number of times in a gene pool. The fraction of genes within the gene pool that are a particular allele is called the allele frequency. Evolution occurs when there are changes in the frequencies of alleles within a population of interbreeding organisms. Suppose birds more commonly notice the brown beetles and eat them before they can reproduce whereas the green beetles, successfully camouflaged by the tree foliage, continue to breed. In each generation, the allele for green body color in the population would become more common and the brown allele, less so.

Over time, unless some other factor favored brown beetles enough to overcome this difference, a population of green beetles would evolve.

Under what conditions would a population not evolve? One way to examine whether a population is undergoing evolutionary change is through the use of the *Hardy-Weinberg equilibrium.* The Hardy-Weinberg principle is an example of a null model. Just as a null hypothesis is a hypothesis of no difference, this null model tells us what to expect when no evolutionary forces are at work. Based on the frequency of alleles, Hardy-Weinberg predicts the frequency of (diploid) genotypes in the absence of evolution. If the genotype frequencies we observe in our study population are the same as those determined by the principle, our population is said to be in Hardy-Weinberg equilibrium; it is not evolving. If we observe different frequencies in our study population, we can conclude that some evolutionary force is at work.

Like the fine print in an insurance policy, the Hardy-Weinberg equilibrium has a great many restrictions. The equilibrium is relevant only for diploid organisms with sexual reproduction. Mating must be random. The gene under consideration has only two alleles, and allele frequencies are identical in males and females. Population size is very large, so that genetic drift is essential imperceptible. Gene flow and mutation are so small as to be negligible. Finally, natural selection is not acting on the alleles under consideration. Of what possible use can such a restrictive formula be? The answer lies in some of its permutations, which allow a researcher to sample a population at one point in time and to determine whether it is at equilibrium for a set of alleles without having to take repeated samples across several generations.

A major condition under which evolution would slow or halt would be when there is little or no genetic variability for natural selection to act upon. Clearly, for some species, genetic variability is very important, as illustrated by those insect species that seem to have enough persistent allelic diversity to be able to evolve resistance to one insecticide after another. Genetic variability is also important in the ability of both invaders and insects imported for biological control to establish themselves, as well as in their potential to attack new and non-target hosts. On the other hand, genetic diversity seems fairly unimportant for some species. For example, many parasitoid wasps such as *Melittobia* (see Fig. 9.13), typically undergo one generation after another of brother-sister matings, and are assumed to be highly inbred. In the case of some invasive insects, lack of variability may actually contribute to their success. Research has shown that invasive populations of the Argentine ant *Linepithea humile* have lost the genetic ability to distinguish one colony from another; as a result, they escape from population control imposed by deadly conflicts between colonies. So how important is genetic diversity itself to the persistence of insect populations? Surprisingly, this question is still an open one, and difficult to answer in a general way.

Ultimately, one of the goals of a behaviorist is to pair a particular behavioral component with a particular gene, determining the actual site at which the gene wields its influence and how it does so. In fruit flies (*Drosophila*), probably the single best genetically studied insect genus, a host of intriguing behavioral abnormalities have

been traced to mutations of single genes. Intensive inbreeding of laboratory stocks has produced populations identical genetically in every respect except for a single mutant gene induced by radiation or certain chemicals. Such populations have been demonstrated to differ behaviorally, often in several traits.

However, in general the task of pairing behaviors and genes is complicated by the fact that the behavioral impact of a mutant gene may not be its primary effect. A functional nervous or muscular system must be constructed in a precise way for 'typical' behavior to occur. Since genes code for proteins such as enzymes, even a single gene mutation may have broad ramifications on the construction of entire systems. A detailed look at the field of behavioral genetics is outside the scope of this book. However, throughout the chapters that follow we repeatedly assume the genetic determination of behaviors. For this reason, it is worth noting two useful methods by which such genetic assumptions might be verified: crossing experiments and selection experiments.

In order for natural selection to act on a trait, that trait must be passed down from one generation to the next and there must be genetic variation in it. However, when we see differences in a trait (such as different behaviors, for example) we cannot just assume they are genetically based. Perhaps the differences occurred because individuals were raised on different diets, had different experiences, or were exposed to different environments. How can we determine what portion of these differences is genetic and thus is accessible to natural selection? A *crossing experiment* depends upon mating individuals that differ in a particular kind of behavior and then examining the behavior of their offspring. For such experiments to be meaningful, of course, the environment must be constant or very well controlled.

The simplest type of crossing experiment would be to use individuals that exhibit certain behaviors that are known by previous crossing experiments to differ at only a single gene locus. Many complex behavior changes have been produced by artificially inducing single-gene mutations in the laboratory, but such simple systems have been difficult to identify in nature. A famous early example was Walter Rothenbuhler's 1960s study of two strains of honey bees that differ in their reaction to a serious bacterial infection called American foulbrood. One strain is very susceptible to the infection; the other is resistant. This difference is largely due to a single behavioral difference: worker bees of the resistant strain consistently remove dead larvae before the infection can spread (Fig. 1.7).

When Rothenbuhler crossed this 'hygienic' strain and the susceptible 'nonhygienic' strain, the resultant offspring were nonhygienic, indicating that the genes conferring resistance were recessive. Going further, Rothenbuhler did a series of backcrosses to the homozygous recessive resistant line; roughly a quarter of the resultant colonies were hygienic. Among the nonhygienic colonies produced, a third uncapped the cells of dead larvae but would not remove the larvae. Another third would remove the larvae, but only if the researcher removed the caps for them. The remaining third would do neither. Thus, the behavioral and genetic results were consistent in indicating that two loci—one controlling uncapping, the other affecting removal—were involved in the difference in hygienic behavior between the two strains (Fig. 1.8).
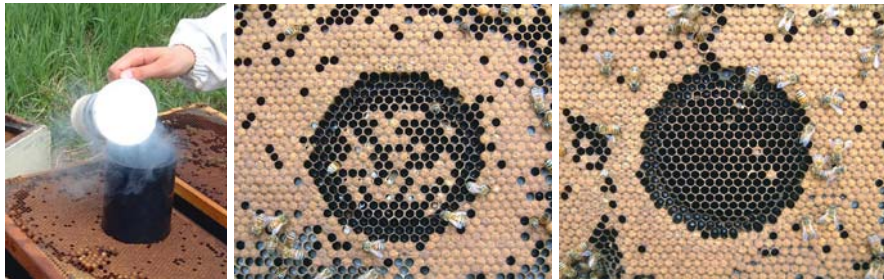
Fig. 1.7 Testing for hygienic behavior. Honey bees of some strains will remove diseased and dead larvae and pupae from brood combs infected with American foulbrood so rapidly and thoroughly that they effectively control the disease. (*left*) To test his or her breeding stock, a beekeeper can pour 250–300 ml of liquid nitrogen through an open-ended soup can, freeze-killing the brood in this spot, and then after 48 hours, count the number of dead brood the bees have removed. (*center, right*) The response shown in the center frame indicates a lower level of hygienic behavior in this colony than that of the colony at the right

Parents	F_1 hybrids	Backcrosses (n=29)
Females showing hygienic behavior X Males that do not	Non-hygienic generation	F_1 males X original hygienic females = ? *Offspring prediction:* If 1/2 hygienic: 1 gene If 1/4 hygienic: 2 genes If 1/8 hygienic: 3 genes *Offspring results:* 6 hygienic 9 uncapped 14 non-hygienic (6 of these would remove the dead, but can't because they don't uncap them first)
(Conclusion: Difference in the two lines)	(Conclusion: Hygienic behavior due to one or more recessive genes)	(Conclusion: Two genes are involved, one for uncapping and one for removal)

Fig. 1.8 Determining hygienic behavior genetics. Experimental crosses and backcrosses done by Walter Rothenbuhler in the 1960s suggested that two recessive genes were responsible for hygienic behavior; later studies have indicated that additional genes are also involved

Rothenbuhler's model has been widely cited as an instance where a natural
behavior is controlled by a few Mendelian genes of large effect, but if it holds up
it will be the only known example of naturally occurring variation in a complex
behavior of a higher organism that is under such strict genetic control. When Marla
Spivak and two Australian colleagues reexamined hygienic behavior in 2002 using
molecular techniques, they found evidence that the actual genetic basis is probably
more complex, and that many genes probably contribute to the behavior.

More commonly in nature a trait will appear to vary along a continuum; these
are often called quantitative traits. The influence of a single gene is usually unde-
tectable because genes at many loci have small additive effects, and the environment
may have a large influence upon the trait's expression. With such polygenic systems,
statistical approaches are necessary to estimate the roles of inheritance and environ-
ment; the principal one used is analysis of variance, a powerful tool of behavioral
genetics.

A second important way to measure the degree of genetic involvement is through
selection experiments, which involve choosing only a certain part of each gener-
ation to become parents of the next generation. By such 'artificial selection' the
population becomes altered through time for the quantitative character under con-
sideration, in a direction that depends upon which part of the population is chosen
for succeeding generations (Fig. 1.9).
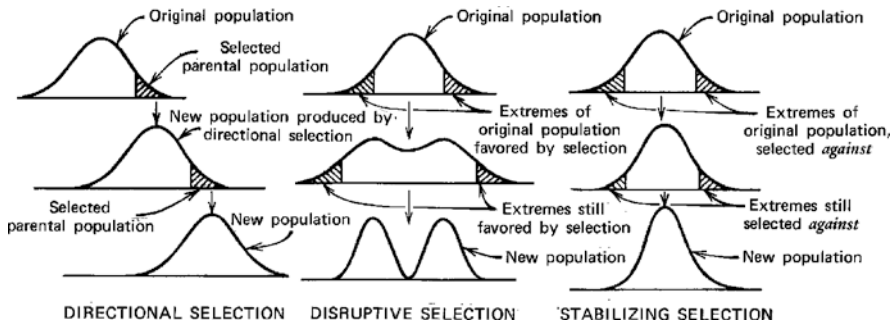
Fig. 1.9   Choosing one's (insect) parents. Three different modes of selection yield quite different
characteristic means and frequency distributions in the subsequent generations. Ordinate indicates
the frequency of individuals in the population. Abscissa indicates variation for the quantitative
character being considered, as expressed in some linear metric measure. Directional selection is
the most common mode

With artificial selection of the type called a 'truncation selection experiment' a
three-step approach is used. In the first step, the trait is measured in all the individ-
uals of the population, and the numbers are averaged together to obtain a mean. In
the second step, the variation in measurements for that trait is truncated, or cut off,
at some value, and a new mean is calculated for just those individuals that measure
below that value. In the third step, only those selected individuals in the truncated

group are allowed to breed, and the mean score for their offspring (called the 'filial generation') is determined.

These measurements are all we need to determine what proportion of our observed trait variation can be attributed to genetic variance. As a result of our truncated selection experiments, two measures can easily be determined empirically (Fig. 1.10). One is the magnitude of the response (R)—how much the mean values differ between the parent and offspring generations. The other is the selection differential (S)—how much the chosen parents deviate from the whole population in their mean value for the trait under selection. Dividing R/S gives a very useful measure called *heritability* (h^2). It is defined as the degree of genetic determination of the variability that is present in the sample population, for the kind of behavior observed and for the precise method of observation used.
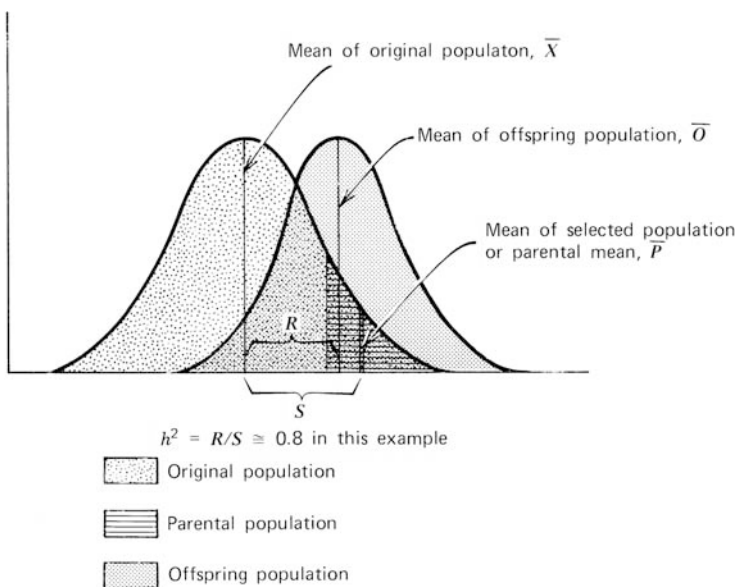
Fig. 1.10 **Determining heritability.** See text for further explanation

What would happen if artificial selection were attempted on an inbred homozygous strain? In this case, none of the variation present has a genetic basis. Thus, the population mean will not significantly change, regardless of the sort of selection being practiced. The mean of the filial population will not differ significantly from that of the parental population, regardless of the selection differential. Therefore, h^2 would be 0.

What if the filial population turned out to have a mean that was more or less identical to that of the selected sample? This would indicate that the trait was completely under genetic determination, and h^2 would be equal to 1. Most cases, of course, lie somewhere between these two extremes. Studies within evolutionary biology,

population genetics, and animal behavior have found that many traits show low (0.1–0.1) to moderate (0.1–0.4) heritability.

As a general rule, most arthropod behavior is highly stereotyped and will tend to yield rather high heritability measures relative to those of vertebrates. For example, selection experiments on milkweed bugs under laboratory conditions shifted the age at first oviposition from 63.5 days to 16.7 days in seven generations. Average heritability from all generations was 1.18, which indicates that heritability for this trait must be very close to 1.0, since additive genetic variance cannot be greater than total variance.

One caution should be noted before concluding this section. After several generations in the laboratory, artificial selection may alter the cultured insects' behavior in ways that adapt the insect for the more simplified environment. Therefore, behavioral data based on laboratory-reared insects may not accurately reflect the behavior of natural populations of the same species. In fact, different behavioral results obtained by investigators working on the same insect in separate laboratories may be explained as strain differences arising in cultures. Few behaviorists maintain careful checks on the 'quality' of the laboratory-reared insects that serve as their research subjects, but all should consider it.

1.2.3 The Comparative Approach

Biologists have long used the technique of comparing different species in order to understand a trait better. If the first important development for the rigorous scientific study of animal behavior was publication of the theory of evolution by natural selection, and the second was the rise of genetics, the third almost certainly was the development of a systematic comparative method, a development that is usually credited to two Englishmen, George John Romanes and C. Lloyd Morgan.

The name of George John Romanes is much less well known than the names Darwin, Wallace, and Mendel, probably because although he is generally credited as being the first to formally use comparative methods to study animal behavior, his motives and methods were a bit unorthodox. Romanes' interest lay in studying animals to gain insights into the behavior of humans. Specifically, he wanted to show that mental processes evolve in a continuous way from lower to higher forms, with humans at the top of the list. Without much direct evidence, Romanes constructed an elaborate scale for emotional states. Worms were lowest because he judged them capable of feeling only surprise and fear. Insects were higher, being capable of various social feelings and curiosity; fish showed play, jealousy, and anger; reptiles displayed affection; birds showed pride and terror; finally, various mammals were credited with hate, cruelty, and shame.

A British psychologist, C. Lloyd Morgan was also interested in this field, which he called 'mental evolution'. Dismayed by the ways in which people like Romanes relied on inferences and anecdotes rather than recorded facts or direct behavioral observations, Morgan developed and promoted the use of the *observational method*:

only data gathered by direct experimentation and observation could be used to make generalizations and develop theories. He also developed an approach called 'Morgan's canon'. As Morgan envisioned it applying to his 'mental evolution', his canon stated that an action should never be interpreted as the outcome of the exercise of a higher mental faculty if it could be interpreted as the exercise of one that stands lower in the psychological scale. For example, an animal's behavior was only to be considered 'conscious' if there was no simpler explanation.

Morgan's canon was a special case of a common principle in medieval philosophy called Occam's (or Ockham's) razor or the *principle of parsimony*. These days in many different areas of study it is interpreted to mean something like 'the simpler the explanation, the better' or 'don't multiply hypotheses unnecessarily.' At its broadest interpretation, the principle of parsimony is sometimes interpreted to mean that one should always seek out the simplest explanation for observed facts, and whenever possible one should reduce complex hypotheses to their simplest terms. Doing so can make a problem easier to study and easier to explain to other people. However, although this 'law' has become almost axiomatic in animal behavior studies, there also are times when it can lead to interpretations that are not just simple but simplistic and misleading because they do not account for all the facts. Likewise, when faced with two competing theories, we cannot just assume that the simpler theory is correct and the more complex one is false, even though we know from experience that, more often than not, the theory that requires more complicated machinations is more likely to be wrong. It is important to remember that a more complex theory competing with a simpler explanation can be temporarily put aside, but it cannot be thrown onto the trash heap of history until it is actually proven to be false. As Albert Einstein is famously paraphrased, 'Explanations should be as simple as possible, but no simpler.'

As used today, the idea and logic of the comparative approach is to look at the occurrence of a particular behavioral trait in both closely related and distantly related species. If hypotheses and predictions about the adaptive value of a behavior for one species are supported, then convergent evolution could result in similar behavior in quite unrelated species subject to similar selective pressures (see wasp prey carriage in Section 1.3.1). The converse is that behavior traits expected due to shared ancestry may in some cases be overridden due to novel selection pressures arising, resulting in divergent evolution. As used today, application of the comparative method relies on well-supported phylogenies (see Section 1.3.2), but, historically, phylogenetic rigor was not so important.

1.2.4 Conceptual Pitfalls

When discussing the conceptual frameworks that inform insect behavior, it is important to acknowledge some other hazards that need to be watched for and avoided. One set of traps arises from the nature of language itself.

All behavioral study rests on the bedrock of detailed description. However, human language arises from human experience and thus we lack the words to

describe the behaviors of another species in a way that is fully divorced from our own experiences. For one thing, almost all descriptive terms possess inherent human connotations that often imply human purpose and/or motivation. Attributing human characteristics to other species of animals is termed *anthropomorphism* (Fig. 1.11). Even though this practice is generally unwarranted, anthropomorphic terms catch people's attention better than blander text does, so they are often used to describe animal behaviors, particularly in items written for the general public. However, when a scientist uses or encounters an anthropomorphic term, it should be with full understanding that an interpretation is being made of the motivations of the animal and that any such interpretation is highly suspect. Descriptions of a cricket 'happily' chirping on the hearth or a 'fearful' cockroach scurrying across the floor may be commonplace in nature books for children but have no rightful place in the scientific study of behavior. We simply don't know what the sensation of happiness is to a cricket or fear to a cockroach.

Fig. 1.11   Casting insects in human terms. Anthropomorphism has been common since the dawn of human experience. A familiar example to most people is the story of the grasshopper and the ants, which goes back at least to Aesop (620–560 B.C.), a slave and storyteller who lived in Ancient Greece

A second difficulty with language use, more insidious and surprisingly pervasive in the field of animal behavior, is the problem of *teleology*. A form of anthropomorphism, teleology is the doctrine that the processes of nature are directed toward some discernible 'goal'. In effect, teleology endows animals with motivations similar to those that humans might show under similar circumstances. Much human behavior is goal directed, or purposive; for example, when hungry, one goes to the table or refrigerator in anticipation of food. However, most animal behavior is directive, that is, the outcome of the response is not foreseen by the organism. Thus, there is a confounding of ends and means in statements such as 'bees visit flowers because they want nectar.' The bee is brought to the nectar by its response to the stimulus provided by the flower, not because it consciously anticipates the outcome of its actions.

A third language-related problem is that, because most behavior is described in terms of its end result, the very act of labeling a particular observed behavior tends to color subsequent interpretations of it. For example, labeling a chemical secreted by a female moth as a 'sex attractant' is done because the end result of her secretion is that males arrive and attempt to mate with her. This label suggests that such chemicals provide directional clues of use to an approaching insect orienting over some distance, but such cues may have not been demonstrated. Furthermore, use of the label 'sex attractant' potentially masks appreciation of a whole congregation of other behaviors by the respondent such as orientation to wind and light.

In a larger context, it is customary to label communication signals by apparent function such as sexual, aggressive, alarm, etc. However, it is often difficult to distinguish the responses that such categories of signals will actually elicit because the environment or 'context' of a signal may alter its message (see Chapter 6). For example, the same chemical in harvester ants may elicit alarm under one set of circumstances but elicit approach in another situation. A second problem is that the respondent's first detectable behavioral response to many signals is just to change positions; as it moves, it enters new stimulus situations. In analyzing the insect's ultimate behavior, it is difficult to separate the influence of these new situations from that of the initial signals.

Even labeling behavior in order to catalog it can color one's observations. A widespread system for classifying communication sets its categories as visual, acoustic, chemical, tactile, or electrical, for example; for convenience, a similar system is used in this book. However, for insects this is admittedly simplistic. An insect may be receiving information simultaneously in a number of sensory modes, and in many cases the total message and its specificity may depend upon receipt of all these different channels together.

A different set of conceptual pitfalls concerns the theory of evolution by natural selection. Although this theory remains the single best unifying explanation for the ultimate causes of the traits that organisms possess, it is important not to assume automatically that the behaviors one sees represent some sort of optimized state and are the best of all possible choices, even though simplistically it might seem that over time, evolution by natural selection would result in every organism being homozygous for the most favorable alleles.

Clearly, this is not what happens. The real picture is much more complex, for at least five reasons. First, not all traits are heritable. Many behaviors may be caused entirely by actions of the environment; this can be particularly true in animals that are capable of learning.

Second, natural selection is not the only evolutionary force as work. For example, as noted above, genetic drift and gene flow both can influence the evolution of traits. Another driving force in the evolution of animal behavior is the concept of an evolutionary stable strategy, a term derived from game theory; it recognizes that animal behavior is governed not only by what is optimal, but also by what other strategies are found in the population, and at what frequency.

Third, selection pressures can change as a result of many factors. Environments change over time; what might be good behavior today, for example, might not be

the best behavior in 10,000 years or even in 10 years. A previously beneficial trait may become deleterious, or vice versa, under new conditions such as a changed or different environment.

Fourth, not every trait can be optimized by natural selection, because traits are linked together in many ways. In some situations a heterozygote has greater fitness than either homozygote. In other situations, epistasis—where genes at different loci interact to produce the phenotype—results in selection acting differently on genes in different genetic backgrounds. Many genes affect more than one trait; one allele may produce a positive effect on one trait but a negative effect on another. Thus, by necessity, tradeoffs must occur. Furthermore, genes can also be physically so close together on the same chromosome that they tend to be inherited together, making it difficult for natural selection to optimize each trait independently.

Fifth, evolution does not have a predetermined goal for any species. There often may be cases where an organism simply cannot evolve a particular trait that would suit it well, because it does not have the relevant genes in its gene pool to do so. Mutations are random; they do not arise to fulfill a need.

If these precautions can be kept in mind, adaptation and natural selection can provide a powerful framework within which to generate sound, testable hypotheses.

1.3 Phylogeny's Role

Phylogeny, the presumed history of ancestry of a group of taxa, provides a strong evidence line to help decipher the evolution of a trait. In a sense, phylogenetics can be thought of as 'evolutionary geneology'. Its tools include the twin fields of taxonomy and systematics, the sciences involved in finding, describing, and naming organisms by an agreed-upon set of rules, and then classifying them into increasingly broader categories that are based on shared features that presumably reflect evolutionary relationships.

Incidentally, we have these fields to thank for introducing the useful general term *taxon* (plural taxa), meaning any taxonomic unit without specifying its rank. Thus, a species is a taxon, but so is a group of species or an entire order. A related term, *clade*, is a group of organisms that includes an ancestor and all its descendents (see Section 1.3.2).

As we have seen, much of behavior has a genetic basis, and traits with a genetic basis are capable of evolving over time. But what is the evidence for behavioral evolution? To answer this, using the comparative approach is a necessity, but in addition, one must consider phylogeny, which involves both microevolution and macroevolution.

1.3.1 Microevolution and Macroevolution

Long before it was ever given its name, people have recognized the reality of *microevolution* (genetic changes within populations or species) because of two

easily recognized phenomena: domestication, and observations of natural selection in the field. Dog behavior is probably the best-known example of evolution under domestication, but even in Darwin's day any farmer worth his salt recognized that the animals under his care changed from one generation to the next in ways that could be guided by selective breeding. Likewise, although long-term studies were not always possible, differences often were quite obvious when populations of the same animal species from different environmental conditions were compared. Knowing the examples would be familiar to his readers, Darwin went to some length to address such domestications and natural changes as background for his new ideas.

While microevolutionary patterns can often be directly seen, *macroevolution* (change of evolutionary patterns recognizable above the species level) usually operates over such a long time frame that it is more apt to depend on indirect evidence such as the fossil record and/or a reconstruction of presumed relationships between similar-seeming species. Although one might think that the fossil record would not be much help for behavioral studies, given that behavior itself does not leave fossil remains, sometimes a great deal can be inferred from morphological structures, tracks, and artifacts such as preserved nests and burrows. However, in general the fossil record does not usually shed much light on how a behavior pattern evolved; rather, it is more apt to demonstrate the antiquity of the particular behavior that is preserved. Some examples include an entire colony of weaver ants from the Oligocene in Africa, fossil dung balls fashioned by scarab bettles in the Lower Oligocene, and fossil lepidopterous leaf mines from the early Eocene of Wyoming. The fossil ant nest demonstrates that distinct morphological castes in ants evolved very early and that social life in ants has apparently changed but little over the past 60 million years. The fossil dung balls similarly demonstrate scarab beetle nesting behavior (see Chapter 10) to have been at a fairly advanced level very early in the history of the group.

Species that share a recent common ancestor tend to resemble one another in many respects simply because they share a common ancestor. Behavioral differences and similarities within a group of species generally reflect the phylogenetic relationships as determined morphologically or genetically.

Perhaps one of the most elegant examples supporting this assertion is found among the cockroaches, an ancient but highly successful group. Cockroaches reached their highest development during the late Carboniferous, and have shown relatively little morphological change in the intervening 250 million years; a fossil roach generally resembles a recently swatted roach except that early forms tended to have visible exerted ovipositors much like those of present-day katydids.

If you have ever tried to swat a cockroach, you know the creature's main defense is extreme proficiency at quick getaways (see Case Study 2.1). What you may not appreciate is that the common household varieties of roach represent only a miniscule proportion of some 5,000 living blattid species that have invaded nearly every conceivable ecological niche from desert to aquatic habitats. Despite a comparatively good fossil record, the classification and phylogeny of these thousands of species were subject to dispute by various authorities. As a result, three classifications arose, based on different sets of morphological characteristics. Rehn's system,

based primarily on wing venation (thereby excluding the many wingless forms), classified cockroaches into five families and 17 subfamilies. Two other cockroach classification systems, Princis' system and Bey-Bienko's system were based on diverse and apparently unrelated structural differences. Princis divided the group into four suborders and 28 families, and Bey-Bienko recognized just three families with a total of 15 subfamilies.

Behavioral characteristics and internal morphology were given little attention in any of these early schemes, yet cockroach reproductive biology is exceedingly diverse. Although it is unusual to find more than one mode of oviposition behavior in a particular insect group, cockroaches display an almost complete spectrum. Like most insects and birds, females of many cockroach species lay eggs in packets (*oothecae*). Such reproduction, where fertilized eggs develop outside the female's body, is termed *oviparity*. Other cockroach species exhibit *ovoviviparity*—the eggs are first extruded and then retracted into a brood sac where the embryos absorb water from their mother until they mature; then the ootheca is again extruded and the nymphs hatch and drop free from their mother. A third type of reproduction, *viviparity*, is found in still other roach species. This oviposition method is superficially similar to the previous type, but when first formed the eggs lack sufficient yolk to allow complete development, so both nutrients and water must be absorbed during embryonic development in the brood pouch.

When the species having these three types of reproduction are superimposed on the three older classifications they intermingle throughout the suborders, families, and subfamilies rather than sorting out into any consistent pattern. In 1964, this puzzling fact prompted Frances McKittrick to undertake a new look at cockroach classification. For comparative study, she chose four character systems: female genitalia, male genitalia, the proventriculus (a portion of the intestinal tract specialized for grinding food, also referred to as the gizzard), and oviposition behavior. Upon analyzing her results, McKittrick was able to recognize two phyletic lineages based primarily on reproductive behavior. In one lineage all species remained oviparous, undoubtedly the ancestral form of reproduction. This group (Blattidae) is exemplified by the notorious American roach, *Periplaneta americana*. The other lineage encompassed the ovoviviparous and viviparous species, including the equally notorious German roach, *Blattella germanica*. In the years since her work was published, McKittrick's conclusions have gained widespread acceptance and support from a variety of other studies (Fig. 1.12), and she is still recognized for being the first researcher to stress reproductive behavior as an important trait in the evolution of cockroaches.

The most recent systematic studies of the group, including both extensive morphological and molecular analyses, still leave some phylogenetic details unresolved and uncertainties remain. The one striking and fundamental difference between the earlier and current phylogenies is that the increasing weight of available evidence has revealed that the termites (Isoptera) properly fall within the cockroach lineage as a sister group to the oviparous Cryptocercidae, a group of uncertain affinity in the earlier classifications.

When comparative behavioral studies uncover a seeming progression in one or more characters within a set of related species, it is tempting to conclude that
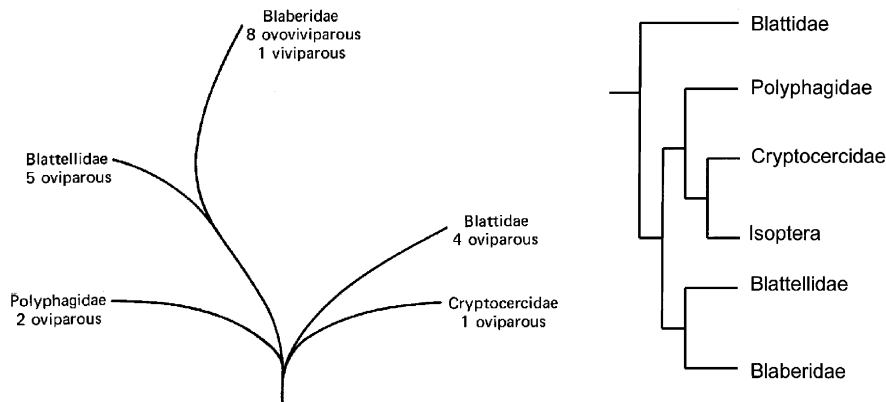
Fig. 1.12 Classifying cockroaches. (*left*) Three older competing schemes (see text) based solely on external features observed in museum specimens gave way to one in 1964 based primarily on female reproductive behavior. (*right*) The currently accepted higher classification and phylogeny of the Blattaria based on a much more extensive data set, including molecular data, also incorporates the termites

evolution has actually proceeded through such a series. However, such a conclusion should be tempered with caution. The fact that intermediate forms are possible and do exist indicates only that evolution *might* have proceeded through a similar (but probably not identical) series. In the absence of a fossil record or some compelling logical argument, it does not even indicate the direction of the evolution of the trait in question.

Prey transport, for example, varies considerably among predatory solitary wasps (Fig. 1.13). Many species carry paralyzed prey back to the nest in their jaws; others always hold the prey with their middle legs, and still others use their hind legs. Some fly hunters even carry the prey impaled on their stinger, but perhaps the most remarkable prey-carrying adaptation is found in a crabronid wasp, *Clypeadon laticinctus*, that transports paralyzed ants on a specialized 'ant clamp' formed by the modified apical abdominal segments. While prey carriage seems to be constant among all members of a particular morphologically defined genus, there appears to be no correlation of prey carriage type with wasp phylogeny beyond this, nor with nest type or phylogenetic position of the prey. This appears to be a case where similar selective pressures have molded the evolution of prey carriage mechanisms.

What are these selective factors? In 1962, Howard E. Evans suggested some answers. In the soil-nesting species, mandibular prey carriage tends both to obstruct the major sense organs and to impede the wasps' ability to dig into their nest entrance. Furthermore, species that use their mouthparts in prey transport either tend to leave the nest open between foraging trips or use such large prey that they must drag them back to the nest; if they were to close the nest between prey trips, they would be forced to lay the prey down temporarily while they reopened it, thereby leaving the prey vulnerable to attack by predators and parasites. Shifting the prey beneath their body and back from the head or even clamped or impaled on the stinger

Fig. 1.13   Carrying prey. (*Top*) A female of the Australian eumenid wasp, *Pseudabispa* clasps her caterpillar prey in her jaws, supported by her middle and hind legs as she flies to her nest

would increase their own efficiency and better protect their offspring from intruders. The relative rarity of abdominal clamp prey carriage mechanisms suggests that the advantage of having all three pairs of legs free may be offset by the relatively greater risk of exposure of the prey to parasites, especially to attacks by parasitic satellite flies (Fig. 1.14).

Another important line of evidence is provided by detailed studies of *adaptive radiation* (the rapid evolution of new lineages). Isolated areas such as oceanic islands are particularly good places to look for examples of adaptive radiation; only a few species may manage to invade such remote areas, and in the relative absence of interspecific competition, new forms may rapidly evolve. The famous case of the adaptive radiation of Darwin's finches on the Galapagos Islands is almost certainly the world's best-known example. The *Bembix* sand wasps of Australia provide a behavioral example of adaptive radiation. Although flies are the prey of nearly all of the 300-plus species of *Bembix* throughout the world, 11 of the 28 Australian species for which biological data exist have switched to other prey (Fig. 1.15). This unique radiation in prey preferences in Australia is presumably related to the absence of related genera of sand wasps that occupy these food niches elsewhere in the world. Other factors may also be involved, such as scarcity of usual prey in some habitats, especially arid ones. Species such as *B. variabilis* may be in the earliest stages of splitting into two distinct species because different populations seem to have specialized on quite different prey. Throughout most of Australia *B. variabilis* use flies

Fig. 1.14   Looting its host. A satellite fly, *Senotainia trilineata* (Sarcophagidae), rests on a nest-marker nail. Such flies typically follow just behind prey-laden wasps like a satellite, and attempt to swiftly dart in and deposit their live larvae on the wasp's prey as the wasp enters its nest. Smaller prey slung under the wasp's body may be less vulnerable to such parasites

as prey, but a population discovered in the far northwest of the continent seem to exclusively use damselflies as prey.

1.3.2 Phylogenetic Systematics and Cladistics

To deduce the evolutionary direction of apparent behavioral progressions, a useful procedure is to plot the behavioral evidence against a 'family tree' (see Figs. 1.2 and 1.12). Recognizing that closely related species are more likely to share traits than are distantly related species, Darwin himself introduced the metaphor of a tree to describe the relationships among taxa.

Many of these trees have their roots in traditional taxonomy and systematics, and owe an intellectual debt to Carolus (Carl) Linneaus, the Swedish botanist, physician and zoologist who laid the foundations for the modern scheme of binomial nomenclature. Linnaeus also developed what became known as the Linnaean taxonomy. This system of scientific classification, still widely used in the biological sciences, assigned every organism its position within a nested hierarchy based on observable characteristics. Thus, above the basic level of genus and species, Linnaean classification placed groups of organisms into families, orders, classes, phyla, and kingdoms.

The underlying details concerning what are considered to be scientifically valid 'observable characteristics' have changed with expanding knowledge (for example, DNA sequencing was unavailable in Linnaeus' time), but the fundamental principle remains sound. Some taxonomists point out, however, that Linnaean classification can be misleading because it implies that different groupings with the same rank
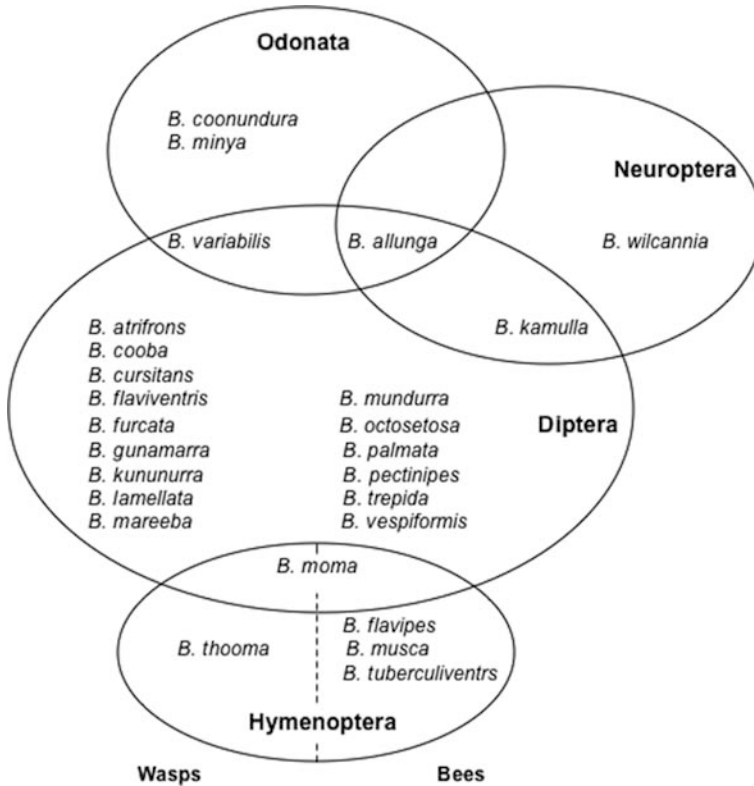
Fig. 1.15   Undergoing adaptive radiation. Known prey preferences of 28 Australian *Bembix* species. Most species hunt only flies (Diptera), the prey used exclusively by studied species of this genus elsewhere in the world. However, seven species are specialists on three other orders while three species (*variabilis, kamulla,* and *moma*) hunt both flies and species from a different order, and one species (*allunga*) takes prey from three very different insect orders

level are equivalent. For example, although cats (Felidae) and orchids (Orchidaceae) are both ranked as family level groups in Linnaean classification, the two groups are not comparable. One has a longer history than the other and the extent of diversity within each group differs dramatically.

In response to these concerns, scientists have developed other ways to show evolutionary relationships in a tree-like or bush-like form. The best-known alternative is based on an approach called *cladistics.* Cladistics began in the 1950s with the work of the German entomologist, Willi Hennig, who referred to it as phylogenetic systematics.

Cladistics differs from other taxonomic systems in its strong focus on evolution rather than similarities between species, and in its heavy emphasis on objective, quantitative analysis, particularly using DNA and RNA sequencing data. The cladistic approach relies on identifying *monophyletic* groups, clusters of taxa that share a more recent ancestor with each other than they do with other groups. Polyphyletic

groups, by contrast, are 'mixed bags' that may seem to share similarities but actually arose from two or more different ancestors. This approach has two main differences from the Linnaean system. First, phylogenetic classification tells you something important about the organism: its evolutionary history. Second, phylogenetic classification does not even attempt to rank organisms. In contrast to the traditional Linnaean system of classification, phylogenetic classification names only clades, or groups that include both a single ancestor and all its descendents.

The most important assumption in cladistics is that characteristics of organisms change over time, because it is only when characteristics change that different lineages or groups can be recognized. The original state of the characteristic before it changed is called plesiomorphic; the new state after the change, apomorphic. Though some people use the term 'primitive' instead of plesiomorphic and 'derived' instead of apomorphic, biologists generally avoid using these words because they have inaccurate connotations. It is all too easy to think of primitive things as being simpler and inferior, but in many cases the original plesiomorphic state of a character is more complex than the changed, apomorphic state. For example, as they have evolved, many cave insects have lost effective vision, and many island-dwelling species have reduced wings.

Instead of a Linnean-based evolutionary tree, cladists construct (or in the words of some, 'reconstruct') a *phylogenetic tree.* This is a diagram intended to represent the evolutionary history of modern taxa. The trunk, or earliest ancestor, gives rise to limbs that give rise to branches that terminate in twigs. The tips of the twigs represent species that are alive today. Sometimes branches fall off, representing extinction. (Some scientists prefer to think of a phylogenetic bush with many branches, rather than a tree with a single trunk; both terms are used.)

How does one go about constructing such a phylogenetic tree? No diagram can take every trait into consideration, so the first thing one must do is identify the particular characters (inherited traits) one will consider, and then describe the ways they vary, i.e. their character states. Traits can be almost anything that has an assumed genetic base and that can consistently be measured. Historically, trait measurements were morphological or anatomical, and many were gathered from fossil evidence. Sometimes traits corresponded to a single structure (such as hind leg lengths in various grasshopper species). In other cases, traits were expressed as ratios that described the measurements of a set of related structures (such as the tibia: femur ratio for various grasshopper species). These ratios were helpful to account for environmental influences on factors such as absolute body size. Behavioral (see Section 1.3.3 below) or physiological traits, such as reproductive modes (see Fig. 1.12), can be useful as well. With the advent of molecular genetics, many traits are measured as DNA sequences, and molecular genetic maps are used to help build phylogenies by comparing and contrasting sequences across different species. Hopefully, one's wise choices will lead to trees that approximate reality. However, there is always the possibility that choosing different characters might have led to different results. Cladistics can produce profoundly complex analyses, so it is important to remember that however fancy an analysis may look or how many molecular data have gone into it, the result is still a tree or bush that represents a hypothesis. New and better

data could change the outcome and support a different hypothesis about the way that the organisms are evolutionarily related.

Next, one must judge which species are most closely related to each other and thus are descended from a more recent common ancestor. This involves decisions concerning *homologies*—characteristics assumed to be shared by species through descent from a common ancestor rather than being a product of a similar environment. As theories go, homology is relatively simple, but since it involves judgments about past events that can never be known with absolute certainty, in actual practice it sometimes can be quite controversial. For whatever character set one has chosen, the most similar pairs are considered the most closely related; more differences are taken to mean a more ancient split in ancestry, based on the fact that it takes more time for multiple mutations to occur. Unfortunately, all this is assumptive. History is not something we can see. It happens only once, and only leaves clues behind for those who attempt to reconstruct evolutionary history.

Whereas evidence for homology can help one make sound phylogenetic decisions, a related possibility can sabotage it. *Evolutionary convergence* is the tendency of different clearly unrelated species to develop similar characteristics in response to a set of environmental conditions. For example, sociality appears in both ants and termites, though they are only distantly related (see Chapter 10). Although the selection pressures under which sociality evolved may have been similar, the trait was not shared with a common ancestor.

After determining the characters and examining each taxon to establish its character states, some types of cladistic analysis require that one decide the polarity, or direction of evolution, for each character; this can take some work. Then the taxa must be grouped by synapomorphies—'changed' character states that they share. If conflicts arise, they must resolved by some clearly stated method; the usual one is parsimony (see Section 1.2.3).

Finally, when it is time to actually construct the phylogenetic tree, ideally it should follow two rules. First, all taxa go on the endpoints of the tree, never 'lower down' at nodes as Linnaean trees would. Instead, all nodes must have a list of synapomorphies that are common to all taxa above the node (unless the character is later modified). Second, all synapomorphies must appear on the tree only once (unless the character state was derived separately by parallel evolution). In practice, 'hybrid' trees often appear.

Once constructed, a phylogenetic tree is a very helpful tool that can be employed to make predictions about fossils or about poorly studied species. It also can help scientists learn about the order of the evolution of a particular trait, a complex feature, or observed diversity.

1.3.3 Behavior and Speciation

Can behavioral patterns be used like morphological or genetic characters in constructing a phylogeny? At first the idea was hard to sell. Many scientists said no; behavior is too variable, and is under too much environmental influence. However, one of the cornerstone beliefs of ethological research has always been

that behavioral patterns can be treated like morphological ones, and this included showing homologies. Behaviors also could act as barriers that interrupt gene flow, thus starting in motion the process of speciation, the division of a species into two or more new biological species that are genetically unique.

Differences in mating behavior often constitute the strongest sort of species-isolating devices. For example, consider the fireflies of eastern North America. This is a confusing group in which the males show almost no differences in structure or body coloring but much variation in flash pattern used to attract females during courtship. This problem attracted the attention of Harry S. Barber; after much study, in 1951 he published a description of 18 species of *Photuris* fireflies classified mainly on the basis of male flash patterns. Ten of these were named as new since they had not been previously recognized by morphology alone. Similarly, when studying the common smaller fireflies of the United States, Jim Lloyd found several such 'hidden species' in the related genus *Photinus*. First recognized by consistent differences in flash signals (Fig. 1.16), these fireflies later were found to differ
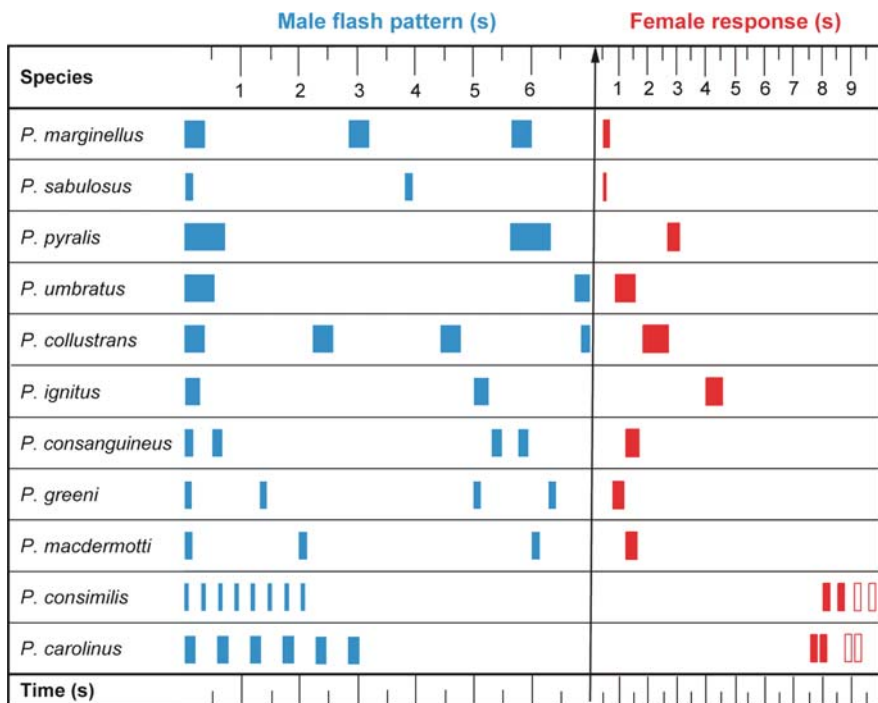
Fig. 1.16 Sorting species by flash. Using behavior to inform decisions about speciation, Lloyd compared flash patterns of *Photinus* fireflies. Differences among several North American species in the male flash signals (*left*) and female response flashes (*right*; note different time scales) are shown at typical field temperatures (signal timing is temperature dependent). Female responses are timed from initiation of the last pulse in the male flash pattern (open bars indicate optional responses)

in minor morphological details. In many places, two or more species of *Photinus* fly together but are prevented from interbreeding by their specific courtship patterns. The males fly at different heights and in different flight patterns (see Fig. 7.2); their flashes differ in length, number of pulses per flash, and sometimes in color or intensity of the light.

One cannot construct a tree using behavioral characters and then use it to test hypotheses about those characters, of course; that would be circular reasoning. However, a very useful approach can be to construct a phylogenetic tree using morphological and/or genetic traits, and then map behavioral characters onto it and see if they match. By examining the tree, it is also sometimes possible to determine the evolutionary direction of a behavioral trait.

One example of this practice involved Herbert Ross's study of the aquatic insect order Trichoptera. The caddisflies make up a very large insect order, with about 10,000 described extant species distributed among 45 families. Their aquatic larvae are found in almost all freshwater communities, where they occupy a diversity of microhabitats and trophic niches. Larvae of certain caddisfly families construct a fixed retreat; those of others construct a portable case; and still others are free living. In 1967, Herbert H. Ross provided the first modern phylogenetic hypotheses of subordinal and superfamily relationships in the Trichoptera. Superimposing larval behavior upon a morphologically based phylogeny indicated to him that fixed retreat construction was the ancestral behavior and portable case building the derived state, with a series of steps leading from one to the other. However, through the years after his work, his view was challenged by at least four very different morphologically-based hypotheses of the relationships between the Trichoptera suborders (Fig. 1.17 top). In 2001, a research team of cladistically-oriented entomologists began their own analyses of the Trichoptera that included both a reevaluation of others' morphological data sets and newly collected molecular sequence data. The first of its kind for the Trichoptera, the project is large and ongoing, but satisfyingly, the phylogenetic relationships among the suborders so far seem to closely resemble those proposed by Ross over 40 years ago on the basis of larval behavior (Fig. 1.17 bottom).

1.4 Questions and Perspectives

In various versions of an old tale from India, a group of blind men (or men in the dark) each touch one different part of an elephant to learn what it is like. When they compare notes on what they felt, they find they are in complete disagreement. The story is used to indicate that reality may be viewed differently depending upon one's perspective, suggesting that what seems an absolute truth may be relative due to the deceptive nature of half-truths.

Over the years, behaviorists and non-scientists alike have asked questions about almost every aspect of animal behavior, while trying to avoid being like these fabled blind men. Even today, such attempts are sometimes successful, sometimes not. Different ways of looking at a behavior clearly lead to different answers.
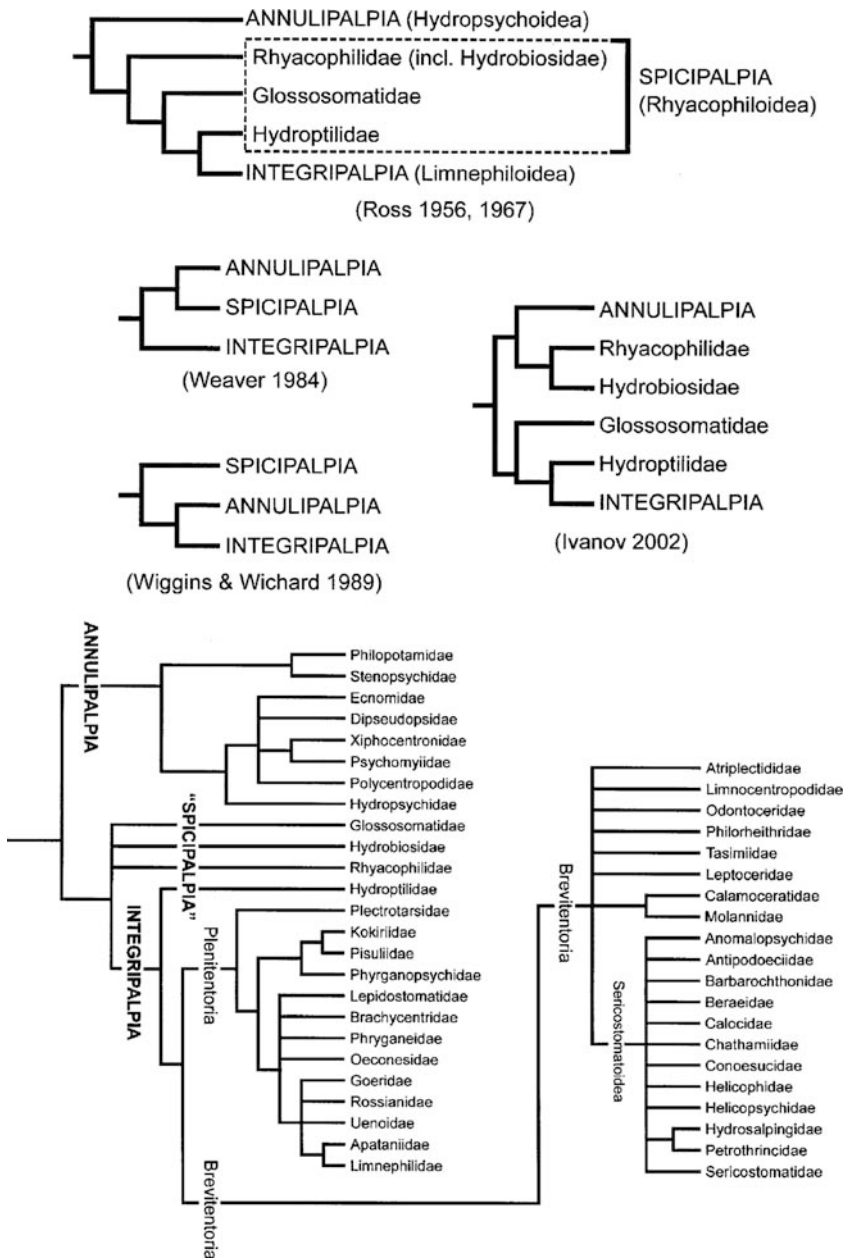
Fig. 1.17 Evaluating Trichoptera relationships. (*top*) The original hypothesis of Ross about Trichoptera (caddisflies) phylogeny compared to subsequent worker's hypotheses of subordinal relationships based on differing character sets that show a lack of consensus. (*below*) A recent composite phylogeny of family group taxa of Trichoptera proposed by K. M. Kjer and colleagues incorporating data from molecular analyses strongly supports five monophyletic clades. With respect to the relationships among the three suborders it closely resembles that proposed by Ross on the basis of caddisfly behavior

Table 1.1   Tinbergen's four questions: Basic approaches to the study of animal behavior

Types of questions	Types of explanation	
Proximate—how organisms work	Causational—mechanistic explanations of individual responses to stimuli, both internal and external	Developmental—explanations based on ontogeny starting with DNA and progressing through life stages from immatures to adult
Ultimate—why organisms are the way they are	Functional—explanations of adaptive significance based on presumed selective advantage	Evolutionary—explanations that attempt to reconstruct the phylogenetic history of a lineage often using a comparative approach

In a classic paper the pioneering ethologist Niko Tinbergen pointed out that essentially all research questions address one of four major concerns about a behavior: the nature of the immediate stimuli that evoke it, the way in which it develops, the survival function it has, and how it has evolved (Table 1.1).

1.4.1 Proximate and Ultimate Analyses

While Tinbergen's Four Questions have become axiomatic in behavior study, others viewing the list realized that they could be grouped into just two kinds of analyses: proximate analysis and ultimate analysis. *Proximate analysis* focuses on the immediate causes of a behavior—those that occur during a given organism's life. *Ultimate analysis* is defined in terms of the evolutionary forces that have shaped a trait over time. For example, a group of scientists might ask why house flies are drawn to sugar. Those favoring a proximate explanation might consider factors such as the way sugar acts on the fly's sensory system (Tinbergen's 'immediate stimuli') or perhaps the physiological events that occur in the fly's brain ('development'). Other scientists in the group might approach the same question from a different analytical viewpoint, an ultimate analysis in terms of the ways that sugar attraction might increase flies' chances of surviving long enough to reproduce ('survival function') or the selective forces in the evolutionary past that favored sugar-preferring individuals ('evolutionary history') and whether relatives of the house fly display similar responses to sugar.

It is sometimes said that proximate questions generally ask 'how' and 'what' whereas ultimate questions tend to ask 'why' but this simplistic division can be confusing. It may also seem to imply that proximate analyses are less important than ultimate analyses, but that is not the case. There are fundamental links between the two analyses. Proximate analysis, by shedding light on neurobiology, endocrinology, molecular genetics, and so on, illuminates the variation available for natural selection to act on. At the same time, understanding something about the natural selection pressures that have acted on a behavior can help in designing the best way to do a proximate analysis. While each explanation of the fly's attraction to sugar is perfectly reasonable, none is inherently superior to the others. However, taken

together, the different explanations and approaches to studying the question provide a fairly complete understanding of the behavior.

1.4.2 Types of Approach

In addition to the differing viewpoints of proximate and ultimate analyses, scientists have different intellectual approaches to a given set of observations and experiments. A *conceptual approach* typically seeks to join together formerly unconnected ideas in new cohesive ways. Natural history and experimentation may be taken into account, but the broad-based concepts that result are usually not tied directly to any specific observation or experiment. For this reason, this approach is sometimes (somewhat disparagingly) called 'arm-chair science'. However, new concepts tend to generate a great deal of new experimental work by others, and a new conceptual advance can be a powerful tool that entirely reshapes the way that a discipline views itself. A clear example would be William D. Hamilton's ideas about kin selection and its role in the evolution of social behavior in the Hymenoptera (see Chapter 10).

Theoreticians come at behavioral study from a different intellectual direction. The *theoretical approach* entails the generation of some sort of mathematical model to explain observations. The first major studies applying this approach to animal behavior involved foraging. Out of all the foods available to an animal, which ones should it choose to eat? Under what conditions? To address such questions, a mathematical tool called optimality theory was developed (see Chapter 4). Critics of the mathematical theory approach are wont to point out that such theories often do not match the details of any given system. However, that is not the theoreticians' aim. They are not trying to mimic the natural world with their model. Instead, they are trying to strip away the specific details to uncover the barest ingredients that will allow them to make general predictions that might apply to many systems.

The *empirical approach* essentially has two bases, observation and experimentation. It basically equates to the 'scientific method' taught in introductory biology classes. One begins with a question, devises a possible answer with an explicit prediction or hypothesis about what one expects to observe, and then uses this potential explanation to design and then conduct relevant experiments or observations. After collecting data in a way that minimizes the influence of other variables, one evaluates the results in an appropriate way (which generally includes the use of statistical analyses). If the actual results do not correspond to the expected ones, the underlying hypothesis is probably false; if the evidence does match the prediction, the hypothesis is tentatively accepted as true, though it can never be absolutely proved so.

In practice, of course, insect behaviorists can and do combine perspectives and approaches in countless ways. Many aspects of behavior are examined from both proximate and ultimate perspectives; others lend themselves more readily to one perspective than the other. Various approaches are also used (though the empirical approach remains the most common).

The most powerful investigations always have been the multi-faceted ones in which research shines new light on a phenomenon from every possible direction.

A premier example is the honey bee, *Apis mellifera*. Because of its importance to agriculture and its advanced social system, it has become one of the most-studied insects in the world. In Chapter 8, a case study considers its foraging from the aspect of communication. Case Study 1.1 considers factors that start the bee out of the hive door in the first place, and out into the world outside.

Case Study 1.1: Foraging Onset in the Honey Bee, *Apis mellifera*

Proximate causation can be considered to have four components—hormonal, neurobiological, molecular genetic, and developmental. These areas interact in complex ways and boundaries between them can be difficult to define, as illustrated by a single species, the honey bee.

For centuries, honey bees have enthralled scientists and the general public alike. Their development and colony life have been subjects of special fascination, but perhaps most of all, observers have been entranced by their foraging. When a new bee-pollinated flowering plant begins to bloom, some time may pass before a single bee arrives. Soon after this initial visit, however, the plant is buzzing with visitors. Clearly, some sort of communication is involved; deducing its nature has been one of the major accomplishments in insect ethology (see Chapter 8). The effects of neural structures, genes, development, and hormones have been a lesser-told story. Much of this proximate analysis comes from the work of Gene Robinson and his colleagues at the University of Illinois.

Honey bees have an age-based task allocation system. Younger bees generally stay within the hive, doing housekeeping tasks such as cleaning the hive and feeding the larvae. Older bees give up these tasks and switch to searching outside for pollen, nectar, water and propolis (gummy plant resins used in nest repair). Like other insects that search for food away from their nests, these foraging honey bees must remember and retrieve information from the environment.

In most invertebrates where it has been studied, such spatial navigation is linked to cell clusters called mushroom bodies (see Plate 1) located in front of the brain. Do honey bees also rely on their mushroom bodies? Robinson's research team dissected bees with known ages and jobs. The researchers found that the mushroom bodies of foragers were almost 15% larger than those of bees that remained in the colony, but the relative volume of other nerve clusters in the bees' brains remained relatively unchanged as a function of age and task allocation.

Was foraging the sole reason? By removing a significant number of the current foragers from a hive, researchers induced week-old bees from the hive to take on the forager role immediately rather than waiting until the normal age of about 20 days old. When they examined these precocious foragers,

their mushroom bodies resembled those of the normal-aged foragers. Thus, it seemed that foraging behavior actually changed the brain, rather than vice versa.

How might this developmental shift be influenced at the molecular level? A gene called *period (per)* affects circadian rhythms and development time in fruit flies (see Chapter 2). Alberto Toma and his colleagues asked how *per* messenger RNA (mRNA) levels in bees might influence the developmental changes associated with becoming foragers. They measured mRNA levels of groups of laboratory-reared bees of different ages, marked a group of their bees that were only one day old, and added them to a natural bee colony in the field. At days seven and 24, they recaptured these marked bees and measured their mRNA as well. In both laboratory-raised and outdoor-living bees, *per* mRNA was significantly greater in older individuals that foraged than in younger bees that stayed home (see Fig. 1.18).

Was *per* mRNA higher simply because of age? To answer this, Toma used precocious week-old foragers. When he measured their mRNA, it did not differ from those of typical older foragers. This showed that there was a fundamental link between *per* mRNA and foraging, not just a more general correlation between *per* mRNA and development. Of course mRNA does not directly cause the behavioral change; rather quantity of mRNA can be assumed to reliably indicate the extent of gene expression, in this case the *per* protein translated from the mRNA.
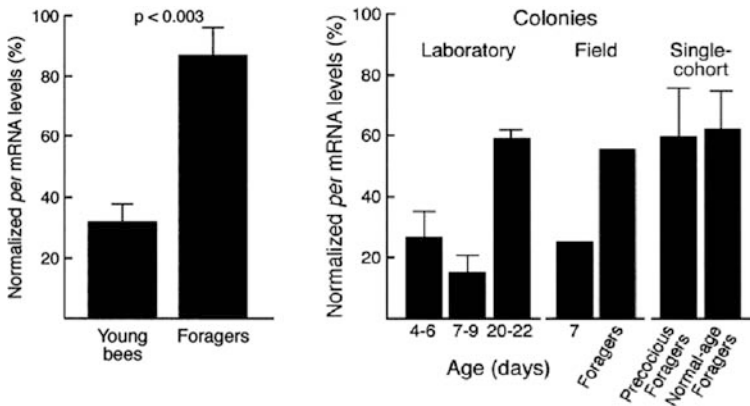
Fig. 1.18   Switching jobs. As they grow older, worker bees shift from hive work to foraging. How might genes affect this behavior? Toma and colleagues measured mRNA. (*left*) Foraging bees have substantially higher levels of *per* mRNA than younger, nonforaging hive bees. This difference could be due to various factors such as age, behavior (forager vs. nonforager), or both. (*right*) Tricking bees into searching for food much earlier than usual, Toma's team produced 10-day-old precocious foragers; when they were compared to normal 22-day-old foragers, there were no statistical differences in *per* mRNA levels

The ways in which genes affect the switch from hive work to foraging have received a great deal of attention (Fig. 1.18). Rapid advances in molecular genetic technology are leading to ever more detailed glimpses into honeybee foraging. In a large-scale 2003 study of 5,500 genes, changes in mRNA levels were found to be associated with about 2,145 genes involved in the hive work/foraging transition. As such large-scale genomic approaches to behavior become more common, the challenge will be to figure out how to handle the massive amounts of data they are capable of gathering. One way to facilitate the molecular analysis of a complex behavior such as honey bee foraging is to dissect it into simpler behavioral components. This is currently a very active area of research. A *foraging (for)* gene has been found to influence the phototactic elements of foraging, and a *malvolio* (*mvl*) gene influences the responsiveness of honey bee workers to sucrose and through that response, the age at onset of foraging and the tendency to forage for either pollen or nectar. Presumably these are only two of many genes that will be found to play a causal role in honey bee behavioral maturation.

Chapter 2
Programming and Integrating Behavior

2.1 Introduction

Lacewing males, *Chrysoperla downesi*, sit among the branches of an evergreen tree, softly drumming their abdomens against terminal twigs and needles in a long, complex pattern of volleys that attracts females. Moths of the black cutworm, *Agrotis ipsilon*, fly by at recorded ground speeds of between 97 and113 km/h (60–70 mph). Foraging *Cataglyphis* ants scurry around upon the floor in the Sahara Desert at surface temperatures of up to 70°C (158°F), scavenging upon the corpses of insects and other arthropods that have succumbed to heat stress in this extreme environment.

Insect behavior—hidden and obtrusive, incredible and yet somehow familiar, often admirable and at other times repulsive—has always been a source of amazement and curiosity. Even with their extra legs and inexpressive faces, insects look and act enough like little people to make one wonder how and what they think, or whether they think at all. What regulatory and integrative mechanisms coordinate the expression of their behavior?

Instead of answering the question, a bit of observation only leads to many more. A headless male preying mantis can complete a sequence of mating behavior (see Fig. 9.16). A decapitated cricket will sing several of its song patterns when its neck connectives are stimulated. Headless cockroaches can learn to keep a leg flexed to avoid an electrical shock. How necessary is an insect brain?

Having followed a tail-wagging dance for the first time, novice honey bees can fly in the indicated direction and distance. The first time it strikes, a hand-raised preying mantis will react to exactly the same stimuli as experienced mantises do. How much of insect behavior is controlled by instinct?

Honey bees learn to avoid a food source from which they have received an electric shock, and can remember the previous location of a displaced hive even 12 days later. Female sand wasps return to their temporarily closed nest and, on the basis of a quick inspection, decide whether many or few caterpillars must be provided to the young larva inside. How much reasoning can insects do?

Such questions have a long history and are still far from fully answered. Yet behavior fairly begs for some degree of functional explanation, because ultimately behavior means making physiological decisions—when to move and when to

remain still, what objects to approach and what to avoid, which muscles to contract and which to relax. For any organism, such decisions require some sort of internal communication system that can organize, manage, and synchronize incoming information and outgoing responses. Like most other complex organisms, insects have two such internal communication systems: a nervous system and an endocrine system. The *nervous system* is electrochemical, and acts through impulses traveling over the surface of specialized cells called neurons. The specificity of the messages in this system resides in the nature of the pathways over which they travel, not in the differing nature of the messages, because all are due to the same type of physio-chemical event. The *endocrine system*, on the other hand, is more purely chemical. Messages are encoded in specific substances produced and released by specific body cells. As these chemicals are transported through the body, many cells are exposed to them, but only certain uniquely sensitive cells respond.

There are real advantages in this duality, two systems existing side by side. Nerves send electrical messages rapidly, but a nervous system that reached every cell would take an enormous amount of space. Hormones, on the other hand, can bathe each cell; however, rapid responses such as escape would be poorly served by the relatively slower speed of the hormonal bath. In effect, by evolving a dual system, organisms have made a reasonable trade-off between response speed and system complexity.

In another sense, however, one might also argue that the insect system is not dual at all but a continuum broken only by imposition of the human need to classify. Neurosecretory cells occur throughout the central nervous system and their secretory products are important functional parts of it. Neurosecretory cells emit products that serve as hormones, neuromodulators, neurotransmitters, regulators of hormonal secretion, and a variety of other functions. Almost all are peptides or small proteins that control physiological or biochemical processes in which sustained stimulation is needed. Although over 100 have been identified in insects, clearly defined functions have been demonstrated for very few.

2.2 Nerve-Based Coordination

'What is the difference between a vertebrate and an invertebrate?' 'One goes squish-crunch; the other goes crunch-squish.' It's an old riddle, but it sums up a vital difference. The characteristic feature of arthropods, including the insects, is a hard, jointed exoskeleton or cuticle made up of a series of hard plates, the sclerites.

For an insect, having its support frame on the outside is a mixed blessing, because the same cuticle that provides a defense against assault and dehydration also separates the insect from its environment. If the insect is to make behaviorally appropriate responses, the nervous system inside this shell must be able to receive information across the barrier and that requires a moist receptor surface, but for such a small organism, water loss absolutely must be minimized. The compromise for insects has been to expose receptor surface only through pores that, while open

continuously, are so extremely small that they minimize the potential for water loss. The receptors also have been concentrated on a very few body areas, such as the mouthparts, antennae, legs and cerci. Most of the body has remained waterproof but also insensitive to external stimuli. Where sensory reception occurs, the basic unit is the *sensillum*, which usually looks like a tiny hair in a socket (see Fig. 6.2). The sensory neurons inside are bipolar—one end extends into the cuticular portion to receive stimuli and the other end sends messages to the central nervous system. Sensilla have many structures and functions, including not only those one might expect such as taste perception, but also unexpected ones such as the infra-red irradiation detectors in species of buprestid beetles that breed only in trees recently killed by fire.

All receptors code their information in units called *action potentials*, which are self-regenerating standard signals that travel through other nerve cells along the length of long cytoplasmic cell projections (axons) through small gaps (synapses), the switchboards of the nervous system, where they are transmitted by the release of chemicals having specific effects upon the neuron or muscle cell across the synapse. Stimulation usually leads to the production of not one but many nerve impulses all of the same amplitude. Information about the stimulus is coded in the number and frequency with which they follow each other, within limits of the system.

2.2.1 The Insect Nervous System

The insect nervous system (Fig. 2.1) is made up of two highly structured, intertwined systems. The first is the visceral (also called stomatogastric or sympathetic) system that controls alimentary canal movements and is closely concerned with the process of neurosecretion. The second is the *central nervous system* (CNS), which coordinates the peripheral sense organs and muscles. As concerns insect behavior, the latter is of the most direct relevance. (A third term, peripheral nervous system, is also sometimes used; it refers to all the nerves that radiate from the CNS to innervate muscles, stretch receptors, sensory receptors, etc.)

Because insects evolved from the segmented system of annelid worms, their organization still reflects that past. In the earliest insects, each body segment probably contained a knot-like cluster of nerve cells, called a *ganglion* (plural, ganglia) that was responsible for the activities of that segment. However, in all living insects today, different parts of the system have fused together in various ways. A ganglion typically contains a mass of neuron cell bodies at its outer edges and a central region, the *neuropil*, where synapses occur. The largest and most complex neuropil occurs in the brain, but all ganglia contain neuropil regions. The neuropil appears to keep growing, even after rest of the nervous system stops; this suggests the importance of new information processing and integration throughout an insect's life.

Nerve cells, like highways, have many shapes, and no single shape can be called characteristic. Like superhighway systems connecting cities, nerves radiate from

Ocellar nerve
Optic lobe
Antennal nerve
Protocerebrum
Deutocerebrum
Tritocerebrum
Frontal ganglion
Bilateral nerve
Labral nerve
Pharynx

Circumesophageal
connective

Aorta
Crop
Hypocerebral
ganglion
Recurrent nerve
Ventricular nerve
Corpus allatum
Circumesophageal
connective
Subesophageal
ganglion

First thoracic
ganglion

(a)

Ocellar nerve
Protocerebrum
Neurosecretory cells
Tritocerebrum
Circumesophageal
connective

Optic lobe
Antennal nerve
Deutocerebrum
Frontal ganglion
Subesophageal
ganglion

(b)

Fig. 2.1 Visualizing the insect nervous system. (**a**) Side view of a representative grasshopper head. A chain of ganglia trail from the brain, dipping below the gut to lie just inside the ventral cuticle; nerves from the ganglia branch out to the sense organs and muscle systems, while neurosecretory cells in the ganglia chemically link the nervous and endocrine systems. (**b**) Front view shows the three main regions of the brain—the protocerebrum, the deutocerebrum, and the small tritocerebrum—and the nerves that connect the tritocerebrum with the frontal ganglion and labrum; circumesophageal connectives at the back of the tritocerebrum connect the brain to the subesophageal ganglion, a complex structure supplying nerves to mouthparts, neck, and salivary glands

the ganglia to organs and muscles, generally within the segment where the ganglion resides. Also, like most superhighways, they generally (but not always), are two-way streets, with sensory (or afferent) neurons delivering signals to the central nervous system, and motor (or efferent) neurons carrying output back to muscles, glands, and organs. The few that act like one-way streets (such as the purely sensory ocellar nerve) do not directly synapse with one another; instead they connect through one or many interneurons.

In most insects, the *brain* is a large group of neurons that lies above the esophagus. For that reason it is sometimes called the supraesophageal ganglion. (Surprisingly, while the brain is in the head of most insects, in dipterous maggots it is several body segments back.) There is still some disagreement among insect physiologists about the brain's precise origins and number of primitive segments that comprise it. However, three parts are generally recognized (Fig. 2.1b). The most anterior section, called the *protocerebrum*, is the most complex part of the insect brain. It directs neural traffic at the crossroads between sensory input and motor output. At each side, optic lobes extend to the compound eyes; at its center, a pair of large *mushroom bodies* (corpora pedunculata) process olfactory information and control tasks that require visual coordination of locomotor activity and spatial orientation (see also Plate 1). The mushroom bodies and associated cells provide a structure for elaborate interconnections that allow learning and memory to occur.

The second brain section, called the *deutocerebrum*, connects to the antennae. Its neurons are of two types—one type processes chemosensory information; the other, mechanosensory. The former have received a great deal of research attention because of the importance of the chemosensory neuropil in mediating feeding, sexual, and social behaviors.

The third and smallest part of the brain, the *tritocerebrum*, connects the central nervous system to the ventral nerve cord through the circumesophageal connectives. It also innervates the labrum (upper lip), pharynx (region between mouth and digestive system), and the rest of the visceral nervous system.

Beyond the brain, ganglia line up along a nerve cord that runs along the underside of the insect's thorax and abdomen. The first ganglion of this *ventral nerve cord* (and the only one still in the head) is the *subesophageal ganglion*. Another nerve supercenter, it controls the rest of the mouthparts, salivary glands, and neck muscles; axons from its neurons travel both forward to the brain and posterior to the thoracic ganglion. The subesophageal ganglion influences motor patterns involved with walking, flying, and breathing, although those motor patterns actually begin in other ganglia.

The rest of the ventral nerve cord consists of a further series of paired ganglia joined by lateral connectives. Typically, the first three are in the thorax and control the wings and the legs. The number of abdominal ganglia varies because they have fused in various ways in different insect groups.

The brain and central nervous system almost certainly are not merely simple relay stations; rather, they function as integrative machines. Part of the evidence for this comes from ablation experiments, in which anatomically distinct parts of the system are surgically removed and their role is deduced by comparing behaviors

before and after excision. The crudest of these is simply to cut off the insect's head, an 'experiment' that has been performed since far antiquity.

Ablation experiments have confirmed that for many stereotyped behaviors the insect brain actually is unnecessary—an observation which led many early biologists to believe that insects had none. The confusion was understandable. A decapitated insect may even show complex behavior for many days, because (in contrast to the vertebrates) insects have not concentrated their life support systems within the brain. Crucial controls of functions such as respiration are decentralized; so are many postural, locomotory, sexual, and grooming mechanisms. At the same time, however, certain crucial differences can be noted when an insect is deprived of various parts of its brain. Most notable is that the relative incidence of various types of actions changes markedly. Often, there is an uncontrolled release of competing behavior modes.

In a well-studied example, a preying mantis deprived of its protocerebrum simultaneously and continuously performs two opposed behaviors—grasping, which holds it back, and walking, which pulls it forward. This is behavioral nonsense, resulting in a hopelessly entangled and exhausted mantis. Intact mantises, of course, spend most of their time doing neither; rather, they wait motionless, often for hours, to ambush unsuspecting prey.

When the subesophageal ganglion is removed along with the protocerebrum, however, the mantis becomes permanently immobile. Does the neural program for leg movement reside in the subesophageal ganglion? No, because electrical stimulation of a disconnected thoracic ganglion produces vigorous and complete limb movements. Rather, *neural inhibition* occurs—the capacity of a neuron to exert a blocking action on cells connected to it. In an intact mantis, the protocerebral lobes apparently send out inhibitory messages that differentially block parts of the excitatory activity being generated by the subesophageal ganglion. The excitatory messages that are allowed to pass are transmitted to the thoracic ganglia where grasping or locomotion is initiated.

How, then, does one explain the copulatory behavior of the decapitated male mantis? When his head is destroyed, as often occurs during courtship with the predatory female (see Fig. 9.16), the mantis walks in a circle while vigorously performing continuous copulatory movements. Here, the ventral ganglia themselves possess an endogenous activity that is usually inhibited by the subesophageal ganglion. Such inhibition is a fundamental property of nervous systems. If a nervous system were unable to inhibit those circuits competing with the one responsible for a desired behavior, the result would be behavioral chaos.

2.2.2 Simple Reflexes and Repeated Motor Patterns

Many rapid autonomous behavior patterns in insects depend upon relatively simple neural circuitry. One set of such patterns includes reflexes. These are familiar to us; a gentle tap on one's knee elicits a knee jerk reflex, for example. Movement is the most

common form of response to a stimulus. It is also the least complex, because the input and output have a one-to-one relationship. A knee jerk, for example, does not repeat itself unless the knee is tapped repeatedly. Because of their relative simplicity, reflexes provide some of the clearest examples of the ways in which behavioral stereotypy depends on properties of nervous systems. Other examples include kineses and taxes, two locomotory responses that will be covered in more detail in the next chapter.

A related set of simple behaviors are those involved in various rhythmically repeated motor patterns such as insect songs, flight, and walking. How are these physiologically generated, maintained, and coordinated? Historically, one explanation (called the cyclic-reflex hypothesis) stated that feedback from the act itself was sufficient to cause the act to be repeated. Thus, such rhythmic actions would continue in a repetitive circular loop (like perpetual motion) until inhibited by other reflex paths or by the brain. Since the 1960s, however, accumulating evidence has supported the concept that many patterns are generated in the central nervous system—the *central pattern generator* (CPG) hypothesis.

In the 1960s, Donald Wilson conducted a series of now-classic studies supporting the CPG hypothesis. Technical advances in electrophysiology had made extracellular recording with cathode ray oscilloscopes into a powerful new tool for studying the neural basis of behavior when Wilson began collaborating with Torkel Weis Fogh, who had developed an experimental system in which a tethered locust could be induced to fly normally in a wind tunnel.

Working together, the two men built a detailed picture of neural output to the locust's flight muscles, then compiled a catalog of sensory inputs to the thoracic ganglia. Next, in a series of skillful experiments, Wilson successively eliminated sensory input to the thoracic ganglia while recording motor output. First, he removed the locust's head and subesophageal ganglion; lacking its wind-sensitive sensory hairs, the locust flew slowly but otherwise normally. Step by step, further operations severed one source of sensory input after another, until Wilson was able to show that even total removal of all sources of periodic input did not abolish patterned motor output (Fig. 2.2). When the breezes in the wind tunnel were kept still, the basic pattern of flight motor nerve discharge remained unaltered. When Wilson severed the nerve fibers from the stretch receptors that register wing movement, the pattern persisted. When he dispensed with timing cues from other moving body parts, nothing changed. Clearly, the locust was not timing its wing beat through sensory cues created by wing movement. The motor pattern must have originated within the thoracic ganglia.

The concept of central coordination does not exclude peripheral influences, however. Though the sensory and motor systems were not linked in the locust in terms of timing, the average frequency of wing beat was correlated with the discharge rate in the receptor nerves and it slowed when receptor nerves were cut. Sensory feedback did not cue sequences, Wilson postulated, but instead modulated genetically determined motor programs. Subsequent studies have added a layer of complexity to Wilson's conclusions, however, with the recognition of neurohormonal modulations of these central circuits. Even though locomotion (and
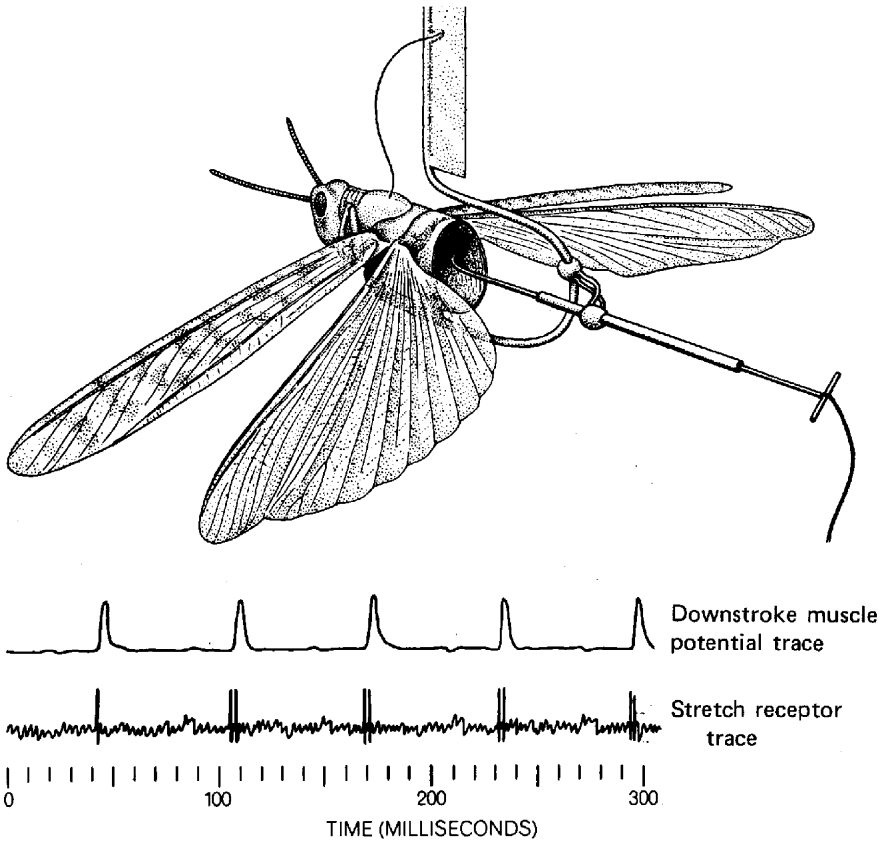
Fig. 2.2 Demonstrating the central pattern generator. Experiments with tethered locusts, which will perform normal flight movements in a wind tunnel, demonstrated that the insect central nervous system, without sensory input from wing sense organs, generates a pattern of motor neuron output that closely resembles the pattern produced in normal flight. Sensory discharges in nerves from the wing and wing hinge were recorded by manipulating wires into a locust's largely eviscerated thoracic cavity. Down-stroke muscle potentials repeat at the wing beat frequency, while stretch receptors fire two to three times per wing beat

a great many other rhythmic behaviors) may depend on genetically determined central pattern generators, they usually can be modified by sensory feedback that serves to adjust them to various real-world factors such as turbulence, injury, and aging.

Partly for the simple reason that so much is known about it already, cockroach escape behavior continues to be an active research area today (see Case Study 2.1). It has been shown that the behavior has two distinct parts, an initial directional turn to orient away from the threat, followed by a run of more random direction. Variants in the initial turn have been described, but leg kinematic motions appear quite stereotyped.

Case Study 2.1: Escape Behavior in the Cockroach, *Periplaneta*

Perhaps the most striking characteristic of many simple reflex-like actions of insects is their speed. To an escaping insect, a few thousandths of a second may be the difference between the quick and the dead. How are cockroaches, for example, so proficient at reacting to our approach, even from behind?

One of the advantages of studying neuroethology in invertebrates is the possibility of working at the level of individually identified neurons. Escape reactions are one of the easier behaviors for such work because the rapid nerve impulses necessary to evade a predator are conducted along axons of especially large diameter. Unlike the numerous small interneurons that characterize many other circuits, these giant interneurons (also called giant axons) run for relatively long intervals before synapsing. *Periplaneta americana,* the American cockroach, has 14 of them, each of which can be easily identified and distinguished with a microscope.

In pioneering research that began in the 1940s with simple eqiupment (Fig. 2.3), Kenneth Roeder showed that although touching a cockroach will make it flee, actually the major (and often only) sensory cue a cockroach needs to detect a predator's approach is the tiny wind gust that precedes the predator's moving body. Two cerci, thin projecting appendages at the end of its abdomen, detect the air puff, and in response, the cockroach turns and runs away, legs scurrying along in classic CPG manner. It happens so quickly a cockroach can successfully detect and flee the displacement wave preceding the tongue of a striking toad. A slowly walking cockroach can take as little as 11 ms to respond to an air puff of particularly high acceleration. The situation is considered a model example of mechanoreception of ultra-low frequency signals.

Both high wind acceleration and a certain critical velocity are important in causing the insects to run. On the underside of cockroach cerci, Roeder observed delicate hairs that bend in their sockets, each exciting a single sensory neuron at its base. Because stimulation of the cerci excites many of these sense cells at once, a volley of action potentials arrives at the synapse more or less simultaneously. This source-related additive effect, called *spatial summation*, generates an impulse in a giant fiber. These in turn excite motor neurons of the cockroach leg. Spatial summation is the reason why cockroaches do not dash madly off in response to minor stimuli such as kitchen drafts, which would cause only a few cercal setae to be deflected and fire their sense cells.

Likewise, impulses also would not be propagated along a motor axon, Roeder discovered, until at least two (often three or four) volleys of impulses
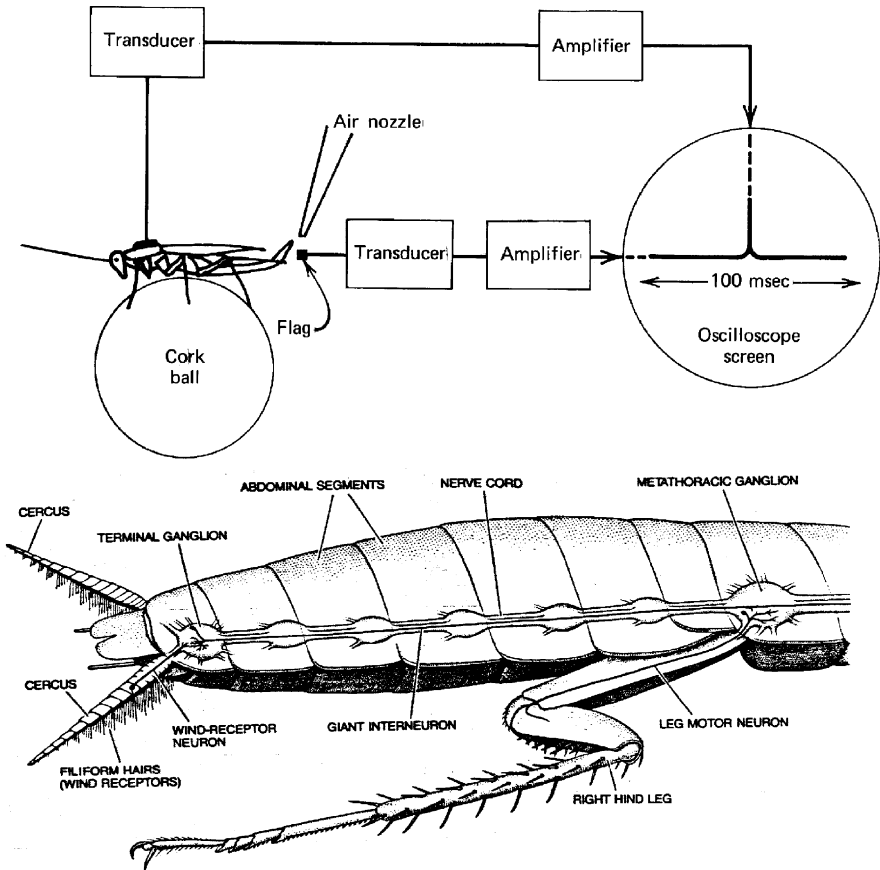
Fig. 2.3 Signaling cockroach escape. (*above*) Apparatus used by Kenneth Roeder to study startle response in the American cockroach, *Periplaneta americana*, one of the commonest cockroaches throughout the world. Glued to a stick, the cockroach is allowed to grasp an unattached cork ball that turns as the roach runs. Near the cockroach's cerci are an air nozzle and a small paper flag. As a puff of air is delivered to the cerci the flag is deflected and an impulse registers on the oscilloscope screen. As the cockroach reacts a second deflection is registered and the difference between the two is the startle response time. (*Below*) Air puffs stimulate receptor hairs on the cerci that relay impulses to giant interneurons running up the central nerve cord to the metathoracic ganglia, from which signals activate motor neurons in the legs. Though the sensory hairs hang below the cerci, they can detect wind from all directions

had arrived at this synapse in a time-related additive effect (*temporal summation*). When he continued to send more volleys of impulses along the giant axons, they quickly stopped responding. On behavioral grounds, this was logical—in a natural situation, continual directives to begin running are redundant information to a cockroach that is already fleeing! Roeder also found that when impulses in the motor fibers were generated, they continued to repeat for

several seconds after all input from the giant fibers had ceased. This illustrated an important adaptive aspect of evasive behavior—movement continues for some time after contact with the stimulus, thereby taking the animal out of harm's way.

Since Roeder's studies, others have confirmed that for most invertebrates, the receptor system associated with detecting danger is associated with a rapidly conducting nervous system that can bring about action through the shortest/fastest neuronal route. In most cases, this is via rapidly conducting giant fibers in the ventral nerve cord. For a number of species, a single interneuron is enough to trigger normal escape. In many cases, all the neural circuitry needed for the basic oriented response occurs in the ventral nerve cord and thoracic ganglia.

While the nerve circuits guiding escape reactions superficially seem quite simple, detailed studies over the past forty years have shown that cockroach escape behavior is actually quite complex, both behaviorally and physiologically. Jeffrey Camhi and colleagues have been major contributors to this new understanding. They began with a few simple questions. Could cockroaches actually determine a threat's direction from a puff of air, or were they simply scurrying off in a random direction after being startled? Plotting many trials showed that the insects usually did turn away from the source of the wind before running away, so they must be able to determine wind direction. How? In a series of trials, various areas on the cerci were covered with wax. When the cerci's upper side was covered, the cockroach's directional response was unaltered. When the underside of either appendage was covered, most of the turns were away from the uncovered one, regardless of the wind direction. When the underside of both cerci was covered, the cockroaches no longer responded to an air puff at all.

Close examination of the bottom side of the cerci shows that the many tiny pivoting hairs run in columns from the front to the rear. In the late 1960s, R. Nicklaus, a German researcher, had shown that in any given column, all the hairs deflect most easily in the same two opposite directions, and that the directions of maximum pliancy differ from one column to the next. By recording sensory output from a number of individual hairs, Nicklaus showed that deflection of a hair in one direction maximized the number of action potentials fired by its sensory cell. Deflecting it in the other direction inhibited even spontaneously occurring action potentials.

Researchers in Camhi's laboratory set out to determine the best excitatory direction for each of the nine columns of cercal hairs of *P. americana,* and to show the range of wind directions to which each column responded. Their results showed that each sensory axon responds maximally to a fairly narrow range of wind directions. However, as a group, the hairs provide 360-degree

coverage. (Thus, even if you approach a cockroach head-on, the cerci at its tail end sense you coming!)

What happens to this directional information as it transfers up the neural chain of command? Camhi and his colleagues made intracellular recordings from individual giant interneurons, then marked each with various colors of injected dyes. They learned that each giant interneuron responds characteristically to air puffs from different directions, and each also differs in its breadth of response. Moreover, each giant interneuron has a characteristic firing rate for a particular wind velocity. Comparing the firing rates of two or more giant interneurons reveals differences uniquely related to wind direction. But how do the interneurons 'decide' where the wind is coming from and which direction to turn in response? Various mechanistic theories have been proposed; in recent years, Camhi and colleagues have been addressing these by stimulating cells of identified giant neurons with artificial spikes added during the sensory-induced behavior, then analyzing the resulting directional leg movements. Though the jury is still out, it appears that directional determination is based on collaborative calculations of direction by the giant interneurons as a group, an approach called *distributed neural processing.*

Currently, a generalized picture of insect escape reactions sees a system in which all the neural circuitry for a basic oriented response is found in the ventral nerve cord and thoracic ganglia. A threat activates sensory neurons associated with peripheral sensory structures such as abdominal cerci. The sensory neurons synapse onto interganglionic interneurons (such as the giant interneurons) or touch-sensitive interneurons in the abdominal nerve cord. In each of the thoracic ganglia, various pathways converge onto interganglionic interneurons that are thought to be the locus of control of the escape system. They determine whether an escape turn is to be initiated and in what direction the insect is to turn. They also connect to the leg motor neurons in their own and adjacent ganglia, both directly and indirectly by way of local interneurons.

Initially, researchers such as Wilson and Roeder believed that the 'higher centers' of the insect nervous system acted mostly to start or stop lower pattern generators. Evidence now suggests that whereas fast-acting behaviors of short latency such as being startled (often called 'ballistic' responses) probably do usually rely upon circuits outside of central control, higher centers interact to initiate, maintain, and modulate ongoing rhythmic patterns in ways that produce advantageous behavior in a complex environment. Interestingly, research engineers and the US military establishment currently are showing interest in this central pattern generator/peripheral feedback model as a basis for the design of controllers for autonomous hexapod robots.

2.2.3 Ethological Explanations

Sand wasps, with no contact with members of a previous generation, perform complex nest-burrowing behaviors. Caddisflies reared in isolation spin perfect cases.

Male crickets reared in solitary confinement still sing species-typical aggressive and rivalry songs when confronted with another male.

In many ways, the behavior of insects gives the impression of acting from a prewritten script. Faced with a given situation, even the novice behaves appropriately. Perhaps for this reason, the concept of *instinct*, so emotionally controversial in vertebrate behavioral studies, has been more easily accepted when applied to insect behavior. As numerous studies have shown, even among insects that have never been in contact with conspecifics, all individuals of the species still exhibit many species-specific motor patterns in exactly the same form.

While their counterparts in physiology and neurology were examining insect behavior from a mechanistic viewpoint, the early ethologists (see Chapter 1) were more interested in a functional view of behavior. Where the physiologists and neurologists saw pre-wired endogenous motor programs, the ethologists saw *fixed action patterns* (FAPs). First described and elucidated by the pioneering ethologists Konrad Lorenz and Niko Tinbergen in the 1930s, fixed action patterns generally have several common characteristics. First, once initiated, fixed action patterns require few or no external stimuli or additional sensory cues for their maintenance or completion. For example, even after certain body parts are removed, many insects will proceed to clean the missing appendages as though they were still there; FAPs have been likened to a piece of memorized music played by a pianist without hearing, seeing, or feeling tactile sensation from his hands.

Second, fixed action patterns can be evoked by a variety of stimuli, sometimes from different sensory modes, and they may show variability in orientation. However, once evoked, their basic structure is stereotyped. Third, they are found in all individuals of the species that displays them. Like morphological characters, FAPs are subject to selective pressures and have a genetic basis. Fourth, once they are initiated, fixed action patterns occur in the absence of positive feedback. Nothing additional is necessary to keep them going to completion.

Finally, fixed action patterns generally involve the coordination of several different muscle groups, and can be quite complex. In crickets, 48 separate FAPs are involved with molting; the system, coordinated by a hormonal cascade, is multifaceted and intricate. Why such complexity? The general explanation is that selection has been intense. With behaviors as fundamental as eclosion, there is no room for error; mistakes are deadly.

What triggers the release of a fixed action pattern? Tinbergen, Lorenz, and other ethologists studied dozens of instincts seeking an inclusive theory. They found that first, an organism's internal physiological state has to be such that it is in a condition of readiness to respond, and second, the sensory-neural mechanism involved has to be exposed to very specific forms of stimulation to set a given FAP into motion. They called these cues *releasers* or *sign stimuli*. In some situations, the releaser appeared to be the total stimulus configuration, or *Gestalt*. However, in most cases, only certain simple, specific aspects of the stimulus were needed. For example, the attraction of a male mosquito to conspecific females may be evoked by a particular sound frequency, which we recognize as the females' distinctive hum; artificially produced sounds will produce exactly the same behaviors in the complete absence of females.

A releaser need not in itself have any inherent relevance to survival. Rather, it may be some property of a particular situation that has biological importance and a property that is shared by all other similar situations. For example, skatol and ammonia release feeding behavior in both dung beetles and blowflies; these substances are produced by decaying matter, but neither are by themselves of any nutritive value nor do they owe their existence to dung beetles or blowflies. This type of releaser has been termed a *token stimulus* (see also Chapter 4).

In passing, it should be noted that the naturally occurring releaser for a behavior is not necessarily the optimally effective one. Male *Argynnis* butterflies are more strongly attracted to solid orange than to the orange-black pattern of the female. Such a *supernormal stimulus*—a signal that is even more effective in eliciting a given behavior than the natural signal is—usually represents an evolutionary compromise. For example, in the sexual approach of *Heliconius* butterfly males, use of experimental models has shown that pure red wings upon the female would be the optimal attractant. However, since the coloration also has mimicry functions, natural selection has dictated limiting the red signal to a stripe.

A releaser that is simple can maximize an animal's recognition of biologically important stimuli while minimizing the amount of neural circuitry required, but it also increases the risk of exploitation by other species that use the FAP for their own purposes, a tactic known as *code breaking.* A well known example of this is the way in which many tropical orchid flowers provide the visual and olfactory releasers that trick male wasps into attempted copulation (see Fig. 9.8).

These classic ethological observations interface with modern insect physiology through the useful concept that for each FAP, there exists a sensory-neural release-controlling mechanism called the *innate releasing mechanism* (IRM) that evaluates incoming signals from one or several sense organs and triggers (or fails to trigger) the signals that go out to initiate a reaction. Complex behaviors resolve into a sequence of stereotyped motor patterns; each step depends on the presence of appropriate external stimuli and internal physiological state before the IRM will act. If any link in the chain is broken, the preprogrammed sequence of behaviors (*reaction chain*) does not continue and hence cannot run to completion.

By itself, the IRM is a 'black box' sort of concept, because it considers only input–output without considering the physiological components behind the control of fixed action patterns. At each step, the IRM activation threshold may be highly variable and may respond to both internal and external influences. In common experience, we say an organism shows varied *motivation* to perform the act. A highly motivated individual may be so ready to act that it will perform a fixed action pattern when confronted by a stimulus bearing but slight resemblance to the typical releaser. For example, if the sand wasp *Ammophila* is thwarted too long from pulling a paralyzed caterpillar into her nest, she will begin to retrieve substitutes. Most motivation initially generates quite unspecific behavior, sometimes simply locomotion. The behaviors that follow become increasingly specific until they ultimately culminate. For example, in the chain-like reciprocal signal exchange that occurs between the two sexes during courtship (see Fig. 9.4), the culminating act of copulation can occur only at the end of a hierarchical sequence of several releasers and FAPs. The

prey-catching behavior of the bee wolf (see Chapter 4) is another example of such hierarchial sequences.

What happens when the environment contains sign stimuli for quite different or even contradictory forms of behavior? Or when motivations conflict? Under normal circumstances, behavior outcome depends on the relative strengths and effectiveness of the different motivational factors and sign stimuli involved, and the behavior that is activated partially or wholly suppresses other non-compatible behaviors. In most insects, escape behavior is inhibited during copulation. In aphids, flight and settling behaviors inhibit each other. If honey bees are exposed to releasers for activation and inhibition of their communicative dances simultaneously, trembling dances may take place. When stimuli for completely contradictory behaviors compete for attention, apparently nonfunctional stereotyped actions called *displacement activities* often occur. Most recognized cases have involved cleaning or preening behaviors. Faced with the opposing behavioral motivations to stay at a food source and to leave it, bees will begin grooming, independent of actual grime. Dusting the bee with pollen or flour does not change the frequency of this behavior; rather, it merely directs the preening movements toward the dustier body parts.

Most behaviors are continuously influenced through feedback from both their internal environment and the external one that surrounds them. A classic example of internal feedback is provided by the feeding behavior of the blowfly (see Fig. 4.3). When stimuli that release feeding are continuously present, more or less continuous food uptake ends only when inhibitory stimuli arise; these come from stretch receptors in the gut wall that serve as internal monitors, firing as the gut fills. Action potentials carried to the brain via the recurrent nerve trigger the eventual motor response, namely, retraction of the fly's proboscis from the food. Cutting the recurrent nerve eliminates the negative feedback from the stretch receptors, with the result that the fly literally explodes from overeating!

2.3 Life in a Stimulus-Rich World

A rabbit possesses over 100 olfactory receptor cells. A representative caterpillar has only 48. Both herbivores successfully find and discriminate between potential food plants. The caterpillar's receptor system seems comparatively limited in comparison to the rabbit's array of receptors. How do insects maximize the amount of biologically significant information sent to higher levels in their nervous systems?

At any given moment the environment contains a kaleidoscopic array of stimuli, only a fraction of which contain biologically relevant information. Our rabbit and larva are surrounded by myriad smells arising from the earth, sky, competing plants, other animals—the list could go on and on. In what ways might they most efficiently ignore irrelevant elements and non-appropriate stimuli?

One way to treat different kinds of stimuli differentially is to evolve a receptor system that is designed to screen out some kinds of stimulation while reacting to other kinds. Every animal species has done this to one degree or another for the stimuli that are requisite to their survival and reproduction. The simplest receptor

takes the form of one cell that both receives the environmental stimuli and relays it. All sensory receptors of insects are *primary sense cells*. The same cell produces both a receptor potential and an action potential, and there is no need for a second neuron. Vertebrates have secondary sense cells—cells of non-neural origin that receive a stimulus and link to a neuron to send the message along. For example, touch receptors in the vertebrate skin are modified epidermal cells. More complex sense organs may contain thousands of tiny sensory devices comprised of specialized nerve cells. Uniquely sensitive to particular kinds of environmental energy, they simultaneously screen out all stimuli outside a selected signal range.

2.3.1 Sensory Tuning and Filtering

Honey bees learn landmarks around a nectar feeder, but ignore these same landmarks when presented at a novel location. Studies with mutant *Drosophila* suggest that mushroom bodies (see Fig. 2.1) are important for odor learning, but not for visual or tactile learning. Several species of butterflies land preferentially on leaves of particular shapes, with further discrimination occurring only after landing.

Ever since ethologists first recognized releasers and sign stimuli, it has been clear that certain types of receptors are tuned to very specific aspects of a general stimulus (see Fig. 6.4). One could envision neural information processing as a hierarchical system through which the various stimulus properties are filtered until a particular behavioral response is ultimately released. Ethologists suggested the concept of two *sensory filters*, one peripheral and the other central. Peripheral filters functioned at the level of the sensory receptors. Central filters occurred within the nervous system, sorting out incoming information, selecting relevant stimuli for further action, and eventually producing a particular response. Central filters thus were components of what they called innate releasing mechanisms, or IRMs (see Section 2.2.3).

Chemosensory systems provide many examples. Partially because insects are known to live in a chemical sensory world and partially for the practical reasons of control of agricultural pests, chemoreception has received a great deal of research attention in the context of stimulus filtering. There are an inestimable number of odors in the world. How can the sensory and nervous system of any given insect species decipher them all? The answer, as numerous studies have shown, is that among both taste receptors and olfactory receptors, some are relative specialists. For example, each feathery antenna of a male polyphemus moth has about 150,000 sensory neurons; 60–70% of these are specialized for detecting female-produced sex odors. Other receptors are generalists that respond to several or many kinds of chemicals but varying in their pattern of sensitivity. By summing the responses of the different chemoreceptors, the CNS could obtain characteristic total response profiles, each uniquely representative of a particular chemical compound. An additional dimension of information would be acquired if instead of being silent in the non-stimulated (resting) state, chemoreceptor cells maintained some constant spontaneous baseline level of firing activity. Then a

particular stimulus could be recorded as either an increase or decrease in firing over the spontaneous rate. The resulting code of neural activity from a field of generalist receptors, known as *across-fiber patterning*, allows a large number of different stimuli to create different patterns that can be coded by the central nervous system without requiring large numbers of specific receptors for each molecule.

The olfactory sense of many caterpillars seems to operate in just this fashion, resulting in different response profiles for each receptor (Fig. 2.4). Since the caterpillar receives information from all chemoreceptors simultaneously, discriminations between numerous natural plant odors, even in excess of those likely to be encountered in nature, are easily within the caterpillar's sensory powers using only
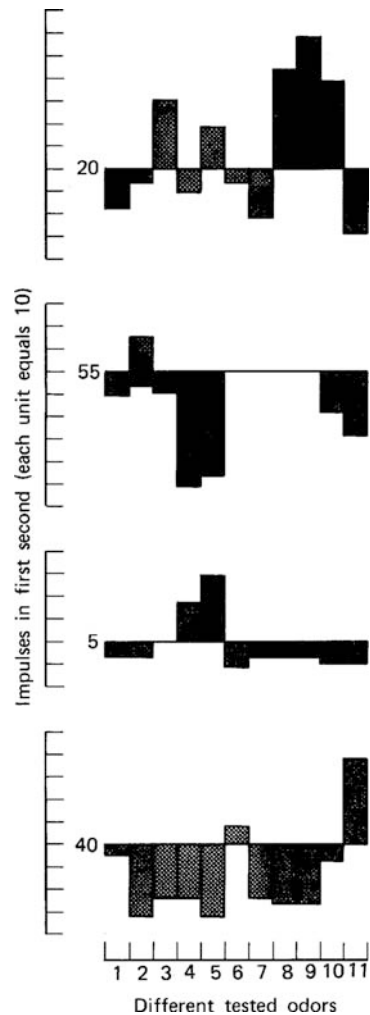

Fig. 2.4 Discriminating between plants. Activity spectra of each of four olfactory receptors of the tobacco hornworm (*Manduca sexta*) in response to 11 different odors show that a lot of information can be encoded with only a few chemoreceptors. Each receptor's sensitivity takes the form of an increase or decrease over its unique spontaneous firing rate

a few receptors. It is likely that the relative sensitivity of different receptors also regularly fluctuates, since it is known, for example, that many insects are rhythmic in their degree of susceptibility to insecticides.

A supreme example of sensory tuning occurs in predatory bats and the moths on which they prey. As a simple experiment, suddenly jingle a bunch of keys near a group of moths flying around a streetlight or window screen. The response of the moths will at first seem chaotic. Some nearly fall to the ground, while the flight of others becomes quickened and more erratic. Some that were fluttering may become motionless, while others, previously motionless, may take flight.

What pattern can there possibly be to all of this? To answer this question, one must appreciate the importance of a principal predator of moths, namely, bats. Fifty years ago, precise and ingenious experimentation by Donald Griffin revealed a bat echolocation system (Fig. 2.5) capable of indicating size, distance, location, and considerable detail about its surroundings, down to items smaller than midges. However, taking the story to the next level took the work of several researchers, including the same Kenneth Roeder that unlocked the basis of the cockroach escape reaction. Case Study 2.2 presents some of the story.
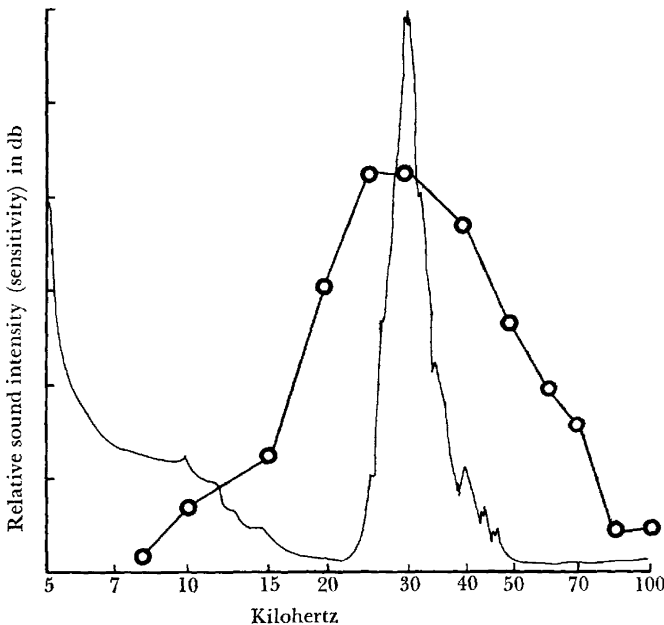
Fig. 2.5 Listening for bats. The relative acoustic sensitivity of a noctuid moth at various frequencies (*open circles*), contrasted with summed intensities of all natural environmental noise recorded in the moth's environment at night (*solid line*). Sounds below 15 kHz were mostly of insect origin. Those between 23 and 50 kHz came from passing bats. It is apparent that moth ears are maximally sensitive to sounds in the latter range and relatively insensitive to other sounds

Case Study 2.2: How Noctuid Moths Hear Bats

Bats and moths have been playing the proverbial cat-and-mouse game for millions of years. Moths are one of the main sources of food for certain families of bats. Yet the game is clearly a balanced one. While all bats in these families probably locate and capture some moths, some moths recognize and evade all bats. How does all this work?

Except in the case of certain 'singing' insects, one does not usually think of insects as possessing ears, but members of certain moth families, especially the Noctuidae, possess true tympanic organs, located in the thorax just below the second pair of wings. From the physiologist's standpoint, a simpler system for experimental analysis would be difficult to find. Each of the moth's tympanic organs consists of only two acoustic sense cells, each with a different threshold, coupled to a thin tympanic membrane. The more sensitive acoustic cell is known as A1, the less sensitive, as A2. Although unable to discriminate between tones of different pitch, the tympanic organs are tuned for the reception of ultrasound.

The first verification that moth tympanic nerves respond to bat chirps was obtained quite by accident at Tufts University, when a hibernating bat was brought out of a refrigerator into the laboratory near a moth tympanic nerve preparation linked to an oscilloscope and microphone. Unexpectedly the bat recovered from the cold enough to shriek, bite the investigator's hand, and escape into the room, where it flew 'silently' around near the ceiling. Throughout this flight, the tympanic nerve proceeded to deliver a rapid series of short spike bursts.

Excited and encouraged at this, Kenneth Roeder and his students eagerly lugged some 300 pounds of electronic gear out onto a grassy hillside where bats were known to feed in the evening and set up a moth for tympanic recording. Very soon, they found themselves able to decode the movements of bats from the nature of the moth's tympanic nerve responses. Rigging up a floodlight so they could actually see the bats (since they were unable to hear them independent of the moth's ears), they quickly learned that the range of the moth ear was much greater than they had expected. Later experiments, in fact, showed it to be in the nature of 100–200 ft when bats were flying toward the moth at an altitude of about 20 ft. In contrast, a bat is unable to track a moth at ranges greater than about 10 ft. The bat, however, has the advantage of much greater speed.

When Roeder turned his attention to the moth's flight behavior, the complexity of the natural situation seemed almost to defy study—'a dizzy dogfight' was his impression, 'extrapolation of a string of acoustic dots in time . . . pitted against unpredictability; power and speed against maneuverability.' It might be compared to combat between a fighter plane and a helicopter, the

bat flying a time intercept course while the moth undertakes selective evasive tactics on the basis of the bat's range and speed of approach.

To reduce this complexity, Roeder replaced the bat with an artificial one: a stationary multidirectional electronic transmitter of ultrasonic pulses, linked to a camera system and perched 16 ft in the air. When exposed to these electronic bat cries, moths showed the same bewildering variety of reactions as they did to real bats. After many hours of observation and over a thousand photographically recorded moth tracks, Roeder determined that the nature of the evasive tactics of the naturally flying moths was related to the distance between the moth and loudspeaker. Moths that flew close to the loudspeaker, encountering ultrasound that pulsed at 10–30 times a second, responded with a variety of maneuvers that usually ended in a dive. Those cruising at greater distances characteristically turned and flew directly away from the sound source.

The adaptive value of this response difference seems obvious. There would be little survival advantage to the moth in attempting to flee a bat at close range or in making erratic turns and twists while the predator was still distant, but every advantage in erratic behavior when the bat was close. Not surprisingly, straight directed fleeing occurred only in response to low-intensity sounds; when the loudspeaker signals were made progressively weaker, the distance at which directed fleeing was released was correspondingly reduced.

Interestingly, moths cruising at about the same height as the loudspeaker turned and flew away in the horizontal plane; those above it were observed to fly directly upward, or redirected their flight by making a sharp turn before flying straight away. How can a moth equipped with only four sense cells orient and steer itself with respect to a sound that comes from various angles? As background for an answer, one must remember that free-flying moths typically flap their wings many times per second. Unlike an airplane, they rarely fly for long in the same direction on an even keel. Because the moth ear is located below its wing, its wing movement has profound effects on the acoustic sensitivity and directionality; on the downstroke, most sound will be screened from reaching the ear, while at full upstroke the ear is accessible to sound from all directions.

To investigate the effects of wing position more fully, Roeder and his associates devised an elaborate apparatus that would measure the acoustic sensitivity of one ear to sound coming from all points in an imaginary sphere surrounding a moth fixed in different flight positions. Obtaining these recordings was a long and arduous task, and Roeder was fully aware that the surgical insult of implanting electrodes, plus the restriction of wing movements that was necessary, might affect the results. However, recordings of the A fiber responses revealed two types of acoustic asymmetry. One was a left–right

asymmetry. The right ear detected sounds most effectively when they originated on the right half of the sphere, and best of all when the sound source was roughly at right angles to the body axis with the wings at the top of their upstroke; at the same time, hearing in the left ear was at its minimum. Alternating with this was a dorsal–ventral asymmetry. The flapping of the wings had the effect of damping the sound when the wings were in the down position. Thus, the left–right differences in sound intensity would alternate with the temporary disappearance and reoccurrence of sound occurring some 10–40 times per second in synchrony with the rate of wing flapping.

How do these asymmetries relate to a moth's ability to escape a hungry bat? A left–right difference in A-fiber discharge when the wings are up probably provides the moth with a rough horizontal bearing on the position of a bat with respect to its own line of flight. The absence of a left–right differential discharge and the presence of similar levels of on and off from both ears might inform the moth that the bat was above it. If neither variation occurred at the regular wing beat frequency, it would mean that the bat was below or behind the moth (Fig. 2.6).

It would seem that a single sense cell in each ear could transmit enough information to inform the moth of a cruising bat's bearings. Why does each ear have two acoustic sense cells? Roeder suggested that the answer might lie in their differential sensitivities. His comparative measurements showed that A1 responded first, firing over a range of low to moderate intensities. Cell A2 began to fire only at moderate intensities and fired even faster at high sound intensity, a range within which A1 was saturated and therefore incapable of further increase. Thus, by operating in piggyback fashion, A1 and A2 might provide a combined signal from which intensity differences could be discriminated over a range wider than either alone could accomplish. In effect, their combined signal would inform the moth how far away the bat was, which ultimately would decide the form of the moth's evasive behavior. He suggested testing this theory by observing the anti-bat behavior of another group of moths (Notodontidae), because their ears each contain only the A1 cell.

A decade after Roeder's research raised the puzzle about the A2 receptors, a report appeared that European notodontids do, in fact, show a two-part response to approaching bats. However, years passed before the A2 question could begin to be addressed directly rather than inferentially. The problem lay in the difficulty of neurally recording moth auditory responses not just to one set of constant acoustic parameters, but to the complex sounds of real attacking bats. As a bat approaches its prey, its echolocation calls shift in duration, intensity, rate and frequency. The ideal situation would be to record the moth's responses during an actual bat attack, but the recording equipment itself made it impossible to set up this scenario.
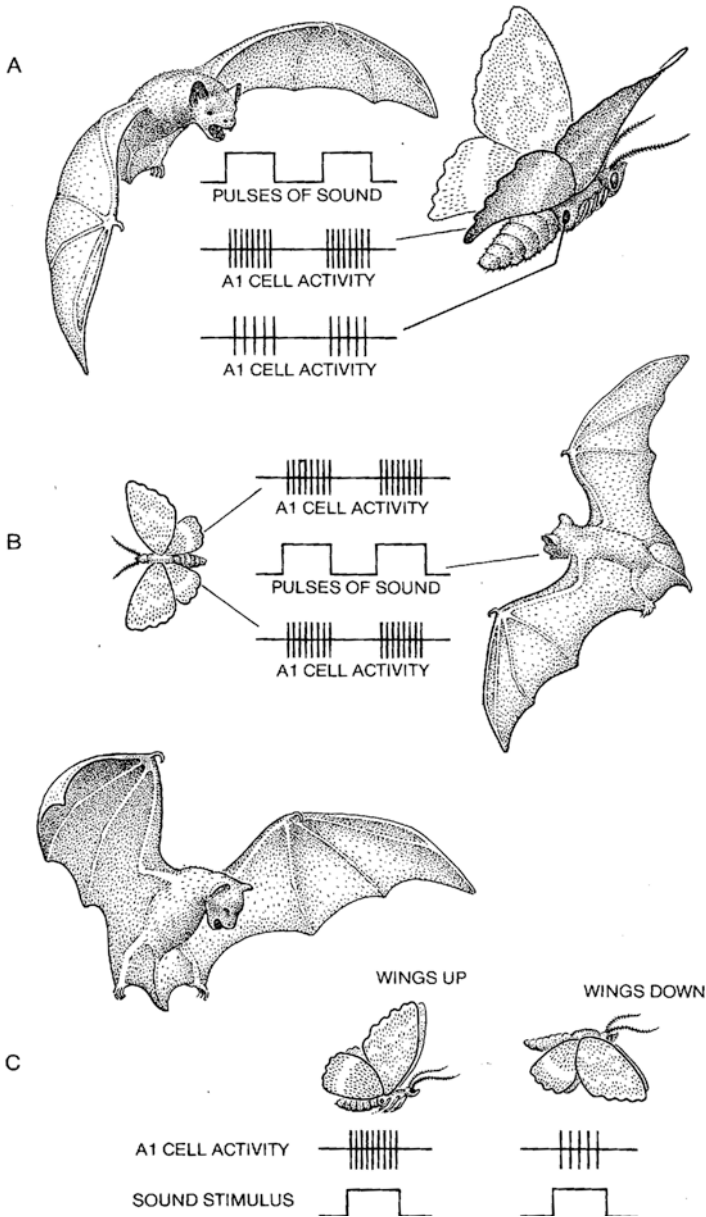
Fig. 2.6 Assessing bat direction. Roeder showed that the activity in the A1 receptors of a moth's ears differs upon detecting bat cries from different points in space. (**A**) When the bat is to one side of the moth, the receptor on the closer side fires more rapidly than the shielded receptor. (**B**) When the bat is directly behind the moth, both A1 fibers fire at the same time and rate. (**C**) When the bat is above the moth, activity in the A1 receptors pulses in synchrony with its wing beat. The role of the A2 receptors, which are missing in some moths, is less clear

In 1994, James Fullard and colleagues found a way around the problem by training a bat in the laboratory to attack a microphone that it expected would be an edible target. These recordings (and a noise-reduced, computer-generated digital replicate) were then broadcast to five species of noctuid-like moths to observe their ears' responses. The results appear to confirm that the A1 cell encodes the approach calls of an attacking bat up to about 100–200 ms before the bat would capture the moth. Then, at this last moment of the moth's life, the A1 firing drops off to a level similar to that detecting a faraway bat. Surprisingly, the A2 cell responses were fundamentally the same, but Fullard found variations among the moth species he tested. In some, the A2 cell response was vigorous; in others it dropped off early, was sporadic, or did not appear at all. Fullard and colleagues have suggested that this may mean that the A2 cell is vestigial, and no longer used in the flight responses of moths.

A sound also has several other features that could convey information to the moth's nervous system, including its intensity, pulse duration, the interval between pulses, and so on. Furthermore, the receptor is but one point along the chain of neurons leading to the brain where selective decoding of stimuli might occur. Thus, in the case of the ultrasonic bat cry, moth ear receptor cells might selectively respond to a particular range of frequencies at one point in the filtering, but after the receptor cells transmit an impulse, subsequent interneurons along the ventral nerve cord would no longer respond to frequency; rather, other sound properties such as pulse intensity, pulse duration, or interval between successive pulses would now be monitored. For example, Kenneth Roeder identified a 'pulse marker' interneuron in the moth that responds to three or four sensory impulses separated by short intervals by firing just once, but the interneuron made no distinction as to duration of a pulse; to it, 0.5 and 500 μs were the same.

The dramatic conflict between moths and bats has caught the attention and imagination of scientists in many disciplines. A number of other insects quite distant from moths have been found to respond evasively to bat ultrasonic cries, from mantises that loop and plummet erratically downward to lacewings that take a power dive. The moth-bat story also has come to include some interesting side plots. One is the production of anti-bat sounds—some arctiid and ctenuchid moths produce clicking sounds at frequencies close to those used by bats, and bats respond by veering away. The click may disorient the bat, jam its echolocation system, and/or act as a warning, signaling the bat that the moth is distasteful (see Chapter 8 and Plate 28).

Another side plot involves mites, common ectoparasitoids that often attack insect tracheal systems. The mite *Dicrocheles phalaenodectes* infects only one ear of its noctuid moth host, destroying the typanum, but leaves the other ear intact; a related species infests both ears, but leaves the tympanum intact. Presumably, both strategies leave the moth host with some chance of still avoiding bats and thus living on to support its parasites.

Since many moths have evolved ways to hear bats, why don't bats evolve a countermeasure such as calls that are too soft for a moth to detect or outside the frequency range of moth hearing? Mostly likely such drastic changes would severely restrict the range and acuity of the bat's sonar system and would only result in related

adaptive changes in the moths. Such an evolutionary arms race may in fact be under-
way now. Studies in Canada indicate that where bat species-diversity is high with a
wide range of sonar frequencies, moth sensitivity covers this frequency range, but in
areas where the range of bat species is small and the sonar range is more restricted,
moths have a similarly reduced frequency sensitivity range. Similar relationships
have been shown in other areas, including between moths of Panama and those of
Hawaii.

2.3.2 Memory and Learning

Dragonfly larvae of the genus *Anax* raised in aquaria soon come to associate the
sight of their caretaker with food; when he or she appears, they may even snap in
anticipation before food actually appears. A mantis, although it originally would
attack, will learn not to strike at an object after it has received an electric shock
or bad taste from this object. Upon emerging from their pupal cases, new adults of
many ant species notice and retain the scent of their colony.

In the past, it was repeatedly suggested that insects show little or no learning,
for 'obvious' reasons such as their small brain and short life span. However, even
little *Drosophila* larvae apparently can easily learn to avoid odors linked to an elec-
tric shock, and parasitoid wasps rapidly learn cues associated with host availability.
In fact, current knowledge indicates that many insects learn extensively during
all major life activities, and furthermore that individuals within a species show
genetically based variation in learning abilities.

Learning may be defined as any relatively permanent, usually adaptive change
in behavior that occurs as a result of experience or practice. This change usually
progresses gradually with continued experience to some asymptote. It often can be
modified by novel experiences, and the effects of experience eventually wane if not
reinforced. *Memory*—the capacity to store information—is a prerequisite, resulting
in a linkage between stimulus and response that would not have occurred without
the previous experience with that stimulus. In physiological terms, one could define
learning and memory as the acquisition and retention of neuronal representations of
new information, respectively.

One of the stranger things about studying learning is that while learning undoubt-
edly involves neuronal modifications, it still can be assessed only indirectly through
its potential effect on behavior; there is no way to directly quantify it. To infer its
presence or absence takes a series of very unusually well controlled experiments
to rule out both observer bias and the presence of feasible alternatives. Likewise,
claims for a lack of learning ability in a certain species could be due to low moti-
vation or be an artifact of the experimental set-up being used, rather than a genuine
inability to learn. Thus, one must be cautious, both in conducting experiments and
in interpreting the published literature.

Not surprisingly, something as widespread and far-reaching as learning eludes
any easy, satisfying categorization, but it can be useful to think of it as coming in
two forms, non-associative and associative. Non-associative learning includes both

habituation and sensitization. *Habituation,* probably the commonest form of insect learning is a gradual waning of responsiveness to a stimulus that occurs as an insect, through experience, finds it to be harmless or at least unavoidable. For example, a variety of insects such as ants and mantises can be 'tamed'; if handled frequently enough, they will come to respond calmly to being picked up and moved about. *Sensitization*, its opposite, occurs when repeated presentation of a stimulus enhances a response to that stimulus and often to related ones.

Associative learning occurs when an organism comes to connect one stimulus with another (or with a motor pattern) such that its response to the first stimulus changes as a result. Associative learning is typically evaluated in one of two ways: by classical (Pavlovian) conditioning or by instrumental conditioning (roughly equivalent to the term, operant conditioning). The former can be thought of as 'learning to recognize' and the latter as 'learning to do'.

In *classical conditioning*, a previously meaningless stimulus (the 'conditioned stimulus' or CS) is paired in time and space with an 'unconditioned' stimulus that already elicits a response, often to some form of reinforcement such as reward or punishment. Afterward, when the CS elicits the same response that the US formerly did, one can say that the two have become 'associated.' In insects, as in most other animals, associative learning is undoubtedly an important part of individual accommodation to a changing environment, a method by which an IRM can be fitted more exactly to the environmental situation. Associative learning studies are now receiving new impetus with advances both in the genetics of learning and memory and in physiological studies of identified neurons and neuronal circuits. Honey bees, *Drosophila* flies, and cockroaches (particularly *Periplaneta americana*) hold particular places of honor in such studies. Recently, associative learning has taken a decidedly practical turn with the development of 'bomb-sniffing bugs' (Fig. 2.7).

Classical conditioning has been widely exploited in experiments designed to delimit the sensory capacities of insect; most classical conditioning studies in insects have used the proboscis extension reflex as the response. A goal of behavioral neurologists has always been to trace specific behaviors all the way back through the neuronal level to their intracellular and genetic roots, and learning has been no exception. However, although *Drosophila* have provided valuable insights into the genetics of learning and memory, they have been extremely difficult to use for physiological studies of identified neurons and neuronal circuits. Cockroaches, on the other hand, have been useful for cellular-level studies of identified neurons and circuits, but because the behavior models in use were designed for free-moving animals, they have not been suitable for studies at the cellular level. However, a 2004 study with cockroaches showed a simple, imaginative approach to bridge this gap.

To study conditioned feeding responses, David Lent and Hyung-Wook Kwon kept adult male cockroaches hungry for 24 hours, then placed them in small plastic tubes that held their heads in place but allowed their antennae to move freely. Each tube holding a restrained cockroach was placed horizontally in the middle of an arena with a red light bulb overhead for warmth and cockroach-invisible illumination. On the arena wall, a green light-emitting diode (LED) provided stationary light flashes. A single red LED was used as a control test to determine whether
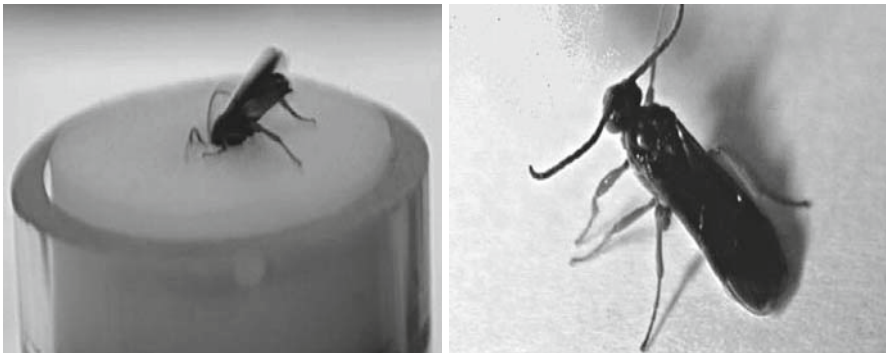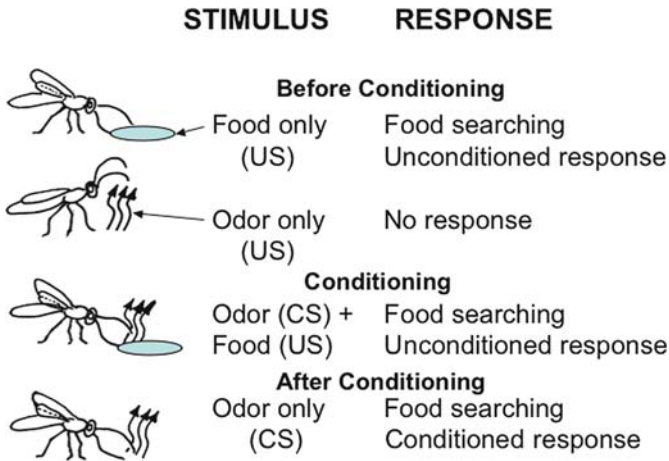
STIMULUS   RESPONSE

Before Conditioning

Food only   Food searching
(US)   Unconditioned response

Odor only   No response
(US)

Conditioning

Odor (CS) +   Food searching
Food (US)   Unconditioned response

After Conditioning

Odor only   Food searching
(CS)   Conditioned response

Fig. 2.7 Bloodhound wasps. Small parasitic wasps such as *Microplitus croceipes* (*above*, inspecting host frass) track their prey from the larva's scent and/or odors in its frass, a mixture of feces and undigested plant materials. This is a learned response; odors differ when the caterpillar feeds on different host plants. As a result, by classical conditioning techniques, the wasps also can be taught to respond to tiny amounts of novel substances that are not biologically relevant. This suggests practical applications such as the detection of explosives, narcotics, or contraband. After even one conditioning trial, these wasps learn to associate a novel odor with successful host-finding, feeding, and oviposition. When exposed to the odor again, they actively antennae and energetically search the vicinity (*bottom left*, a wasp responding to odor wafting through a hole). When the odor is not present or is different, they remain relatively passive or recoil (*bottom, right*)

sounds from the light switches were being detected. To evaluate their unconditioned arousal responses, the cockroaches were treated to an odor cue (a puff of air passed over peanut butter), a light cue (a flash from the green LED), a mechanosensory cue (a high-current air puff), or auditory cues at a frequency of 1.8 kHz; during each trial, antennal movements were videorecorded so that antennal angles could later be measured from the digitized images. Then cockroaches were trained to project their right antenna toward the green light as the peanut butter air puff was presented.

The cockroaches were surprisingly bright (Fig. 2.8), and quickly learned to associate the visual cue through classical conditioning with no other reward than an attractive odor, which could be explained as intrinsically rewarding in itself. After just five training trials, 90% showed significant learning, and it persisted unexpectedly long. Thirty minutes after training, 60% still showed antennal projection responses to the CS, and almost half responded even after 72 hours. Optimal learning performance was achieved when the odor and light cue were simultaneous or nearly so, which one might expect because in nature, foraging animals detect salient cues just before or concurrent with the reward.
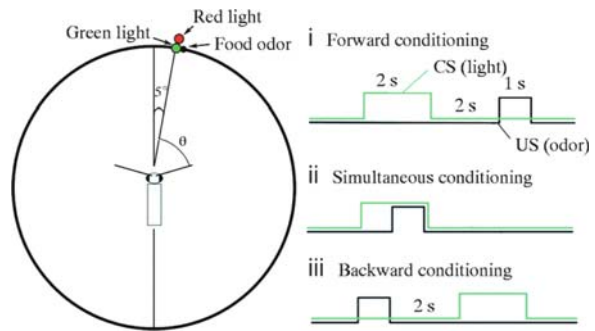
Fig. 2.8 Remembering associations. *Periplaneta americana* cockroaches held in the center of an arena learned to associate a green LED light with the smell of peanut butter by one of three classical conditioning procedures (*i, ii, iii*). Then, after five training trials, at intervals their learning performances were assessed by percentage of antennal projection responses. The roaches showed no significant decline in learning for up to 30 minutes afterward, and retained a considerable degree of memory for up to 72 hours afterward
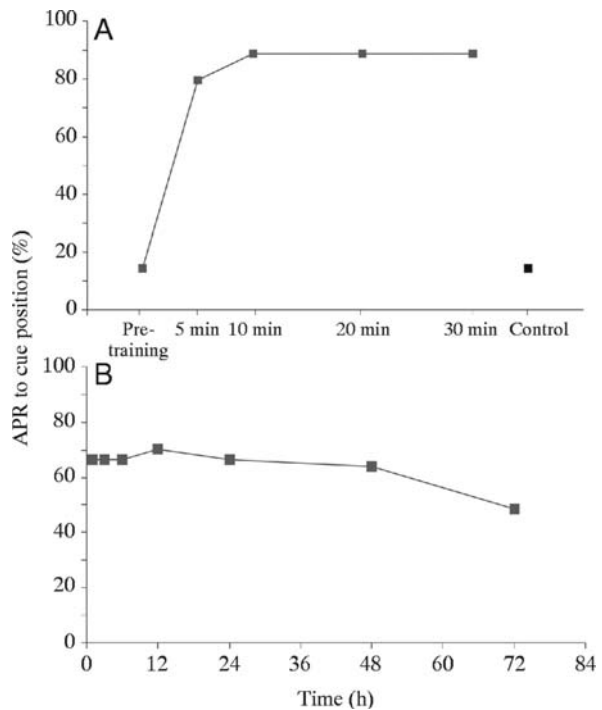
In contrast to classical conditioning, *instrumental conditioning* involves a reinforcing stimulus that is contingent upon the insect's own motor patterns. An example would be the way that a bee or butterfly might learn, through trial and error, how to extract nectar from a newly encountered type of flower. The most widely known laboratory-based example requires a tethered grasshopper or cricket to move its leg in response to an electric shock, heat, or access to food. The fact that a headless cockroach will still learn such a task demonstrates that this type of conditioning can occur at the level of ganglia.

Scientists who specialize on insect learning recognize various other basic categories as well. Food aversion learning is particularly interesting because an aversion can form even when many hours pass between ingestion of a food and the resulting indigestion.

Spatial learning is an area of particular interest to behaviorists. Bees and wasps, for example, learn the location of their nests through landmarks recognized and remembered from a previous orientation flight (Fig. 2.9). Honey bees appear to possess a topographically organized landscape memory that allows them to navigate along a previously untraveled route.

The area over which an animal normally wanders in search of food, shelter, and/or mates is called its *home range*; within it, others of its own species may be tolerated and the space thus shared. Among insects, many species that are long-lived as adults and/or social have a well-defined home range, such as the foraging area of an ant or termite colony. Tropical *Heliconius* butterflies have learned home ranges within which they memorize the location of their food flowers and larval host plants; adults tend to return nightly to a particular communal roosting place for up to six months. Similarly, tropical euglossine bees fly along regular trap-lines to which they return day after day to collect pollen and nectar from newly opening flowers (Fig. 2.10).

It is sometimes said that *observational learning*, in which a subject imitates the motor actions of a demonstrator, is characteristic only of vertebrates. However, this may be splitting hairs, because social interactions clearly influence what insects learn. Young foragers learn from experienced ones how to locate profitable flowers through the well-known honey bee waggle dance (see Figs. 8.13, 8.14). Experienced *Temnothorax* ants teach inexperienced nestmates to locate food sources by a technique known as tandem running, adjusting their speed to that of their pupil. After watching a model land on a flower, inexperienced observer bumblebees are more likely to seek out that flower type than an unvisited alternative. Such behaviors are usually called *social learning*, defined as learning from other individuals. Social learning is distinctive because it allows new behaviors to spread quickly within and between generations. It is faster than individual learning, and saves the fitness costs of errors associated with inexperience.

Social learning has been more thoroughly studied in mammals, birds, and fish than in insects, and until fairly recently, insect social learners were thought to be restricted to social Hymenoptera. However, this view is changing with greater research effort in this area. In fact, social learners may not even be restricted to colonial species. For example, a 2005 study of wood crickets, *Nemobius sylvestris,*
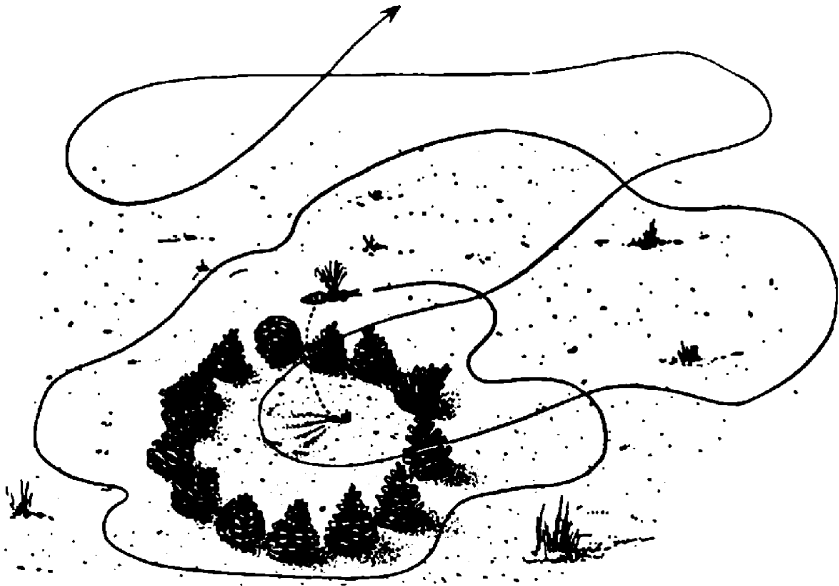
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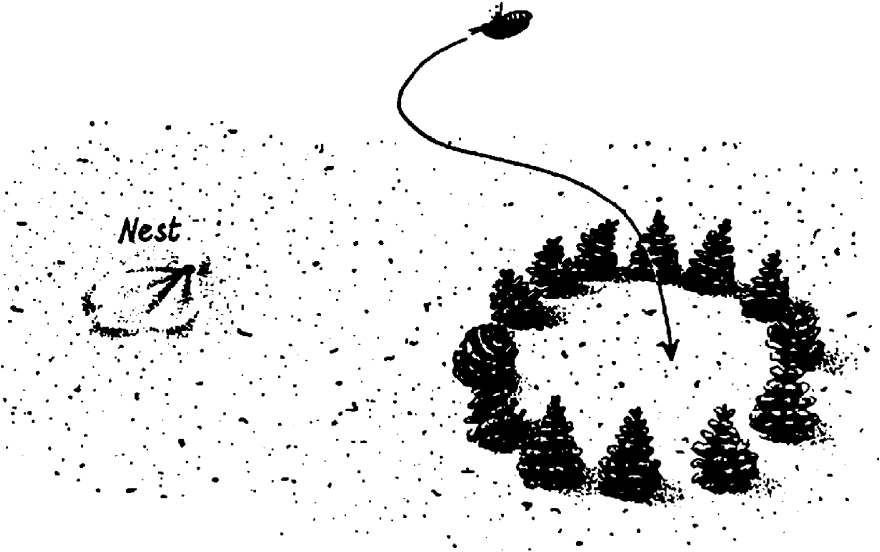
b

Fig. 2.9 Learning landmarks. After the nest entrance of *Philanthus triangulum* is ringed with fir cones, the wasp learns to associate her nest with this distinctive landmark through an orientation flight (**a**). While the bee wolf is away hunting, the ring of cones is displaced. Upon return the prey-laden female flies to the center of the fir cones (**b**)
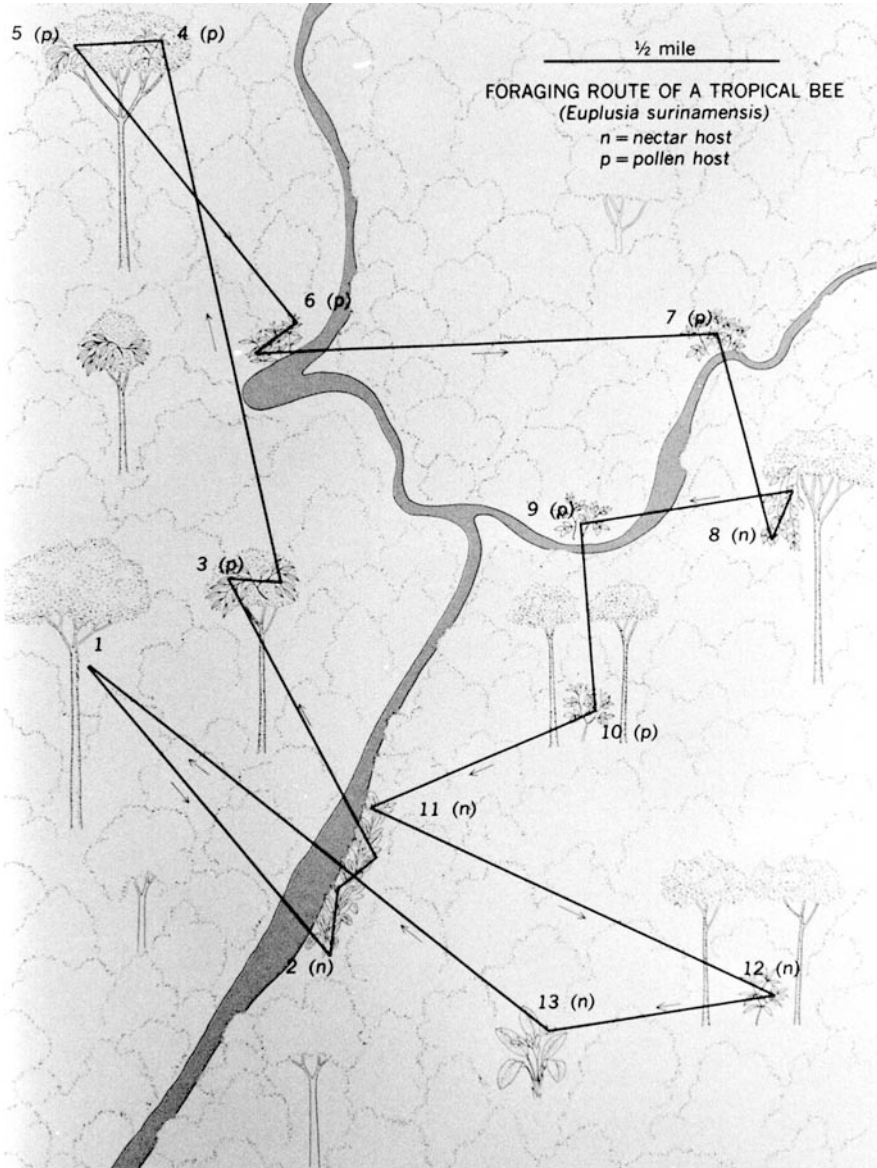
Fig. 2.10 Memorizing a trapline. The tropical bee *Euplusia surinamensis* constructs her nest (1) 130 ft above the ground under loose tree bark. Each day she flies this foraging route through the Costa Rican forest, visiting ground plants (2, 11, 13), shrubs (6, 7, 9), understory trees (10, 12), vines (3, 5, 8), and an epiphytic shrub (4) to collect nectar (*n*) and pollen (*p*) from newly open flowers. It is a trapline worth remembering because although each plant produces only one to a few new flowers each day, flowering may continue for up to six months. Marked females returned to the plants daily even when flowers were artificially removed prior to their visit, showing that they actually memorize the trapline

in France showed that these crickets adapt their predator-avoidance behavior after having observed the behavior of knowledgeable others, and they maintain these behavioral changes in a lasting way after the demonstrators are gone. Moreover, evidence suggests that *Nemobius* are actually more likely to acquire social information about the presence of predatory wolf spiders through encounters with other crickets than to acquire personal information through direct encounters with the spiders.

Many vertebrates have been shown to learn various tasks and concepts most easily during a critical period in development; if learning does not occur during that window of opportunity, it is difficult to nearly impossible. Does a similar phenomenon occur with insects? A few studies suggest it is possible. For example, *Cotesia congregata* are braconid wasps that hunt for hosts and mates among plant foliage. If a young adult female wasp is exposed to wild cherry trees, an inherently unattractive plant, during the first four hours after she ecloses, she will continue to search among wild cherry trees rather than cabbage, a normally attractive plant. Such a general increase in responsiveness is referred to as 'priming.'

Certainly, for many or perhaps most insects, searching behavior relies upon specific host-derived stimuli that the adults recognize innately, often during a critical phase such as the time around adult emergence. However, sometimes cues appear to be learned by the immature insect, a process called 'preimaginal conditioning' and these are subsequently manifested in their responses as adults. Many cases of preimaginal conditioning have been documented. Early in the twentieth century, researchers observed that phytophagous beetles selected oviposition sites on plant species similar to the ones on which they had been reared. This phenomenon, sometimes called the *Hopkins' host-selection principle*, has been used to explain host preference or selection in various groups. For example, in one of the earliest detailed studies on parasitoid learning, when the ichneumonid parasitoid *Venturia (Nemeritis) canescens* was reared on wax moths, a species they do not attack under natural conditions, as adults they preferred the odor of wax moth larvae over that of their natural meal moth host. Likewise in a much later study, when tobacco hornworm caterpillars were trained to avoid the odor of ethyl acetate by pairing it with a mild electric shock, they retained this response as adult moths.

Does actual learning persist through complete metamorphosis? This is still a debated topic, and although some research suggests it might be so, the idea has its skeptics. Metamorphosis is an extreme event; not too long ago, it was generally thought that a larva's body essentially turned back into a sort of soup during the pupal stage, only to be completely restructured into an adult insect. Yet despite the drastic nature of the metamorphosis process, neurophysiological evidence from *Drosophila* and various Lepidoptera that indicates that parts of the brain involved in learning do remain intact. An interesting one involves a parasitoid that attacks the codling moth, the insect responsible for the 'worm' that is (hopefully not) in your apple (Fig. 2.11).

The study of *Hyssopus pallidus* outlined in Case Study 2.3 was one of the first to study preimaginal learning with such careful attention to detail and control of variables. For example, a major criticism applied to other preimaginal learning studies
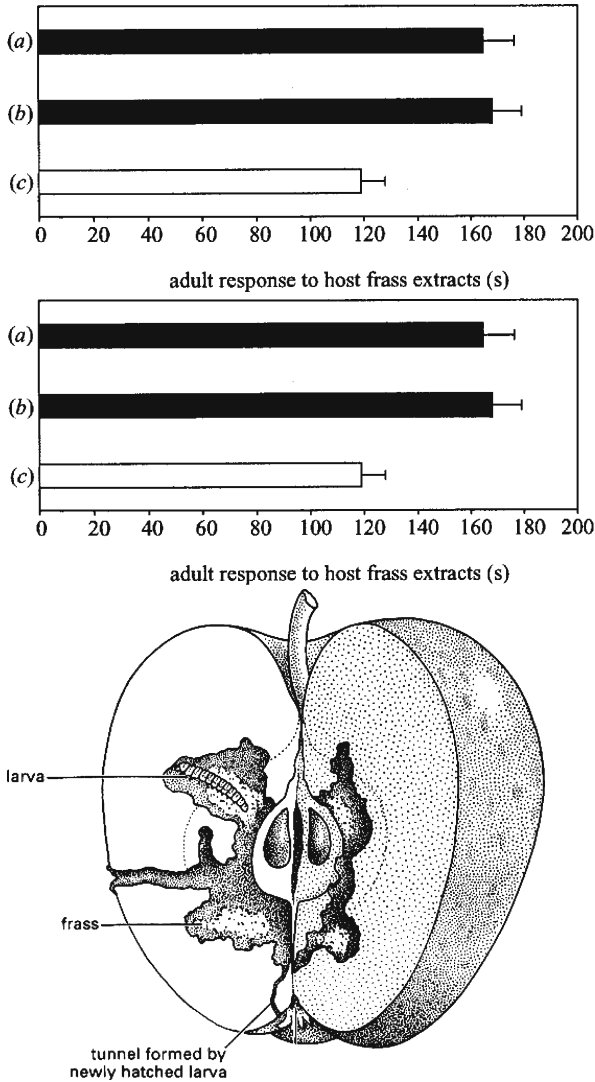
Fig. 2.11 Learning as a youngster. The parasitoid wasp, *Hyssopus pallidus*, finds the concealed caterpillar of its codling moth (*Cydia pomenella*) host by chemical cues in the host's frass. (*above*) Exposure to either apple fruit extract (*a*) or apple fruit (*b*) during the parasitoid's larval stage resulted in significantly higher response to moth larval frass as an adult female compared to controls (*c*). (*center*) Addition of apple fruit extract either to the host moth larval diet (*a*) or to the diet of the developing parasitoid (*b*) also resulted in significantly higher adult female responses to moth larval frass compared to controls (*c*) lacking apple fruit extracts. These findings suggest the adult parasitoid 'remembers' its larval experiences

was the difficulty of excluding a 'chemical legacy' of contamination from the larval to the adult environment, especially when learned cues are directly present in the insect food or in the host cocoon. For this reason, these researchers did not offer their chemical cue as a liquid or solid substrate, but as a volatile substance that was removed long before pupation and adult emergence. To counter the possibility that test organisms might have become contaminated by the relevant chemical cues as they eclosed into adulthood, in each case the researchers placed their treated filter papers 4 cm away from the host caterpillar. Because the caterpillar is paralyzed and cannot move during parasitoid development, and the parasitoids do not leave the host, the wasps were never in direct contact with the cue-laden filter papers during the exposure period.

Case Study 2.3: Learning in the Parasitoid Wasp, *Hyssopus*

A parasitoid's host-searching ability depends on responses to chemical cues, and these responses have both genetic and learned components. Is there a critical phase at which a parasitoid is more likely to learn? And does such learning carry through from one life stage to another?

To apple growers, the larvae of the codling moth *Cydia pomonella* are major pests that burrow into fruits, rendering them unfit to sell. However, the little parasitic wasp *Hyssopus pallidus* is a promising candidate for biological control, because females of this parasitoid have the ability to enter infested fruit, irreversibly paralyze the feeding caterpillar within its burrow, and deposit eggs on its body. The hatched parasitoid larvae feed from the outside of the host caterpillar, develop gregariously in large numbers, then disperse as new adults throughout the orchard to find new hosts in other apples.

To find these hosts, *H. pallidus* relies on its response to traces of frass (feces and silk) left behind on the surface and in the channels of the infested fruit. Thus, it was with some dismay that Michela Gandolfi, Letizia Mattiaci, and Silvia Dorne found strong deterioration of the response to frass in their laboratory culture of *H. pallidus* after 30 generations on codling moth caterpillars that were being fed an artificial diet based on wheat germ instead of apples.

Was this behavioral deterioration the result of an inadvertent selection process? Apparently not. When the Swiss researchers reared the parasitoids in the presence of fruit cues, their original level of response was completely restored within a single generation. This suggested that perhaps the parasitoids' responses had two components. Perhaps the host-derived chemical components of the frass were recognized innately, but learning was required before the wasps could recognize the fruit-derived components.

Did the parasitoids need to learn the fruit-related chemicals from fruit-fed caterpillars and their feces? Or was exposure to fruit itself sufficient? Gandolfi, Mattiaci, and Dorne infested apples with first instar codling moth

caterpillars, waited until they reached the fifth instar, then cut apart worm-laden apples to extract them. Rearing the larvae individually in plastic boxes, the researchers fed some with the wheat-germ based diet alone. These would serve as their control group. For a second group of larvae, the artificial diet was treated with a solvent extract of grated apple skin, pulp, and seeds; after the solvent evaporated, the mixture simulated the apple components of frass. In each of a third set of boxes, a piece of apple was suspended; in each of a fourth, a piece of filter paper treated with their apple extract. Then they introduced a mated female parasitoid in with each host so that it could lay eggs.

When the new generation of parasitoids emerged, they were transferred to new cages without ever being exposed to apple cues. As a bioassay, when the mated parasitoid females were four days old, the researchers prepared filter paper discs by treating them with apple extract or host frass extract, transferred these second-generation wasps into individual dishes, and placed the open side of the dishes on top of the filter paper. For ten minutes, they watched each wasp and recorded the amount of time it spent in 'searching', which they defined as intensive antennal examination of the filter paper.

Comparing the groups, it was clear that rearing *Hyssopus* larvae on hosts that were fed either apples or an artificial diet treated with apple extract had a similar effect—the parasitoids showed a significantly greater adult response to host frass than parasitoids reared without apple cues (see Fig. 2.11). Did a high response to host frass require exposure to both the taste and smell of apple? To find out, the researchers compared the responses of parasitoids reared on caterpillars fed with apple-supplemented diet to those reared on caterpillars exposed only to the odor of apple fruit extract. Both of these treatments significantly enhanced female responsiveness to host frass cues, indicating that olfaction alone was as effective as taste and smell together. This was surprising because studies with other insects had suggested taste to be more important than smell in the chemical learning process.

Was there a sensitive window in the parasitoid's life history for learning the relevant stimuli? Gandolfi, Mattiaci, and Dorne reared another set of wasps on caterpillars fed on plain artificial diet, but this time they exposed the wasps to apple fruit extracts at different developmental stages. For comparison, they used both parasitoids exposed to apple extract during their entire development and parasitoids that were never exposed at all. As an extra precaution, a parallel series of experiments was conducted in which female wasps were introduced into untreated vials and into vials from which extract-treated filter papers had just been removed after having been in the vial for 12 hours. Then the searching activity of the wasps in these two groups was bioassayed. The lack of any statistically significant difference between them satisfied the researchers that no contamination had been left on the inner surfaces of the vials after the treated filter papers were removed.

As they emerged, the new adults were either immediately transferred to new cages or allowed to spend one additional day in their rearing situation before transfer. Then, when they were four days old, the mated females were tested for their 'searching' response to extracts prepared from natural frass produced by codling moth caterpillars feeding on apples. When the results were analyzed, it was clear that exposing *Hyssopus* to apple extract at different developmental stages affected the response of adults to host frass cues in different ways (see Fig. 2.12). As before, parasitoids never exposed to the apple extract at all during development showed no significant response to apple extract as adults, but those exposed to extract during development responded strongly to it as adults. The surprise came when the exposure times were compared. Exposure at the beginning of development was the most effective—as effective, in fact, as exposing the parasitoids to extract throughout their entire development. However, exposing them either at the pupal
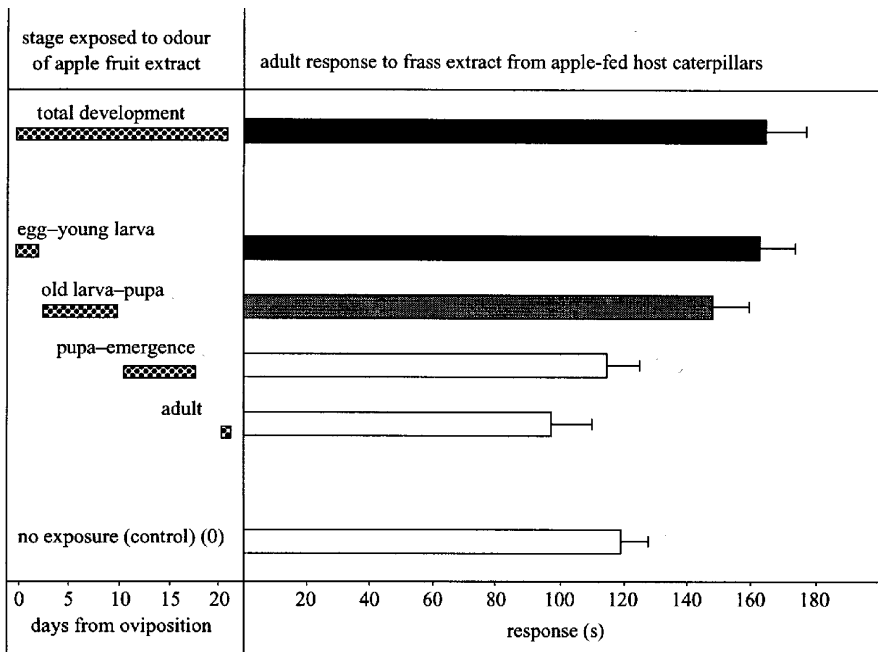
Fig. 2.12 Remembering through metamorphosis. Codling moth parasitoids, *Hyssopus pallidus,* exposed to odors from apple fruit extract at different developmental stages differ in their response as adult females to frass extracts of their apple-fed moth larvae hosts. Those exposed at their earliest stages of development (egg to late larva-pupa) gave significantly stronger responses as adult females to larval frass than those exposed only after pupation or as adults; the latter responding no differently than controls with no exposure to apple fruit extracts at any time in their lives

stage, during emergence, or at the adult stage one day before the bioassay was ineffective, even though in these cases the interval between removal of the bioactive cues and the bioassay was much shorter.

Some other studies had found cases in which an insect showed preimaginal learning of some cues and not others; the presumption was that learning had to be biologically relevant if it was to occur. Gandolfi, Mattiacci, and Dorne wondered if this would be true for *Hyssopus.* Was preimaginal learning confined to fruit cues, or was it a more general phenomenon? They repeated their studies, this time exposing parasitoids from egg to larval stages to menthol, a compound not detectable in apple extracts or codling moth caterpillars. As a control, they used only the solvent. Parasitoids that were never exposed to menthol during development were repelled by it as adults, and actually responded more to the control than to the menthol. However, when parasitoids had been exposed to its odor from egg to larval stages, as adults they showed a significantly higher tolerance to menthol than did parasitoids without menthol exposure, and responded to it in essentially the same way they responded to the filter papers with the solvent control.

Thus, it appears that the parasitic wasp *Hyssopus pallidus* learns to locate its concealed host by zeroing in on its frass, and this recognition is a two-stage process. A high response requires both host-derived chemicals in the frass that are recognized innately, and apple-derived chemicals that must be learned through exposure early in the parasitoid's life cycle. The preimaginal learning is a general phenomenon in which the wasps are capable of learning a variety of cues. While chemical cues are indispensable, for this wasp species at least, physical stimuli such as visual or tactile cues seem to be of only minor importance. The parasitoids did not need to contact the fruit directly; learning occurred just as well when they were reared on hosts fed an apple-supplemented artificial diet. In contrast to general expectations, the sensitive period for learning these olfactory cues was not during eclosion or early adulthood, but in the earliest stages when the wasp was developing from egg to young larva.

The codling moth parasitoids exposed to odors from apple fruit extract at different developmental stages seem to show that some sort of learning persists through metamorphosis. Or is this not 'really' learning? The phenomenon is undoubtedly real; the definitions used to describe the effects of experience on insect responses may be the cause of confusion. One could consider it to be a case of priming, in which certain experiences make the parasitoids more responsive to foraging cues. Alternatively, one might call it preference (and avoidance) learning, a case of associative learning where the increase in responsiveness is specific for the cues that the insects encounter during the experience. Then again, one might say it is at least analogous to sensitization to chemical stimuli, a mechanism well known among

adult insects in which the response to a stimulus gradually increases with repeated exposure to that stimulus.

Such studies offer tantalizing glimpses into the complexity of neuroethology, where questions outnumber answers. Studies that couple behavioral research with detailed neurophysiology and genetics are still embarrassingly meager, and have almost entirely concentrated upon a mere handful of insects from four of the 28 or so insect orders. These animals—mostly cockroaches, grain beetles, fruit flies, blowflies, and a few of the many ants, wasps, and bees—have been chosen not because of their representative nature but primarily for convenience, availability, ease of rearing, and sometimes, perceived importance to society.

2.3.3 Insect Intelligence

Honey bee workers can learn signals quickly and with apparent ease in every known sensory modality. Multiple tasks pose few problems; they can link up to five different visual signals with correct turns in a maze. Nor do sequential tasks pose great difficulty, for bees may learn to visit a single location up to six different feeding times during the day or four different places at four different times. Some ants, such as *Formica pallidifulva* workers, can learn a six-point maze at a rate only two to three times slower than that of a relatively advanced vertebrate, the laboratory rat. Female *Ammophila* wasps that have made an inspection visit to a temporarily closed nest burrow can still remember and properly perform the action determined in that single visit, even 15 hours later.

Faced with a myriad of such examples, it is easy to succumb to a sense of wonder and conclude that some insects are comparable to vertebrates in intelligence. (It is small wonder that many fiction writers have done so.) However, these are but fragments of information from the insect's behavioral repertoire, and intelligence in this sense of the word is a meaningless measure. In fact, in this sense animals do not even possess varying degrees of intelligence; rather, they possess specific abilities to learn selected things. For any organism there are certain types of tasks that can be mastered and others that cannot. This is no less true with insects. Honey bees, which can learn quickly to orient with respect to attractive odors, cannot do so at all with respect to repellents. Thus, one is often struck by an apparent paradox— the contiguous association of a seemingly startling propensity for learning and very inflexible behaviors. For example, the predatory wasp *Liris nigra* is no less able than others of its kind to utilize latent learning to relocate nests after foraging trips. Yet in prey capture, which normally involves stinging a cricket in four ganglia ending with the subesophageal ganglion, the wasp appears intensely frustrated when confronted with a decapitated prey. She will sometimes spend more than an hour vainly searching the cricket for the site of the missing ganglion.

Intelligence can be defined in various ways, but it generally includes the ability to learn facts or skills and apply them in a rational way, that is, to generalize learned information by transferring it from one set of circumstances to another. Insects do not measure up very well in this regard. Their ability to transfer memories to assist in the learning of new situations is nearly or totally absent.

Consider *Ammophila pubescens*, a European wasp that raises its young in burrows that it digs in the soil. Unlike most other digger wasps, it attends to up to 15 nests at a time, remembering the locations of each. Because the nests are begun at different times, the young inside may range from a newly hatched larva capable of consuming but a single caterpillar a day to an older offspring requiring three to seven caterpillars, or a full grown larva does not need more food but should have its burrow sealed so it can safely mature underground. The ability to do so many complex things at once would seem to indicate a fairly high degree of intelligence, but rationality is not this wasp's strong suit.

Watching *Ammophila* closely in the early 1940s entomologist G. P. Baerends noted that the female begins each day with inspection visits, flying from nest to nest and inspecting the contents of each before she begins to bring prey to any of them. Might this behavior provide a clue to her ability to multitask? Baerends located a series of nests being attended by a single female and carefully replaced the nests with plaster of Paris casts he could open and close. In the following days he spent many hours substituting larvae of various sizes for each other and adding and removing caterpillars the female had brought. Very quickly it became apparent that the single morning inspection visit set the wasp's behavior for the rest of the day. Substituting a larger larva after the inspection visit made absolutely no difference, nor did it matter whether he added prey or removed some that she had already brought. If her inspection visit indicated permanent closure, this she would do, even if the larva had subsequently been removed so she now was sealing a completely empty nest! Thus, provisioning behavior in *Ammophila* is paced to meet the needs of each growing larva in a way that is both sophisticated and restricted. Each step in the unfolding behavior patterns of the day is guided by the sign stimuli present in the single brief examination of nests, and after this each appropriate motor pattern is performed in a genetically determined sequence. In nature, in the absence of meddling entomologists, the information obtained through a single daily visit would be, and clearly is, sufficient.

Insects also appear almost entirely incapable of *insight*, that is, reorganizing their memories to construct a new response in the face of a novel problem. The French naturalist Fabré (see Chapter 1) demonstrated this long ago with another hunting wasp that briefly drops her cricket near the hole to enter her burrow before reappearing to drag it inside. While she was inside the burrow, Fabré moved the cricket a short distance away. With insight, a wasp might be expected to recognize that her prey had merely been moved and that her burrow, having been inspected, was ready for stocking. Instead, when the wasp reappeared, she returned the cricket to its proper place at the edge of the hole once more, then descended again, alone. Fabré moved the cricket; again, the wasp reappeared to reposition it and reenter her hole alone. Fabré re-elicited this response 40 times before he lost patience!

For a long time during the twentieth century, the 'nature–nurture' controversy was vigorously debated; instinct and learning were pictured as diametric opposites in command of the behavior of different kinds of animals. However, the controversy really is a spurious one, and few behaviorists nowadays seek to determine whether a particular behavior response is learned or instinctive. Rather, it is

generally agreed that behavior is rarely determined either solely by the type of out-side events impinging on the individual or by inborn heredity alone, but rather by interaction of the two. A high reliance upon learning ability may be adaptive when an animal is relatively long-lived and/or faced with a good deal of uncertainty or variability regarding aspects of its environment that are biologically significant. In contrast, the advantage of a high reliance upon innate behavior patterns lies in their reliability. When a particular environmental cue can be linked dependably to a biologically appropriate response, innate fixed action patterns are certain to be successful responses. Selection also will favor innate behavior when the cost of an initial mistake is high, such as would be true in the case of the cockroach and moth escape reactions. Furthermore, innate behavior presumably permits economy in the nervous system.

2.4 Hormone-Based Coordination

Reproductively active adults of the lacewing *Chrysopa carnea* are green, but they turn brown when they enter diapause in the autumn; in the spring, when they become active, they again turn green. A grasshopper typically goes through a series of five to seven molts over several months between hatching from its egg and becoming a sexually mature adult; if its prothoracic gland is removed when it is still an early nymph, its development halts, and its behavior never matures. A female cockroach produces chemical sex attractants; if the corpora allata in her brain are surgically removed, she is incapable of attracting males and will not mate.

It is well known that insects rely heavily upon circulating chemistry. They pos-sess a traditional endocrine system that produces blood-borne chemicals that act on receptor-bearing target tissues elsewhere in the body. They have nerve cells that rely upon chemical neurotransmitters to propagate their messages (and thus could be considered a hormone that is acting locally within the synapse). And they have functional hybrids of neurons and endocrine glands called neurosecretory cells that cluster in their brains and throughout their central nervous systems.

Hormones, by classical definition, are substances secreted by endocrine glands and transported by the circulatory system to other body parts, where even tiny quantities evoke physiological responses in target tissues. A broader definition recognizes that in addition to endocrine glands, single cells can produce hor-mones. Various body organs, especially those associated with reproduction (such as ovaries, testes, spermatheca, etc.), also are known to have a secondary endocrine function.

Hormones connected with growth, development, sexual maturation and repro-duction (see Chapter 9) have received the most study, but internal hormone secretions have been implicated in nearly every aspect of insect life history, includ-ing important controls on migration, orientation, and periodic behaviors as well as activation of adult behavior.

Behaviorally, hormones often act as primers or modifiers that start the internal motivation of an insect to later perform a particular behavioral act. Strong evidence

is obtained when removal of a particular endocrine center abolishes a specific behavior that can then be restored through gland implantation or hormone application. For example, the *corpora allata* are a pair of endocrine glands behind the brain. Their removal (an operation termed allatectomy) from last instar or newly emerged females of *Gomphocerippus* grasshoppers completely prevents the onset of normal sexual receptivity. Females so treated respond to courting males by kicking defensively and trying to escape. However, implantation of actively secreting corpora allata into such females changes their behavior toward males to a state of copulatory readiness. Allatectomy of previously sexually receptive females leads to loss of this receptivity and reappearance of defensive kicking within six days. Thus, one can state with fair confidence that for these grasshoppers the internal impetus toward mating is directly mediated by secretions from the corpora allata.

A useful conceptual overview places genes at the beginning of all behavior, producing their effects by establishing the parameters that will govern (1) the nature of particular neural pathways that are responsible for the manner in which stimuli are processed, and (2) the production of hormones that trigger the expression of the fixed action patterns present in the nervous system. These hormones can interact with the nervous system and the insect's physiological state immediately (in which case they are called *releasers*) or belatedly (when they are called *modifiers*); in either case, the outcome is that they activate appropriate behaviors. Thus, for example, while she is developing her eggs, a female mosquito releases one hormone that temporarily keeps her from seeking new hosts until after they are laid; a second hormone increases sensory sensitivities that help her find a site to lay them.

Many functions of an insect's life are under endocrine regulation. Here, we will concentrate on molting and metamorphosis, two developmental behaviors well suited to physiological and biochemical control by the hormonal system, which tends to be slower and more sustained than primarily nerve-mediated responses. At the same time, remember that the nervous system still exerts an influence on both events through nervous feedback and by secreting neurohormones.

It is an appropriate place to start, because all insects share a fundamental problem. They have an external skeleton, and as they grow, it becomes too small. Consequently, they must grow a new, larger, more flexible exoskeleton and then shed (molt, ecdyse) the old one. Most insects also metamorphose into an adult form at the last molt. For some groups, this represents no great change beyond adding or maturing functional sex organs; for others, it is a drastic revolution. New structures, musculature, and nervous innervations appear; food choices differ, new sensory receptors arise, and entire behavioral repertoires change. Many larval neurons die; others are remodeled; new adult neurons proliferate from neuroblasts. All of this alteration is linked to endocrine changes and hormones.

Hormones control not only the molt, but also the development or degeneration of many systems that affect behavior. One was discovered when pioneering insect physiologist V. B. Wigglesworth implanted an active corpus allatum into last instar larvae of a bloodsucking bug, *Rhodnius*, and found that they molted into additional larval instars rather than producing adults. At first Wigglesworth thought the new

hormone was an inhibitor, but as soon as he realized its true effect he named it *juvenile hormone (JH)* to reflect that fact. Juvenile hormone is now recognized to be not just a single hormone, but a group of sesquiterpenes having at least six major members. These mediate a wide variety of functions in addition to metamorphosis.

Another, *ecdysone*, was the first insect hormone to be structurally identified. As new techniques have allowed others of its type to be isolated, *ecdysteroid* has become the preferred name for the group. Ecdysteroids' primary claim to fame is that they directly affect gene expression and thus trigger the separation of the epidermis from the overlying cuticle, which begins the molt. Like JH, they now have been shown to have wide-ranging effects at every developmental stage but particularly in embryogenesis and other reproductive and developmental tasks. The primary site of ecdysteroid synthesis is the prothoracic gland, but despite its nervous connections, the primary mode of gland activation is hormonal. The classic understanding is that when a winged (pterygote) insect becomes a full adult, it no longer molts, so this gland is no longer needed. Exposure to ecdysone in the absence of JH then leads to apoptosis (programmed cell death) that causes the gland to degenerate. Apterygote insects, on the other hand, continue to molt as adults, and they retain their active prothoracic glands. Recent discoveries add complexity to this picture but do not change its general outlines.

A third important hormone goes by the acronym *PTTH* (short for a rather unwieldy term, prothoracicotropic hormone). It actually was the first insect hormone to be discovered, but the last major hormone to be structurally identified. In 1917 Stefan Kopec reported that the brain of gypsy moth caterpillars was necessary for successful pupation, based on his well designed experiments in which he surgically removed brains from some larvae while controls had sham surgery (an incision made, but the brain left in place). He also tied silk string tightly around various parts of gypsy moth larvae, then watched their subsequent development. When a caterpillar was tied around its midsection early during its last larval instar, only the head half later pupated; when tied late during that instar, both halves pupated. Based on this, Kopec proposed the concept of a *critical period*, a time period when the brain was necessary for its hormonal influence to be exerted. Removing the brain before the critical period prevented development but afterwards, it had no effect. He postulated a brain hormone was responsible.

Unfortunately, Kopec was ahead of his time, and his work was poorly accepted. The prevailing wisdom was that insects had no hormones. Furthermore, everyone 'knew' the nervous system and the endocrine system were functionally distinct; brains and nervous tissue certainly did not produce hormones. Neurons secreting chemicals at their synapses had not even been envisioned. When later work by others showed that the brain produced not just one but many different hormones, even his terminology fell out of favor.

Today, however, Kopec would be vindicated. His 'brain hormone' has been demonstrated to be PTTH, and it shows a satisfying complexity. The PTTHs from only a few insects have been identified, but they appear to fall into two size groups. The 'small' PTTHs were renamed bombyxin; their exact role is unknown, but they appear insulin-like and may be involved in ovarian development and the utilization

of carbohydrate during egg maturation. The 'big' PTTHs show the activity for which they were named, acting on the prothoracic gland to regulate the synthesis of ecdysteroids. When an insect receives the proper stimuli from the environment (such as photoperiod or temperature) or from its nerves (such as stretch receptors firing after an assassin bug's blood meal), it releases PTTH. This in turn activates the prothoracic glands to produce ecdysteroid, triggering the molt. Interestingly, for many insects that undergo pupal diapause, PTTH release is regulated by photoperiod during a circadian window.

Ecdysteroids, juvenile hormones, and PTTH are still recognized as the three major hormone groups regulating insect development and reproduction, but other important hormones that play more specialized roles are continually being discovered. Though their functions have yet to be fully elucidated, many hormones previously isolated from vertebrates have been found. Insects produce insulin and melatonin. They have counterparts to vertebrate adrenaline and noradrenaline. Their reproductive hormones are close enough that female rabbit fleas depend on the hormones circulating in the blood of the pregnant rabbit host in order to reproduce. Considering that a hundred years ago, insects were thought to lack both hormones and brains, it is somewhat humbling to learn that they have counterparts to so many vertebrate systems—as it is to recognize that, because they are the more ancient group, it would be more correct to salute the insect-type life processes that are found in us.

2.4.1 Clocks and Reiterative Rhythms

After 17 years of silence underground as nymphs, great numbers of periodical cicadas emerge to fill the air with their raucous noise. The snowy tree cricket (see Fig. 8.2) sings in such a rhythmic tempo that one can ascertain the temperature on a summer's eve by listening to its chirp with a watch in hand. Silverfish scurry about each night, resting in cracks and crevices during the light of day. Much of what insects do is rhythmic, from heartbeats and songs to cycles of sleep and wakefulness, to reproductive cycles measured in weeks, months, or even years.

Intuitively, one can see the adaptive advantages of most cycles, but how are they initiated and maintained? In discussions of biological rhythms, the term *clock* is widely used as a convenient analogy. It does not refer to a specific physiological mechanism; instead, it is a convenient catch-all term to describe the largely unknown biochemical systems driving the rhythmic cycles. The discovery of a great many 'clock mutants' in *Drosophila melanogaster* that show different circadian cycle lengths (or no rhythm at all) confirms that the periodicity is innate and genetically coded.

Although further research will probably show many variations in the clocks of different species, investigators are closing in on a general description of the system. Working with vertebrates as varied as hamsters and humans, biologists have identified an area in the hypothalamus of the brain called the suprachiasmatic nucleus (SCN) that appears to contain a master clock. The SCN clock operates via rhythmic changes in the activity of three genes. The first two, called *per* and *tau*, respectively,

code for a protein (PER) and an enzyme that degrades PER. Production of PER varies over a 24-hour schedule, gradually building up inside and outside the cell nucleus. When PER is in peak abundance in the cell, *tau* turns on the enzyme's production, slowing PER's rate of accumulation. At the same time, extra PER bonds with a protein coded by a third gene, *tim*. In this bonded form, PER is carried back to the nucleus, where it blocks the activity of *per*, the gene that produced it. However, this blockage is only temporary, and soon a new cycle begins. Surprisingly, these key genes of vertebrates have also been found in both *Drosophila* and honey bees, where they play an equally critical role in enabling circadian rhythms. Thus it appears likely that they arose early in evolutionary development, perhaps from an ancient animal that lived about 550 million years ago.

Reiterative rhythms occur with a regular repeated periodicity in the life of a single individual. Some reiterative cycles cover a relatively long period, such as the lunar periodicity of nesting behavior in the nocturnal sweat bee, *Sphecodogastra texana* (Fig. 2.13). In many temperate insects, seasonal rhythms are based on changes in photoperiod, involving an assessment of the duration and accumulation of daily changes in day or night length over a period of time. At the other extreme, reiterative cycles of feeding and locomotion may be very short. Typically, however, reiterative
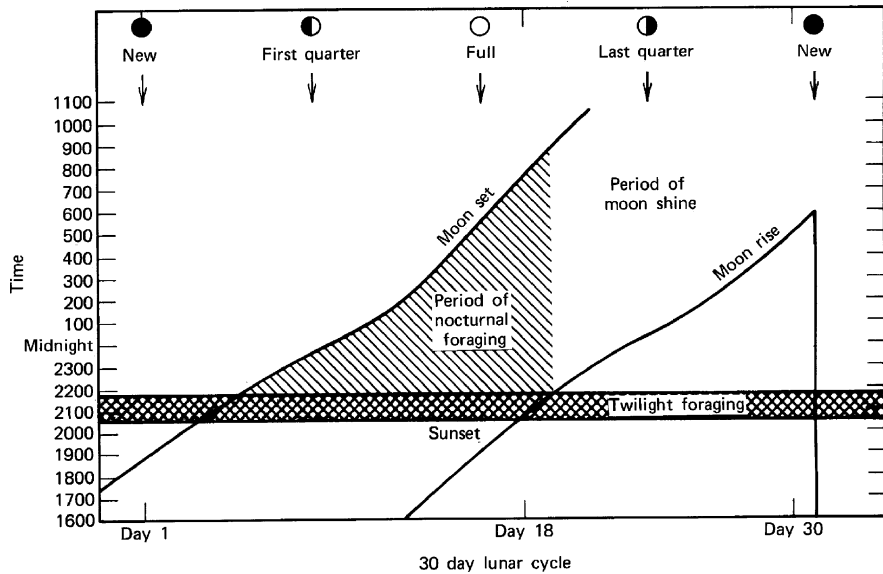

Fig. 2.13   Responding to moonlight. The sweat bee *Sphecodogastra texana* shows lunar periodicity. In good weather adult female activity always begins about sunset. Concentrated pollen collection and nest cell construction occur only during that part of the lunar cycle where moonlight is continuous with the twilight, thus permitting extended nocturnal foraging. When the moon rises after the close of twilight (ca. 9:30 pm), the bees close their nests at the end of twilight and make very few pollen collections from their host plant (the evening primrose, *Oenothera rhombipetala*) even when pollen is abundant. Brood development in excavated nests correlates with the observed foraging activity

behavioral rhythms have a periodicity of about 24 hours and thus are called *circadian rhythms*, derived from the Latin *circa*, about, and *diem*, day. For example, anyone who has cohabited with cockroaches has noticed their characteristic pattern of activity that begins shortly after dusk. The timing of moths' sex odor release is also on a circadian cycle.

Circadian rhythms all share some important characteristics. First, although these cycles average about 24 hours, they are not exactly so, and will drift out of phase or *free run* for some time unless they are entrained (kept in line, reset) by certain external environmental cues. Crickets are a well-studied example. Each evening under natural conditions, males begin singing at about the same time relative to nightfall. In a room with constant bright light, although they still sing, each day their calling starts about 25–26 hours later than it did on the previous day. The very fact that the length of a free-running cycle is not exactly matched to the earth's many 24-hour environmental cycles provides strong evidence that internal components drive a given rhythm. However, it does not prove it, because one cannot always exclude other environmental cues with certainty.

The cyclical environmental cue that entrains a circadian rhythm is called a *Zeitgeber*. Most circadian rhythms studied to date have relied upon light/dark transitions as their Zeitgeber, but other cues may also prove important. Some insects held in continuous darkness, for example, distinguish between long and short days in a temperature cycle. However, in general, circadian rhythms are temperature compensated. Unlike most other physiological processes, within normal biological limits the periodicity remains stable under changing temperature conditions. Consider the midge, *Clunio marinus*, that spends its larval and pupal life among red algae between the tidemarks of certain European beaches. Adults emerge only at low tide; they live for just 2 hours and must mate and oviposit before the tide advances back over their breeding ground. A number of genetically distinct geographical races exist, each with its own emergence rhythm precisely adapted to its local tidal conditions. In southern races the daily periodicity is circadian and free runs in constant light. In the Arctic, however, emergence is strictly tidally controlled and stops in constant light or dark; it is as though an internal alarm clock were measuring 10 hours from the time of first exposure to the previous ebb tide.

Subsequent research has shown that the receptors for circadian rhythms and for seasonal activity are located in the brain of some insects, in the compound eyes of others, and in other cases, in both. Cryptochrome, a light-sensitive pigment that contains the vitamin riboflavin and a protein, is a major player in sensing circadian light information. Interestingly, in *Drosophila*, cryptochrome in the brain regulates the morning activity rhythm and cryptochrome in the compound eyes controls the evening activity peak.

2.4.2 Gated Rhythms

Many behavioral events, such as the periodical cicada's emergence (see Plate 44) or the mass emergence of mayflies from a pond, look like a rhythm when one views the whole synchronous population, but occur only once in any individual's life. These

one-time events are called *gated rhythms*, because at the appropriate stage of the life cycle it is almost as though some mechanism were opening a behavioral 'gate' at the appointed time. All those individuals streaming through are allowed to begin a given behavior, but an individual that misses a given gate opening time must wait for the next one.

Ideally, one attempting to investigate gated rhythms should seek an organism with a relatively simple nervous system, choose neurons important to a clear-cut behavioral alteration, and then follow the changes occurring in those neurons during the course of hormone action. In the 1970s, two researchers found their model system in giant silk moths (family Saturniidae), not to be confused with the silkworm moth, *Bombyx mori*.

Case Study 2.4: Initiation of Adult Behavior in Saturniid Moths

An adult silk moth acts very different than the pupa it previously was. How do hormones and the nervous system interact to produce this change?

In moths, as in most insects, emergence of an adult from its pupal skin occurs only during a specific period of the day; individuals that do not emerge during that particular time cannot eclose until the proper time on the following day. However, simple escape from the pupal skin does not herald the arrival of a fully functional adult. A newly eclosed individual displays little in the way of adult behavior and will make only immature rotary movements of its abdomen. The problem is not lack of appropriate neural machinery; it possesses a fully developed adult nervous system. Nor is the lack of adult behavior merely due to the insect's restraint—peeling the pupal cuticle away from the mature moth within still does not mature the behavioral repertoire before its normal emergence gate. Complex motor patterns such as flight or walking, on the rare occasions when they can be elicited at all, are uncoordinated and abortive. Even simple reflexes, such as the 'righting reflex' when overturned, are missing.

At the arrival of the eclosion gate, however, the behavior of a 'prematurely peeled' moth changes strikingly. In perfect pantomime, the moth sheds its phantom pupal skin and escapes from its nonexistent cocoon. At the end of the performance, it inflates its wings and assumes the full repertoire of adult behavior. This behavior suggested that adult actions must be controlled in a central manner that was closely linked to the timing of eclosion.

Hoping to locate the site of the eclosion clock, James Truman and Lynn Riddiford performed a series of surgical ablation studies on various parts of the pupal nervous system. When the brain itself was removed shortly after the onset of adult development, development proceeded normally and the resulting moths went on to shed their pupal skins. However, their emergence was quite abnormal; some usual behaviors were entirely omitted and others were out of sequence. Even more striking, the eclosion was no longer gated. Moths

emerged at all sorts of odd hours randomly distributed throughout the day and night.

Was all this behavioral confusion simply due to removal of important neural centers? The researchers tackled this suggestion by implanting loose brains into the abdomens of debrained pupae. In these 'loose brain' moths, neural connections between the brain and nervous system were never established. Yet the resultant moths emerged at the proper gating time and displayed proper emergence behaviors! Clearly, the appropriate messages were being carried through chemical channels rather than along nerve fibers. An eclosion hormone appeared likely, and the case was strengthened when injecting brain homogenates into moths prior to their normal eclosion time resulted in moths emerging early.

But what was the actual role of the brain? For example, did the brain include the photoreceptor, the clock measuring the time after lights-on or lights-off, or both? Knowing that different species of giant silk moths have quite different eclosion gating times, the researchers performed brain transplants between species. The results (Fig. 2.14) clearly confirmed their suspicions. The moth brain contained the gating clock. By interchanging the brain, one could interchange the time of emergence.
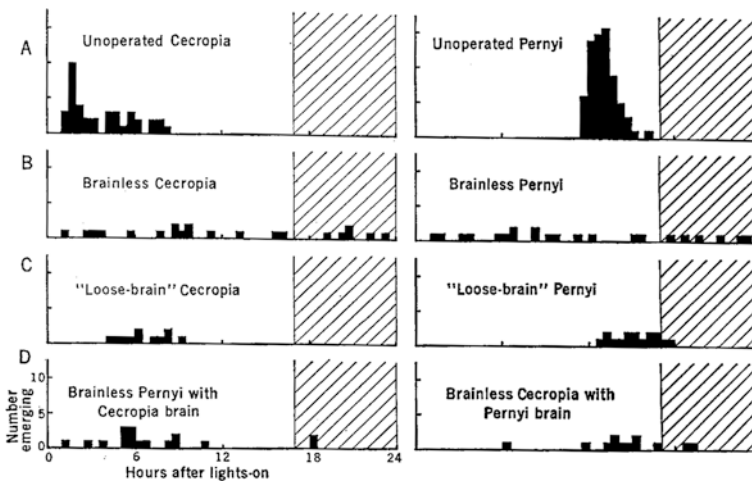

Fig. 2.14 Interchanging brains. *Hyalophora cecropia* silk moths eclose in the morning, whereas *Antheraea pernyi* ecloses just before dark. When their brains are removed, eclosion rhythmicity is abolished in both species. When their brains are reimplanted in their abdomens, rhythmicity returns even though there are no nervous connections between brain and CNS. If the brains are removed and implanted into individuals of the opposite species, the restored rhythmicity is that of the donated brain rather than the recipient body. The hormonal action is not species-specific, only the timing of its release

Were there also photoreceptors in the brain? Removing a moth's compound eyes did not halt its response to light–dark cycles. Truman implanted brains into the head region of ten previously debrained pupae, and into the abdomen of another ten. Then he plugged the pupae into holes in a partition and placed them into a chamber so as to expose their anterior and posterior halves to different photoperiod regimes. In each case the subsequent eclosion of the host depended only upon the photoperiod to which the brain was exposed.

The research outlined in Case Study 2.4 concentrated on one critical point of development. However, molts between larval instars, from larva to pupa, and from pupa to adult differ in the degree of internal morphological change that occurs. The system usually runs smoothly, but errors do occur. As noted for the assassin bug *Rhodnius* given supplemental juvenile hormone (Section 2.4), insects sometimes molt more times than usual, becoming 'supernumerary larvae' rather than changing into adults as expected.

How is a proper degree of change regulated? The brain is in charge, as Truman and Riddiford demonstrated. Upon receiving proper stimuli, it secretes PTTH that in turn stimulates the prothoracic glands to synthesize and secrete ecdysteroids. These combine with a receptor protein in the cell nucleus, bind with DNA, and induce transcription of a few master genes. These transcripts, in turn, start a flurrying cascade of gene activity that ultimately results in everything from changes in morphology and physiology of internal organs to secretion of a new cuticle. However, it is juvenile hormone—through its timing and quantity at target cells—that modulates ecdysteroid-induced gene switching so that the proper amount of change occurs. More exactly how it does so at the gene level is a matter to be elucidated by current and future research.

Chapter 3
Spatial Adjustment

3.1 Introduction

The burrows of most wood-boring cerambycid beetle larvae are very irregularly oriented; why? At temperatures so low that most other insects are inactive, bumblebees still fly about; how? Migrating locusts appear to swarm single-mindedly toward a fixed goal. Do they?

Though the scale of movement varies widely, the ability to change position within the environment is essential to the survival of nearly every animal, including most insects. Escaping predators, gathering food, locating a mate, adjusting to environmental variables such as temperature and humidity—these and other important behaviors all depend upon an insect's ability to adjust its spatial relations.

One of the most generally known facts about insects is that they possess three pairs of legs. This is, in fact, the fundamental ground plan of insects, and one that is amply represented in the fossil record. It is derived from an ancestral arrangement in which serially uniform legs occurred on the majority of body segments. Over time, some legs became modified into various appendages such as mouthparts, thoracic legs, genitalia and cerci, while others on the abdominal segments typically were lost. With the passage of further evolutionary time, insect thoracic legs have developed an enormous diversity of structure and function (Fig. 3.1). In addition to differences between taxa, variation can be found within an individual, between larvae and adults, and between males and females.

The acquisition of wings was a second major development, the importance of which can hardly be overstated. Insects were not only the first organisms to develop the capacity for powered flight, they remain the only group of invertebrates to possess this ability. This development opened the third dimension to insects, setting the stage for improvements in such diverse but crucial behaviors as dispersal, escape, thermoregulation, feeding, and mate location. It probably also led to an expansion in neural capabilities. It has been noted that some of the most 'intelligent' insects (i.e. those that are most capable of learning), as well as those with the most acute vision and olfaction, are found among actively flying predators and pollinators.

Together, diversification in the structure of legs and wings undoubtedly has been a key factor in the overwhelming success of insects worldwide. Through variations
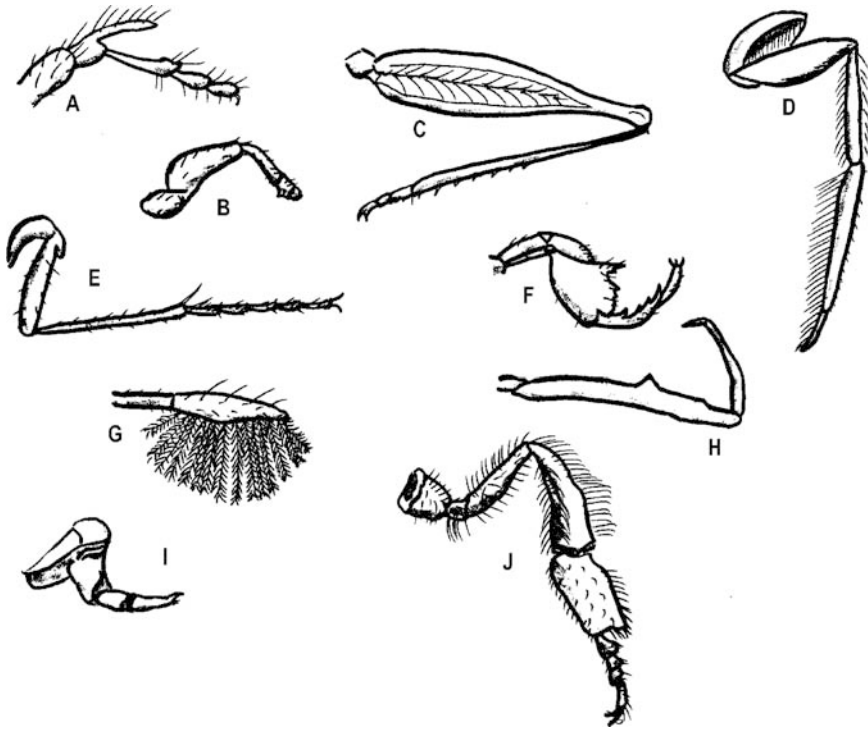
Fig. 3.1 Showing a bit of leg. Diversity of insect legs and some of the purposes of their modifications. (**A**) *Drosophila cracens* foreleg—courtship, (**B**) thrips foreleg—crawling, (**C**) grasshopper hind leg—jumping, (**D**) *Corixa* water boatman hind leg—swimming, (**E**) *Cicindela* tiger beetle hind leg—running, (**F**) cicada nymph fore leg—digging, (**G**) *Rhagovelia obesa* water strider middle tarsus—walking on water, (**H**) *Ranatra fusca* water scorpion fore leg—prey capture, (**I**) caterpillar thoracic leg—crawling, (**J**) honey bee hind leg—pollen transport

on their basic body plan, insects have surmounted the barriers to inhabit nearly every terrain but deep saltwater. Moreover they have done this so elegantly that they have attracted the attention of engineers who study insect locomotion as inspiration for moving robotic devices (Fig. 3.2).

3.2 Locomotion

A tiny flea's jump may be 13 inches long. A blood-sucking bug, *Rhodnius*, may move about with a meal 10–12 times its own body weight, corresponding to a human drinking 200 gallons and subsequently weighing nearly a ton. Click beetles can suddenly flip into the air to a height of four times their body length. Cockroaches have been clocked at speeds of nearly 3 miles per hour—a remarkably high speed in relation to their body size.
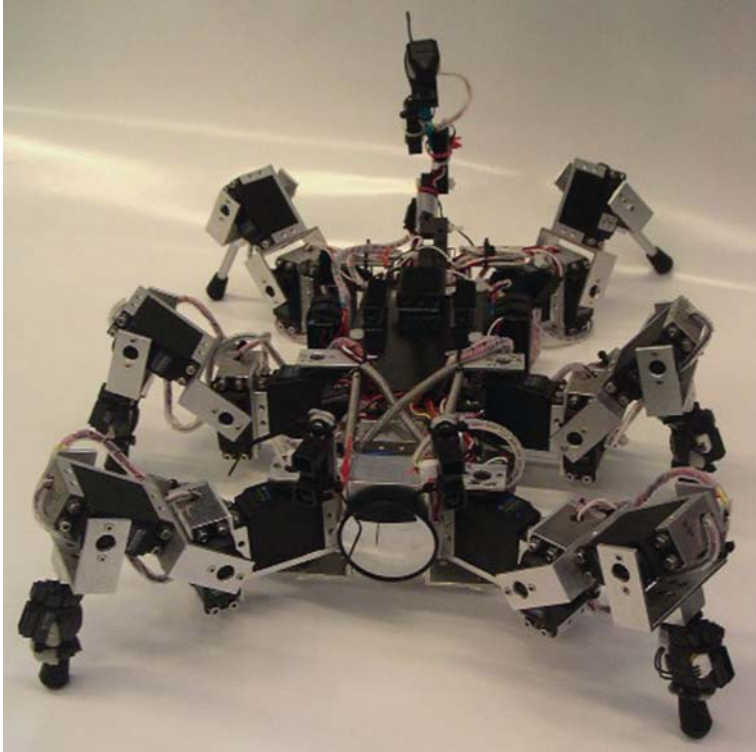
Fig. 3.2   Creating a useful mimic. Hexapodal robots have potential for performing many tasks such as exploring terrain of distant planets. Around the world, robots such as this one are being developed that mimic the analogous working morphology of common insects. The wireless camera mounted atop the robot's rear monitors the environment and gives the robot the appearance of having a stinger like a scorpion

Many insect locomotory activities appear extraordinarily impressive by human standards. Are insects endowed with comparatively tremendous muscular power or a different sort of muscle from those we possess? Not really. Physiological studies have shown that their muscles are quite similar in almost all respects to our own, although the insect may possess many more individual muscles than a human does. Instead, many of the strange powers insects appear to have (as well as many of the problems they face) are the consequence of a simple physical relationship between surface and mass. As the size or mass of any object diminishes, the *relative* amount of its surface increases. (The volume of a sphere is $4/3\pi r^3$, where r is the radius of the sphere; the surface of a sphere, however, is $4\pi r^2$.)

For an organism as small as an insect, this surface to volume relationship has a marked effect on muscle power. The power of a muscle is proportional to the *area* of its cross section, whereas the mass it has to move is proportional to *volume*. We are amazed by the long jump of the flea, which proportionately carried out by a man

would cover 800 ft. However, we must realize that a flea the size of a man would have relatively much more mass per unit cross-sectional area of muscle than does a normal-sized flea.

3.2.1 Terrestrial and Aquatic Locomotion

Houseflies easily walk upside down across the kitchen ceiling. Mole crickets burrow through the soil with their powerful, spade-like forelegs. Many aquatic insects such as dytiscid and gyrinid whirligig beetles use their flattened, fringed legs as oars for paddling or swimming. Although a few insect species have secondarily lost most or all of their use of their legs as locomotory appendages, walking and running are common behaviors for the adults of nearly all flying and non-flying insects and for many immature forms as well.

The power for most terrestrial locomotion comes from the thoracic legs, which move in various sequences at different speeds so that stability is always maintained. Coordination of these patterns, understandably crucial, is mediated both through central mechanisms (often termed central pattern generators) and through segmental reflexes. Two general principles appear to underlie the walking sequence. First, no leg is raised until the leg behind it is in a supporting position. Second, the movements of the two legs of a segment alternate. A pattern of alternating triangles of support is commonly observed; with never fewer than three legs on the ground, an insect can stop at any point without losing stability. Stability is also enhanced by the fact that the insect body is slung between the legs in such a way that the center of gravity is low.

Walking is done by moving the three legs contacting the ground backwards while the other three legs are raised and moved forward. This propels the insect's body forward, and when the raised legs are all the way forward they lower and make contact while the legs that were down are raised and the whole pattern repeated.

Many immature insects move in a manner similar to adults. However, because an insect's thoracic legs can function only when the external skeleton is relatively rigid, soft-bodied larval forms generally employ somewhat different methods. Many larvae crawl, moving about by changing the shape of their body as a result of muscles acting against the body fluids. Caterpillars and sawfly larvae have thoracic legs, but also have hollow cylindrical outgrowths of their abdominal wall. Waves of contractions pass along their body from back to front, progressively lifting body segments and these fleshy prolegs. At each point in time, at least three segments are in different stages of contraction, a process that calls for a high degree of nervous coordination.

Although most insect legs are adapted for walking, climbing, or running, some are modified in ways that aid other forms of locomotion. The ability to leap or jump appears to have repeatedly and independently evolved in insects of all sizes, particularly as an escape reaction. Hind leg modifications are the most common but only one of a variety of specializations, most of which are based upon the sudden release of stored tension.

In groups such as Orthoptera and fleas, jumping has become a pronounced specialization. Efficient long-distance jumping presents a special challenge—in most cases it requires a powerful and rapidly accelerating movement of the jumping legs, and this in turn requires morphological modifications. Even the large femur extensor muscles of grasshoppers' jumping legs cannot generate the quick extension needed for an efficient jump without some mechanical modification within the leg structure for storing energy. Locusts meet this challenge with a tendon of the tibial flexor muscle that moves over a stop; the stop allows the extensor to contract without moving the leg when the muscles are coactivated. This stores energy in the mechanical distortion of the femur, tibia, and extensor tendon in a manner analogous to the bow and arrow of an archer.

Among fleas, a rubbery protein called *resilin* in the cuticle stores and subsequently releases energy for the jump (see Plate 2). The material displays a 97% recovery after stress is applied, exceeding that of elastin, the human elastic protein. In 2005, an Australian research team produced resilin protein in purified form by cloning a portion of the 'resilin gene' in *Drosophila*, with the hopes developing ways to use the material for human spinal disc implants.

As far as is known, all biological pre-launch amplifiers depend on the same mechanism—energy storage in deformed elastic materials. One of the most spectacular jumping strategies does not even involve legs. Click beetles shoot upward as much as four times their body length by rapidly accelerating the joint between two thoracic segments; here again a mechanical stop prevents movement until large isometric force has been achieved.

Aquatic insects have evolved two general sorts of locomotory adaptations—those enabling them to propel themselves upon or up to the top of the water and those by which they 'swim' beneath the water surface. Diving beetles in the family Dytiscidae are Olympic-quality insect swimmers; their body shape is so similar to a small-span wing profile that it is believed to create dynamic lift during fast swimming. Many bottom-dwelling insects such as larval Odonata and Trichoptera walk over the substrate just as terrestrial insects do (even though the larval case of some caddisflies can be quite a hindrance to movement).

Insects that live in lakes and other slow-moving waters generally swim well. The trunks of their bodies are streamlined and well adapted to flow. They generate thrust by synchronous power strokes, and often have adaptations such as flattened rear legs. Most free-swimming insects paddle with their hind legs, sometimes together with the middle legs. Efficiency is often increased by devices such as hairs or cuticular blades and/or modification in the morphology and relative size of the legs. In contrast to the general rule in terrestrial locomotion, in swimming the two legs of a segment sometimes work together like oars.

Surface dwellers take great advantage of the relationship between their body size and the physical properties of water at temperatures and pressures characteristic of their environment. Specifically, under these conditions water tends to have a relatively high surface tension, so that the water-repellent surface of the insect cuticle is sufficient to support many small surface dwellers as though upon a thin elastic membrane. Many insects also secrete additional waxy material upon their tarsi, allowing

them to walk or row across the water film without breaking its surface. Some, such as water striders in the family Gerridae, have hydrophobic tarsal hairs and specialized claws on their long legs that allow them to skate on the water's surface. One of the more spectacular surface dweller adaptations occurs in *Stenus*, a genus of staphylinid beetles that live on grasses along mountain streams. If they accidentally tumble into the water, as they often do, *Stenus* can walk upon the water's surface, but only slowly. In response to apparent danger, however, they release an anal gland secretion that lowers the surface tension of the water behind them. Drawn forward by the higher surface tension in front, the beetles propel themselves along at speeds of 45–70 cm/s, moving their abdomens from side to side to direct their movements.

Insects with gills or other aquatic respiratory adaptations can live permanently submerged. Locomotion methods among insects that live beneath the water surface vary greatly. Most live predominantly at or in the surface layer of the stream bottom, but an unusual behavior occurs among a few species in which normally terrestrial adults dive to reach submerged areas to oviposit. Female black flies dive through shallow moving water to reach the surface of rocks where they affix their eggs. Similarly, some female caddisflies dive vertically and swim to oviposition sites below inclined submerged stones. Although adult stream insects rarely swim, larvae of many insect groups can swim by body undulations. Some mayfly larvae escape from predators or aggressive conspecifics with such strong, active swimming that they can travel against a current. Dragonfly larvae force jets of water rapidly out of the rectal chamber so that the body is driven forward. Still other species use claws, silk, suckers and other devices to help themselves maneuver.

The drift of insects downstream with the current, a behavior that typically occurs at night, is perhaps one of the most frequently studied topics in stream ecology, but because of the diversity of stream insects and the diversity of running water conditions, researchers have found it difficult to identify clear patterns, much less to develop predictive models. It is clear, however, that drift is more than a passive activity. When a habitat patch is overcrowded and resources are low, as much as 10–30% of the insect population of a stream may drift in a single night, traveling between 2 and 20 m during one drift movement. Black fly larvae drift by first fixing a silk thread to a rock on the stream bottom, then prolonging the thread by spinning and in essence rappelling themselves several centimeters downstream before resettling at the bottom.

3.2.2 Aerial Locomotion

Insects alone among the invertebrates possess the ability to fly, and flight is one of the most important reasons for their success. How and when did this remarkable ability arise? The acquisition of wings in vertebrates is a familiar story, but few people realize that insects were actually the first organisms to develop powered flight, and they did so at least 90 million years (and perhaps even 170 million years) before the earliest winged vertebrates.

Insect wings appear to have arisen upon rather large active insects sometime prior to the Late Carboniferous Epoch. They were not modified limbs, but two or three pairs of sideways expansions of the upper part of the thorax, and presumably, at first these expansions only allowed an insect to glide. Flapping and steering would come later.

On one point, scientists agree: Despite a stunning amount of structural diversity in insect wings today, they evolved only once. Throughout the fossil story, wing venation has remained relatively consistent, and the changes that have occurred can be homologized across insect orders, as can many other important morphological aspects. Beyond this, the simple question, 'What is the origin of insect wings?' has been the subject of competing theories for over one hundred years. For one thing, the question is actually two queries. One centers on homology, asking what morphological elements gave rise to wings. The other concerns behavior and evolution, asking what purposes early wing-like structures served and what conditions favored their origin.

Currently, the best accepted theories are that insect wings may have arisen either from pronotal lobes on the thorax or from modified gills. As a result, unlike the wings of birds or bats, the wings of insects contain no intrinsic muscles. Instead, they attach to the thorax by a complicated hinge structure that amplifies the tiny strains of the flight musculature into the large sweeping motions of the wing. To transmit force to the wings, the flight muscles are attached to the thorax by two different systems. In one system, direct flight muscles connect directly to the wing sclerites. In the other, the flight muscles insert within the thorax at some distance from the wing base, and deform the overall shape of the entire thorax so that parts push on the wing base and move it up and down (Fig. 3.3).

Odonata still possess only direct flight muscles, but most other insects possess some combination of direct and indirect muscles so that while the muscles altering wing inclination remain attached to the wings themselves, the muscles responsible for wing flapping are attached to the thoracic walls. Most present-day insects also have developed a musculature that allows the wings to fold backward over the abdomen. Thus while the wings are flapping, wing inclination is synchronously changing, so that the overall wing flight pattern becomes much like that of a pair of small propellers directing an air stream downward and backward. In typical forward flight, each wing traces a pattern that resembles the numeral 8 relative to the body at its base, and many insects can hover or loop by changing the inclinations of this 'figure 8' relative to their body.

By necessity, as insects became smaller their wing movement rate increased. While a house fly may have a rate of about 200 beats per second, mosquitoes have a rate of up to 600 beats. Tiny ceratopogonid midges have been clocked at a wing vibration speed of over 1,000 beats per second. How can this be possible? No known animal nerves are physically capable of transmitting stimuli fast enough to cause contraction and relaxation at these high speeds. The elastic nature of the insect thorax and the action of resonating flight muscles hold the key to this paradox. In many insects, especially certain Diptera and Coleoptera, the wings have two stable positions—completely elevated and completely depressed. As the wings move downward, normal thoracic elasticity resists this motion until a certain point
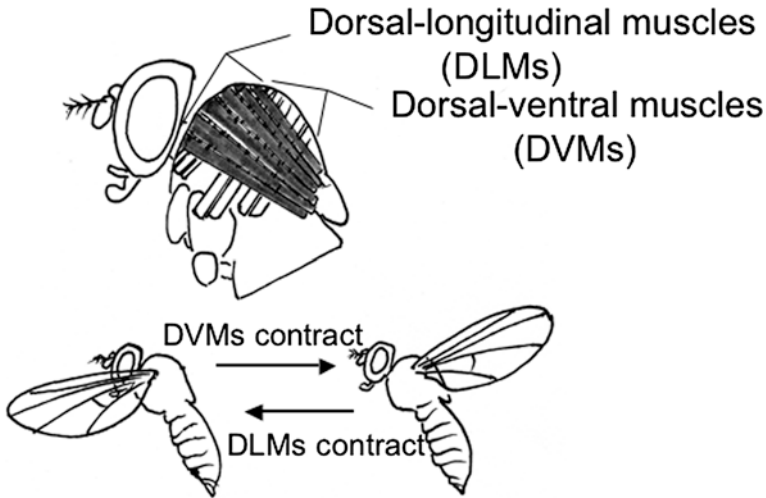
Fig. 3.3 Flapping their wings. Rather than flapping up and down, most insects wings move in a back and forth motion. This is a result of the arrangement of two groups of large antagonistic flight muscles that attach to the inner thorax walls rather than directly to the wings (thus they are called *indirect* flight muscles). One group (DLM = dorsal-longitudinal muscles) is inserted at right angles to the other group (DVM = dorsal-ventral muscles). Alternating self-sustaining contractions of these two muscle groups changes the shape of the thorax driving the wings forward and backward. Tiny steering muscles attached to wing base apodemes alter the wing attack angle, with the result that with each wing stroke the wings move propeller-like around their base before flipping over and sweeping back in the opposite direction, following a figure-8 pattern

is reached. At this 'click point,' three things happen simultaneously. First, the resistance vanishes and the wings click into a new position below the thorax. Second, their inclination automatically changes in readiness for the upstroke. Finally, the muscles that have been contracting are suddenly released. As they relax, the opposing muscles are suddenly stretched, which causes them to contract instantly. In this remarkable oscillating process, these insects have developed a system that does not require the synchronous nervous control for every contraction that is characteristic of dragonflies, locusts, and butterflies. Once initiated, this 'improved model' can be operated at almost any speed, depending on thoracic elasticity, and can be modified by secondary controls as circumstance dictates.

3.3 Orientation

Having briefly viewed *how* insects move, let us turn our attention to *why* and *where* they move, first as individuals and then as populations. The subject of spatial adjustment is a critical one touching many facets of the life of an organism. A major part of an insect's behavior is in fact orientation to factors such as food, mate, prey, host,

etc. Thus, it is unsurprising to find that the study of orientation and navigation is a dynamic part of modern biology, with a rapidly growing literature. We can only be concerned here with some of its more general tenets.

Orientation is the self-controlled maintenance or change of an organism's body position in relation to external cues. It occurs when certain stimuli in the environment elicit a responsive sequence of behaviors that results in a non-random pattern of locomotion, direction of body axis, or both. The fact that orientation is self-controlled in this way distinguishes it from passive transport. That it includes position maintenance means that orientation also may be taken to include postural adjustments such as response to gravity.

3.3.1 Locomotory Responses

When too far from its host plant to receive directional cues, the red cotton bug *Dysdercus* congregates in humid areas; it does not directionally follow a humidity gradient, but simply moves about randomly more actively when in drier areas and more slowly in more humid areas. To escape predators, a male grayling butterfly will fly upward toward the sun; if blinded in one eye, he will 'escape' in circles. Caterpillars move down the stems of their food plant when they are about to pupate in the ground. Sexually mature female crickets turn to face and approach the recorded song of a male cricket.

In the early years of the twentieth century, Jacques Loeb theorized that orientation occurred because of asymmetrical stimulation of an animal's sensory organs. For any bilaterally symmetrical animal, Loeb argued, a stimulus that registered unequally on the animal's two sides would simply cause the animal to turn until the stimulus was equalized. Loeb called such a directed movement a tropism. However, since then, the term tropism has come to refer primarily to movement in plants, and the term *taxis* (plural, taxes) is used when referring to this behavior in animals. Some also broaden the definition of taxis to describe any oriented heading of an animal, whether moving or stationary.

While Loeb's explanation was useful in stimulating research on orientation, investigators soon found many examples like those above that did not fit Loeb's simple scheme. In 1940, Gottfried Fraenkel and Donald L. Gunn proposed a more comprehensive classification of orientation behavior according to the reaction mechanisms involved. A response like that of the red cotton bug would be called a *kinesis* (plural, kineses). This is perhaps the simplest type of locomotory response that an animal can make to a stimulus—moving in a way that is related only to the *intensity* of that stimulus while disregarding any spatial properties that the stimulus might possess.

A response like that of the grayling butterfly continued to be called a *taxis*, now defined as a directed reaction in which the organism's long body axis is aligned with the stimulus and movement is more or less directed toward or away from the stimulus. Movements such as these would seem to be among the most straightforward types of orientation to study because the insect's track appears obviously related in

direction to some physical or chemical polarization of the environment. In fact, such movements were one of the earliest types of orientation response to attract serious biological interest, and they have continued to do so.

With Fraenkel and Gunn's system, it became common to create terms that combined the supposed environmental cue with the form of taxis or kinesis, and an unwieldy terminology soon arose. A number of specific taxes were described, based on whether an animal moved toward or away from certain environmental factors, the complexity of the organism's sensory apparatus, and the manner in which the animal moved. The classifications that resulted are still in use, but they can be slightly overwhelming. For example, an insect that reacts to light is said to show a *phototaxis*. If, as with a maggot, it reacts by bending more vigorously on the lighted side of its body, an action that will move the creature into darker areas, the phototactic orientation is called *klinotaxis*. If instead it can be demonstrated that the organism's eyes mediate the movement so that removal of one eye causes it to move in circles in the light but not in the dark, the behavior is called *tropotaxis* or, more correctly, *phototropotaxis* (Fig. 3.4). Here, like the two reins of a horse, each receptor has a one-way turning action; pulled equally, the horse goes straight but if just one is pulled, the animal turns. In still other cases where orientation with form vision is clearly demonstrable so that some degree of orientation to the light is still possible after unilateral blinding, the taxis is now termed *telotaxis* or, more correctly, *phototelotaxis*. In addition to all this, movements toward a stimulus are generally prefaced by the word 'positive' whereas those oriented away from the stimulus are termed 'negative'.

Fig. 3.4 Learning to adjust. When a honey bee's left eye is blackened, initially it circles toward the intact eye, but after 20+ repeated trials the bee learns to compensate and again moves directly toward the light. Only a sample of trials is shown; the light was directly above the starting point in each case

At first, Loeb's theory had such appeal that taxes were considered to be forced movements over which the animal had little or no control. But gradually the accumulating data began to give biologists a new appreciation of the complexities of animal orientation, and Loeb's simple theory was discredited on several counts. For one, taxes are obviously as variable as the rest of behavior. A given taxis may depend on environment, context, experience, and/or the organism's internal state (nutritional, sexual, developmental, etc.). For example, although when preparing to pupate some caterpillars move downward, their first responses as emerging moths may be to climb upward as high as possible. In addition, a tactic response may change in type or sign at short notice. Thus, the blinded circling grayling butterfly will immediately follow in a straight line should a female grayling pass by.

Tactic responses are often far less simple than they appear, and tactic interactions are common. On the one side, taxes grade into kineses, from which they differ in being *directed* responses of the insect relative to the stimulus source. In another direction, they overlap with such longer-range phenomena as migration, discussed later in this chapter; at times the two are difficult to distinguish. Taxes also grade into still another quite sophisticated set of responses—the whole subject of positional orientations in general and transverse orientations in particular—that may or may not be called a subcategory of them.

Not surprisingly, other systems for classifying orientation behaviors have arisen. One considers that orientation basically involves the positioning of an organism in response to various stimulus fields such as heat, magnetism, light, gravity, pressure, and chemicals. Thus, one may consider chemical orientation, gravity orientation, astronomical orientation, orientation to polarized light, or any of a host of other orientation subdivisions. (For discussion of a variety of sense organs used in perception of chemical, visual, and mechanical stimuli, refer to Chapters 6, 7, and 8, respectively.) Another system is based on the observation that orientation occupies an interface between behavior and ecology. For any organism, the environment contains both positive and negative factors—not only resources needed for sustaining life or their absence but stress sources such as intense sunlight, which can be rapidly debilitating in the absence of compensating behaviors. A maximally fit organism is expected to behave in a manner that consistently works to minimize its body distance from resources (food, shelter, etc.) and maximize its distance from sources of stress. Viewing orientation from the perspective of its adaptive significance has led to a more complete classification of orientation than past attempts. However, for most scientists, taxes and kineses remain a major conceptual scheme for understanding and investigating the actions of insects and other organisms.

3.3.2 Posture and Position

Locusts in flight maintain an even body keel partly through visual reactions to inclination of the horizon. Flies mechanically sense angular acceleration and angular motion by rapid oscillations of their gyroscope-like halteres (modified knoblike

vestiges of their hind wings). Through continual compensatory reactions to a directed light source, a dragonfly banking its wings while flying a curve still keeps its head in a perfectly upright position.

All such examples involve positional orientation—compensatory maneuvers for body stabilization against displacement by wind, water, etc. The most widespread forms of positional orientation in insects are the *transverse orientations*, those in which the body is positioned at a fixed angle relative to the stimulus.

Among the best known transverse orientations are the *dorsal* and *ventral light reactions*. In this type of light orientation, well illustrated by dragonflies, moths, and butterflies, both the long and transverse axes of the body are kept perpendicular to a directed source of light at all times. (Thus, these light reactions contrast with phototaxis, where orientation is parallel to the light rays.) For example, the dragonfly shows a dorsal light response, mediated by the upper ommatidia of its eyes, that assures that the upper part of its head remains turned toward the light. If blinded in one eye and illuminated equally from all sides, the insect will roll continuously toward its seeing side. These reactions are particularly common among both flying and swimming insects (Fig. 3.5).

Light reactions are particularly important in relation to gravity perception, and can involve polarized light (see Chapter 7). Insects lack specialized gravity receptors that function like the inner ear in vertebrates or the statocysts found in various crustaceans. Instead, insects have relatively unspecialized sensory hairs (proprioceptors) that are usually clumped into plates in positions where they can measure the relationship between body parts differentially affected by gravity. For example,
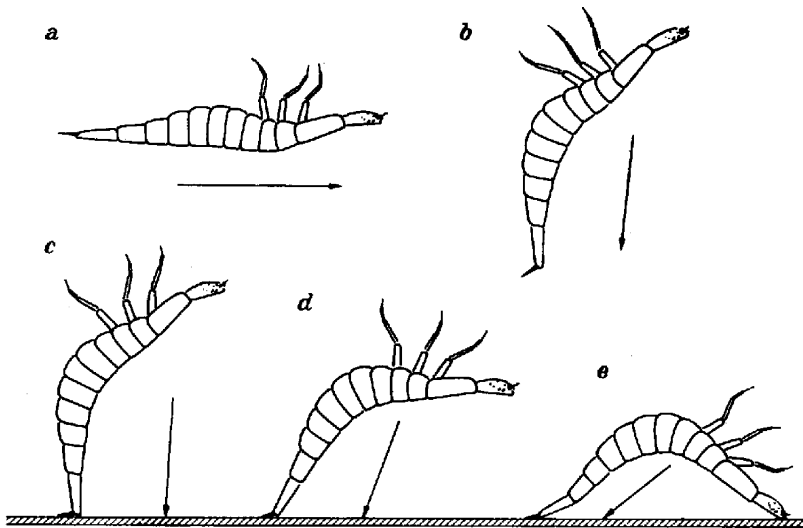

Fig. 3.5 Heeding unnatural cues. The larva of the diving beetle *Acilius* normally swims to the surface for air, cued by its dorsal light reaction; placed in an aquarium lit from below, it will descend with its back down, attempting to get air at the *bottom* as though it were the surface. *Arrows* indicate direction of swimming movement

in ants, gravity receptors are located at points of body articulation (neck, antennal joints, thorax and petiole, petiole and gaster, and joints between thorax and coxae); stimulation of any one point alone is enough for gravity orientation, although the different joints are not equally reliable.

Visual input sometimes serves as an effective substitute for gravitational forces. In fact, phototaxis and geotaxis, two of the best-studied taxes, have several aspects in common. For most insects the sun is upward, and positive phototaxes and negative geotaxes are the norm. One of the most remarkable features of honey bee communication is the two-way transfer from the angle between sun and food source to the angle between vertical and direction of the straight part of the waggle dance, then back again (see Chapter 8). For the dancing honey bee, positive phototaxis is coupled with negative geotaxis; if the food is in the same direction as the sun, the straight run of the waggle dance is directed upward, opposite the direction of gravity. When information about gravity is experimentally altered, the dance performed by the bee reflects the changed input (Fig. 3.6).

Probably the single most striking aspect of postural control among insects is the manner in which it depends upon input from a great number of sources acting in concert to the point of redundancy. For example, an ant can correctly orient to gravity using any one of its five proprioceptive joint systems alone if the others are fixed in position with wax.

3.3.3 Orientation to Radiant Energy

When an ant on its way back to the nest is placed in a dark box for a period of time, how will it orient when released? *Lasius niger* proceeds in the same course as before, relative to the sun, but because the sun has shifted position in the sky during the ant's incarceration, the released ant's orientation is incorrect in terms of its nest.

An orientation like this one—locomotion at a fixed angle relative to light rays— is termed a *light-compass reaction*. It has been demonstrated in a wide variety of insects, including caterpillars, bees, and certain beetles and bugs. Light reactions also have been well studied in the context of navigation during migration (see Section 3.5.3). The polarization of light rays often serves as an orienting cue. In one of the more unusual examples, certain African dung beetles apparently use polarized moonlight to whisk balls of dung in a straight line away from the dung pile.

Have you ever noticed that various crawling and flying insects nearly always travel in a straight line across roads at right angles to their direction? This appears to occur irrespective of compass directions or other external stimuli. One hypothesized explanation is that the insects orient by balancing their reception of a symmetrical source of shortwave (infrared) radiant energy. Although roads are relative newcomers to the environment of insects, the adaptive significance of such behavior may be a survival advantage conferred in crossing large bare spots of earth or bodies of water in the shortest possible time with minimal energy expenditure and exposure to the elements or predators.

A

WAGGLE DANCE PERFORMED
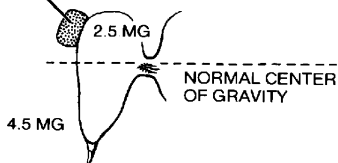BY UNALTERED WORKER
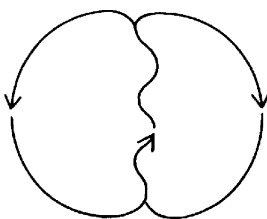
LATERAL VIEW OF BEE ON COMB
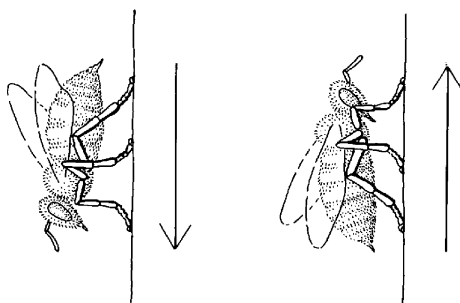
CHIN PULLED FORWARD
UPPER HAIRS ON SENSORY
ORGAN ARE DISTORTED

CHIN PULLED BACKWARD
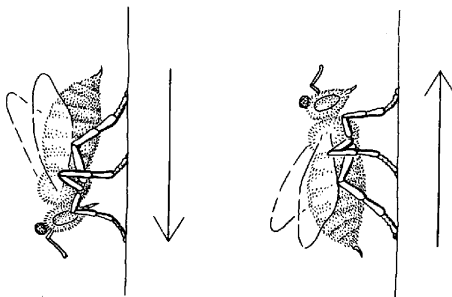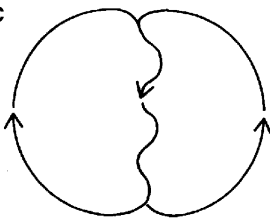LOWER HAIRS ARE DISTORTED

B   ADDED WEIGHT

2.5 MG

NORMAL CENTER
OF GRAVITY

4.5 MG

WAGGLE DANCE PERFORMED
BY *SAME* WORKER AFTER WEIGHT
ADDED TO UPPER PART OF HEAD

EFFECT OF ADDING WEIGHT TO HEAD

C

TOP OF HEAD PULLED FORWARD
LOWER HAIRS ARE DISTORTED
BEE SENSES ITSELF MOVING
UPWARD

TOP OF HEAD PULLED BACKWARD
UPPER HAIRS ARE DISTORTED
BEE SENSES ITSELF MOVING
DOWNWARD

Fig. 3.6 Turning gravity on its head. Proper orientation during the honey bee waggle dance depends on gravity perception. Because of the way it is connected at the neck, the lower half of a honey bee's head weighs almost twice as much as the upper half. (**A**) When an unaltered bee is dancing on the vertical surface of a comb inside the hive, gravity causes this lower portion to swing downward, tilting against the sensitive proprioceptive hairs on the neck, and stimulating nerves at their base. Severing these nerves causes total disorientation. (**B**) A tiny weight glued to the top of the bee's head alters its balance. (**C**) The proprioceptive information received by the bee's brain is reversed, resulting in a dance that is the opposite of normal

Insect reactions to infrared radiation are rarely reported, but they have been demonstrated across diverse taxonomic groups, and with further study they may prove to be more common than expected. Certain wasps that parasitize beetle larvae found in dead timber can detect their hosts by means of infrared receptors on their antennae. The beetle *Melanophila acuminata*, which lays its eggs in freshly killed conifer trees, uses a pair of specialized infrared sensory pits to sense forest fires, even over long distances (Fig. 3.7). Thermoreceptors located in the wings and antennae of species of darkly pigmented butterflies have been shown protect them from heat damage while sun basking. Research has shown that some blood-sucking bugs are able to perceive the radiant heat emitted by their warm-blooded prey, even at a distance, and others have the ability to locate blood vessels under their host's skin by sensing temperature gradients. Likewise, *Atta* leaf-cutter ants can learn the location
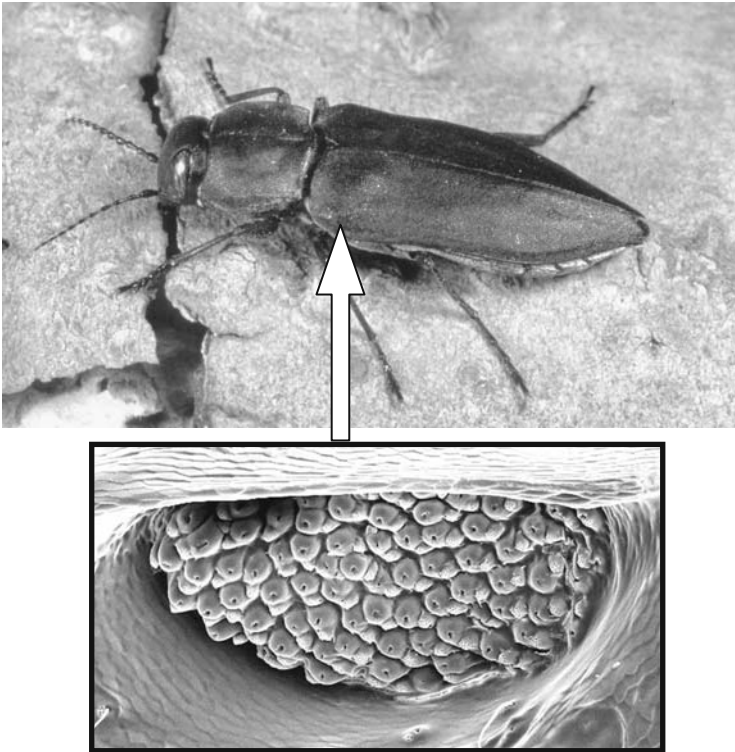

Fig. 3.7 Finding fires. The jewel beetle, *Melanophila acuminata*, possesses a pair of infrared detector organs in pits next to the junction of its middle legs and body. Each organ contains a cluster of about 70 individual dome-shaped sensilla (*below*, highly magnified), which are exposed during flight. Electrophysiological recordings reveal that these receptors respond to infrared radiation, characteristic of a forest fire, enabling the beetle to find smoldering wood in which to lay its eggs. Biomimetic engineers have developed an infrared sensor based on this organ. The beetle is about 10 mm long

of a food reward by using thermal information as an orientation cue; shielding their heads and thoraxes did not weaken this ability, suggesting that only the head and antennae are involved in assessing temperature.

3.3.4 Magnetic Field Orientation

Some Australian termite species build large 'magnetic' mounds oriented perfectly north–south (Fig. 3.8). Resting termites adopt positions aligned with the cardinal axes of a magnetic field. Weaver ants following a foraging trail in dim, diffuse light will reverse their heading when exposed to an artificially induced magnetic field with polarity opposite that of the geomagnetic field.

The ability to sense the earth's magnetic field has long been suspected for some insects, but until fairly recently, experimental evidence has been tenuous, indirect, and often confounded by other factors, particularly the skill with which insects use visual cues such as the sun, polarized light, the moon and landmarks for spatial orientation. In fact, when salient cues such as light are present, an insect's competence in magnetic field orientation may be entirely hidden.

With wax secreted from specialized abdominal glands, the honey bee builds parallel vertical combs that have hexagonal cells on both sides separated by a thin middle wall. The cells are tilted slightly upward at about 13° to the horizontal, an adaptation which serves to keep honey in. When a swarm of bees takes possession of a new home such as a hollow tree, they will reconstruct, literally overnight, a complete series of combs having the regular parallel construction. How do the bees 'decide' how their new combs will be oriented?

About fifty years ago, Martin Lindauer and colleagues decided to attack this question experimentally. They transferred bees from a conventional hive into a plain empty cardboard cylinder with the entrance hole centered in the bottom, and found that the bees produced new combs with an orientation that exactly corresponded

Fig. 3.8 Orienting magnetically. Mounds of the magnetic termite, *Amitermes meridionalis*, in a seasonally flooded field in northern Australia. The long axes of all these nests run north–south

to that of the combs in the original parent colony. Since all directional landmarks had been removed in the round cylinders, the researchers hypothesized that the bees were somehow able to orient to the earth's magnetic field. To test this hypothesis, they placed a powerful magnet outside the experimental nest cylinder so that the natural magnetic field was deflected. Invariably, the same bees that had previously reconstructed faithful new combs in experimental cylinders now built combs that differed from those in the previous nest by 40°—the exact angle of the artificial magnetic deflection.

The magnetic sense of insects and its adaptive importance have been most thoroughly investigated in social insects, especially ants, bees, and termites. There is now growing experimental evidence for magnetic field sensitivity in some Diptera, Coleoptera, and Lepidoptera as well. Contexts for its use have included home range orientation, homing, long-distance migration, and nest and body alignment. In experiments with artificially induced magnetic fields, the insects have always responded to changes in the magnetic field's declination, which implies sensing of magnetic polarity.

Although the sensory system that mediates magnetic signals has not yet been definitively identified, evidence favors the use of intracellular, submicroscopic magnetite particles that have been found in honey bees, monarch butterflies, and some ants. An alternative hypothesis draws on a system that has been demonstrated in some birds, in which certain photochemical reactions are magnetically sensitive; if such reactions are linked to light reception in the eye, then changing the wavelength of ambient visible light could alter the directional orientation to the geomagnetic field. Such effects have been obtained in male *Drosophila melanogaster*.

3.3.5 Orientation to the Evidence of Others' Presence

Both orientation and navigation depend upon perception of environmental features that exist quite independent of the insect itself. One another's actions and adjust their own movements accordingly. Gallery orientation by the larvae of long-horned wood-boring beetles (Cerambycidae) is an example. Larvae are responsive to sounds emanating from other larvae. Experimentally, they will change direction when exposed to simulated gnawing sounds originating ahead of themselves or slightly to one side. As a practical result, examination of gallery complexes reveals that the amount of turning and irregularity of burrows is directly proportional to the degree of infestation, and highly contorted burrows are a characteristic of heavy infestations.

In another example, groups of whirligig beetles (*Gyrinus*) spin crazily about over the surface of most freshwater ponds. As long as they all keep moving, they seem to avoid contact; but if one stops, another beetle may bump into it. Through impulses registered by receptors on a modified second antennal segment, each beetle is aware of the location and direction of the others by the vibrating waves they set up as they ripple over the surface.

3.4 Thermoregulation

The sphinx moth *Celerio lineata* stabilizes its thoracic temperature during flight over a range of ambient temperatures. A wide variety of insects, from butterflies and beetles to cicadas and arctic flies, bask in sunny spots. Male tettigoniid grasshoppers elevate their thoracic temperature prior to singing.

Most people think of insects as being purely 'cold-blooded' (ectothermic) creatures that passively reflect the temperatures that surround them. However, this view is overly simplistic. In most habitats, seasonal and diurnal temperature oscillations are considerable.

Heterothermic is probably a better term to describe the insect's life with fluctuating body temperatures. Because of their very high ratio of surface area to mass, small organisms readily lose and gain heat; insect body temperatures can change abruptly by 10°C (50°F) or more when direct sunlight is obscured by the shade of a passing cloud. This can be a serious matter—for insects, as for other animals, body temperature is closely attuned to activity and energy supplies, and thus affects all aspects of life from the rate at which food can be located and harvested to the ease with which predators can be avoided. Thus, one should perhaps not be surprised to find that insects have ways to control their body temperatures within a far narrower range than that of their surroundings.

Adaptations to temperature fluctuations can (and do) take many forms. Some adaptations are primarily behavioral, whereas others rely more heavily on physiology, but any attempt to strictly divide them soon shows the two systems to be intertwined.

3.4.1 Dormancy and Thermotolerance

Most insects face periods of adverse conditions, in which temperatures are outside their physiological limits and/or food is wanting. However, being heterothermic, they have an advantage that is denied to their homeothermic brethren. As long as the temperature does not reach lethal extremes, insects are capable of ceasing development and reproduction temporarily, then resuming these activities when conditions again become favorable. This ability is undoubtedly one more reason behind the enormous success of Class Insecta, because it allows them to exploit seasonal resources while successfully bridging the harsh periods between.

The external conditions that temperate-zone insects must tolerate differ markedly in summer and winter, so despite some similarities the insects' responses have come to be known under different names. We speak of winter hibernation (although it is not directly comparable to hibernation in mammals) and summer aestivation. Both actually jointly serve two different purposes. One is to promote survival by depressing metabolism and energy utilization during adverse times. The other is to synchronize periods of feeding, growth and reproductive activities with those times of the year when food is available and environmental conditions are suitable.

Short- and long-term shut-downs follow different strategies. To cope with relatively short periods of non-lethal but unfavorable circumstances, insects commonly go into a state of easily reversible, directly temperature-dependent developmental arrest called *quiescence*. Depending upon the temperature, the insect's growth slows, gonads mature more slowly, and feeding and other behaviors lose speed. Quiescence is a rapid response that can occur at any life history stage.

Severely hostile conditions that last several months, such as a temperate-zone winter or a hot, dry desert summer, require a different approach because an insect in the active state simply could not survive. A programmed developmental arrest called *diapause* occurs. Unlike quiescence, diapause happens only during a specific developmental stage, usually (but not always) before adulthood, and its timing depends on the insect species. For example, the European corn borer diapauses only as a fifth instar larva; the cecropia moth, only as a pupa; the Colorado potato beetle, only as an adult.

Diapause can be facultative, occurring in response to environmental cues, or it may be obligatory, occurring during each generation. A number of economically important species (such as the gypsy moth) have an obligatory diapause, but facultative diapause is far more common. For an insect with facultative diapause, a relevant environmental cue must be received during a sensitive period in development for diapause to occur; otherwise, development simply continues to proceed. This system can allow exquisite fine-tuning in the insect-plant arms race, as many home gardeners can attest. Throughout the warm months, these insects can produce multiple non-diapausing generations, building up high populations. Then, in late summer or autumn they produce a generation that goes into diapause and thus escapes the winter months when their plant hosts are unavailable.

While the diapause itself is a physiological event, behavior is intimately and intricately tied to it. Usually, the insect moves to a site (or in the case of cocoons, constructs one!) that offers additional protection from the full onslaught of inclement conditions. Specific behavioral changes are often associated with movement to overwintering sites called *hibernacula.* This may involve short- or long-range migration, a subject covered later in this chapter. It also includes local movements such as are displayed by certain caterpillars that have been feeding up in trees but now climb down and begin burrowing into the soil.

Feeding usually stops during diapause, so it no surprise to find that many species 'fatten up' in preparation. Of course, their exoskeleton does not allow this in a literal sense, but insects that are about to enter diapause often sequester twice as much lipid reserves as their counterparts that are not so programmed. Because metabolism slows with dropping temperatures, energy reserves may be less a problem, however, than water loss. With no access to free water and possession of a large surface-to-volume ratio, diapausing insects are particularly vulnerable to loss of water across their cuticle. Insects that diapause as adults (such as many beetles, bugs, and butterflies) often gather into large aggregations (see Plate 5). For those that are distasteful, this may increase their protection during this inactive life phase. Equally important but perhaps less immediately obvious, an aggregation provides a more stable microenvironment for its members and increases local humidity.

Whereas quiescence occurs in direct response to adversity, diapause begins *before* adverse conditions begin. How can this be? Most commonly, the answer seems to involve changes in two important aspects of the environment—photoperiod and temperature. Other seasonal changes may vary with latitude, altitude, and habitat, but changes in the length of day versus the length of night are a reliable signal that unsuitable conditions are coming. Photoperiod changes are so predictable that in most cases, the developmental period that is sensitive to photoperiod actually occurs far in advance of the actual diapause stage. This is critically important, because such early programming offers the insect the time it needs to prepare for diapause, both physiologically and behaviorally. It is important to remember, however, that photoperiod is not the only trigger for diapause. Daily fluctuations make temperature less reliable as a seasonal cue, but they do act on this basic signal, and can shift the photoperiod-based diapause response over a broad range or in extreme cases even eliminate it. Other environmental cues that have been identified include moisture conditions and changes in host plant quality.

The assumption has been that the programming of diapause has the same genetic basis as other biological rhythms (see Chapter 2). Thus, the basic requirements for a photosensitive diapause system would be a mechanism to distinguish long days from short days and a way to keep track of them—in other words, the insect must have a clock and a counter. A great deal of genetic research in the past few years has centered upon finding, identifying, and characterizing critical clock genes. Only the best known of these—the *period (per)* gene—has been studied in connection with diapause. For the drosophilid fruit flies that have been studied, the somewhat surprising findings indicated that null mutants that fail to express *per* enter diapause just as readily as the wild type.

Diapause does not end immediately after the diapause-inducing conditions disappear. Some time is required before neurohormonal systems return to configurations that support development and reproduction. Interestingly, overwintering insects appear to terminate diapause in early winter and after this point, their continued development is halted only by a direct effect of low temperature. In essence, their diapause turns into quiescence.

It is clear that like all organisms, insects of a given species are adapted to a set temperature range within which they can effectively reproduce and develop, and outside this range, they clearly do so with varying levels of success. What about those insects that do not diapause? Through what behavioral and physiological responses do they counter the effects of high- and low-temperature stress?

Survival at extreme temperatures—called *thermotolerance*—can be increased several ways. One way is through genetic adaptation; differences in thermotolerance can be detected both in diverse geographic populations and in laboratory lines selected for this trait. Another way is through long-term acclimation; rearing individuals for long durations at high temperatures can result in striking increases in thermotolerance. Acclimation is a complex adjustment that involves major body changes; in some insects it actually includes the synthesis of antifreeze proteins. A great many behavioral changes support these physiological alterations. These can

range from forming thicker cocoons to voiding the gut to remove food particles that would be powerful ice nucleators.

A third way to increase thermotolerance is through a response called *rapid heat hardening*, in which brief exposure to an intermediately high temperature provides protection from injury at a more severe temperature. For example, *Sarcophaga* flesh flies live only a brief time at 45°C (113°F) when moved there directly from a 25°C (77°F) chamber. However, if they are first exposed to 40°C (104°F) for two hours, they survive much longer at 45°C (113°F). This protection develops within minutes, reaches a maximum within a few hours, and then decays rather slowly over several days. Does diapause represent a shutdown in gene expression or does it represent the expression of a unique set of genes? Perhaps both. Studying *Sarcophaga* flesh flies, David Denlinger has shown that far fewer proteins are synthesized in the flies' brains during diapause. However, in addition, their brains synthesize a set of proteins that are not observed in brains of non-diapausing flies, and various classes of diapauseupregulated genes can be distinguished based on their expression patterns. Other research suggests that insects respond to heat stress by suppressing the normal pattern of protein synthesis and concurrently synthesizing several new proteins called heat-shock proteins. Several types of heat-shock proteins have been found in organisms ranging from bacteria to plants to insects, and behavioral geneticists suspect their upregulation may be common to many different types of dormancies. The most highly expressed heat-shock proteins are highly conserved; the gene that encodes one group called Hsp70 is over 50% identical in bacteria and *Drosophila melanogaster*.

3.4.2 Regulation of Heat Gain

Certain *Pheidole* ants forage above ground all day during cool, cloudy periods but when the weather is hot and sunny they restrict their foraging to the period from late evening to early morning. The adult form of a flightless midge called *Diamesa* walks on glacier ice even when its body temperature is chilled to –16°C (3.2°F). It is so sensitive to heat that if you were to pick one up in your hand, the warmth of your skin would kill it.

Cryptic insects that rest by day on a matching background, predators that use a lie-in-wait strategy, and many other arthropods that are exposed to sunshine all have at least a potential problem with heat gain. Not surprisingly, various behavioral adaptations have evolved that involve postural adjustments to minimize the body surface area exposed to the heat source or that lead to avoidance of solar radiation totally during certain periods. Structural features also help. For example, the long legs of many ants and beetles living on sand in direct sunlight lift their bodies above the substrate, while light body pigmentation reduces heat input from above.

Especially when the weather is warm, flying insects face an additional problem—dissipating their own body heat. Small insects have much lower body temperatures in flight than large insects do. However, this is not because they produce less heat—instead, they actually produce more. Rather, it is because smaller insects have

more surface area relative to their mass, so that internally generated heat is lost more rapidly by convection. Insect flight is actually one of the most energetically demanding activities known. Most insects produce more heat per unit muscle mass when they fly than almost any organism on earth. Almost 94% of the energy expended by their contracting flight muscles is degraded to heat, while only about 6% appears as mechanical force on the wings.

Most insects apparently do not cool themselves as we do with active evaporative mechanisms, but some of the exceptions are striking. The tsetse fly, *Glossina morsitans*, is able to feed while standing on the hot hide of a mammal's back under the equatorial sun; to lower its body temperature, it opens its spiracles, allowing the water drawn from its blood meal to evaporate. *Diceroprocta* cicadas of the Sonoran desert overheat when they sing in hot weather; to cool down, they actually sweat through large pores on their back, using liquid they suck from deep-rooted shrubs.

Social insects exhibit a variety of architectural and behavioral devices that maintain nest temperature and humidity within carefully controlled tolerance ranges, irrespective of season or outside temperature (see Chapter 10). While such insects are individually heterothermic, socially they are nearly as homeothermic as birds and mammals. Honey bee workers maintain the hive interior at temperatures between 34.5 and 35.5°C (94–96°F) by fanning with their wings to promote air circulation and cooling by water evaporation. (In winter, the bees cluster loosely at warmer temperatures and very tightly during extreme cold, keeping that same range.)

3.4.3 Heat Production

Male *Neoconocephalus* katydids raise their flight-muscle temperatures above 30°C (86°F) before starting their ear-shattering mating concerts. Founding queens of *Vespula* wasp colonies incubate their brood clump by perching upon it and pressing their abdomen over it much as a hen incubates her eggs. Prior to flight, nearly all but the smallest temperature zone butterflies bask in various distinct postures that simultaneously maximize solar input and minimize convective heat loss.

If avoiding too much heat is one important biological task, its flip side is staying warm enough to function. *Endothermy*—the ability to increase body temperature beyond that of the environment—has been long known in insects, but scientists once thought such regulation was accomplished solely by behavioral means such as the basking frequently observed in butterflies. An increasing number of studies now show that some insects use physiological means as well. On the basis of body weight, most flying insects have higher rates of metabolism and hence of heat production than other animals.

In insects, essentially all endothermic increases of body temperature have the same causal mechanism—heat produced by the active flight muscles. Because these are the most metabolically active tissues known, endothermy in flight is largely an obligatory phenomenon. In addition, many species use high-energy fuels and intense metabolic rates to produce body heat at rates sufficient to increase their body temperature beyond that of their environment.

High muscle temperature is, however, not just a consequence of muscle activity. In many situations, especially flight, it is also a prerequisite. Until the temperature of the muscles is sufficiently high, there is little overlap in the contractions of the antagonistic muscles, the wing-beat frequency is very low, and the insect remains grounded. Different relative wing sizes and power requirements determine the muscle temperature and wing-beat frequency necessary for a given insect to become airborne; this varies with body size, between different muscles used for different activities, and between different species.

Large wings are one way around the problem—they allow an insect to fly with a low wing-beat frequency. As a result, some butterflies are able to initiate flight without prior endothermic warm-up and to continue flight by gliding; this also reduces the energy expenditure of locomotion. Another response is to evolve a dense pile coat; this can cut the rate of convective heat loss from the insect's body by half. Bumblebees (*Bombus*) provide an elegant example; their combination of high metabolic rate, relatively large body size, and good insulation helps them not only to elevate thoracic temperatures passively during free flight but also to maintain a sufficiently high thoracic temperature to fly at very low ambient temperatures. Due to their rapid metabolism, their body temperature while flying usually exceeds ambient temperatures by 5–10°C (9–18°F) and sometimes b as much as 20–30°C (36–54°F). However, thermoregulation is still a costly behavior, especially when an insect is not physically active. When temperatures are very low, it takes nearly as much energy for a stationary bumblebee to maintain its body heat as it does to fly. Thus, it is all the more impressive that queen bumblebees use thermoregulation behaviors to raise the temperature of their brood.

The requirement for a high thoracic temperature to *start* flight poses a real behavioral problem. When an insect comes to rest in the shade, its body temperature rapidly becomes practically the same as the ambient temperature. Small flies such as midges and fruit flies have rapid heat loss and little buildup of body heat during flight; their wing-beat frequency and flight speed varies nearly directly with ambient thermal conditions. Some of the larger insects, such as bumblebees and some moths, however, must warm their flight muscles to about 40°C (104°F) before they can attain sufficient wing-beat frequency and lift to support themselves in free flight. Without some means of increasing muscle temperature, the insect could remain permanently grounded.

Shivering is a widespread mechanism for increasing thoracic temperatures before flight. It involves many patterns of flight muscle activation and can work flight muscles harder than flight itself does, but it is well suited for variable rates of heat production because it can occur at a wide range of activation frequencies. Among many Lepidoptera, the rates at which wings vibrate during such shivering have been shown to be directly correlated with muscle temperature. Interestingly, it took scientists a long time to recognize that insects shiver, because it is almost never externally visible even if one looks very closely.

The evolution of shivering is clearly related to the evolution of flight, but it is unrelated to an insect's place on the phylogenetic tree. A physiological warm-up is found in all large, active flyers among the dragonflies, moths and butterflies,

katydids, cicadas, flies, beetles, and wasps and bees. It is missing in small (and therefore non-endothermic) members of the same groups.

In addition, an insect may regulate its body temperature through discontinuous activities such as intermittent flight, intermittent shivering, or some combination of the two. However, some insects are behaviorally better suited to make use of this option than others. For example, a hovering sphinx moth or dragonfly in continuous flight is in a less advantageous position in this regard than is a bee that lands on flowers at frequent intervals while foraging.

3.5 Migration

Foraging army ants, *Eciton hamatum* (see Chapter 10) commonly move out of the nest in columns along branching trails to seize and carry back to the nest all small prey in their way. However, as new brood matures within the colony, instead of simply returning to the nest, workers reverse to lead a mass exodus that carries the whole colony away along one of the day's trails. During their march the ants neither react to prey nor branch off. Meanwhile, in California large numbers of convergent lady beetles, *Hippodamia convergens*, spend the winter at high altitudes in the Sierra Nevada mountains, then move down to agricultural areas in the Central Valley in March to lay their eggs; beginning in June, their offspring fly back to intermediate altitudes, gather into aggregations, then move back to higher altitudes to overwinter. On a much smaller scale, two species of pierid butterflies regularly maintain a directional flight across Gatun Lake in the Panama Canal.

What triggers the mass exodus of army ants? How are the movements of the lady bugs coordinated and maintained? Why do the butterflies go back and forth? Up to this point, we have been viewing insect spatial adjustment primarily as a phenomenon involving a single individual within its immediate environment. Now it is time to step back and view insect movement on a larger scale, considering these behaviors in terms of the population or species.

A fundamental concern for most insects is finding the optimal habitat in which to live and reproduce. For dispersing individuals, the problems are particularly complex and acute. At what point should an individual stop expending energy on the search and settle for whatever situation is available? When should selection favor the evolution of ways for individuals to return to specific sites after displacement from them? How should areas of fluctuating or disparate resources be best exploited? When times are hard, does it make more sense to move, or to just hunker down and ride it out? Such theoretical questions have been receiving much attention in recent years, and some interesting answers are beginning to appear.

In general, insect movements are of two main kinds. The first kind, concerned with resources and home ranges, has the ecological outcome of keeping an insect in the habitat where it can obtain the resources it needs for given stages of its life cycle. The second kind is quite different. *Migration*, one of the most important forms of insect dispersal, has been succinctly defined as 'adaptive traveling.' It involves

leaving the current home range and habitat. (As a fine point of terminology, although migration acts as an active mass movement functioning to displace populations, those who study it usually distinguish between migration as an individual behavior and dispersal and aggregation as population processes; see Section 3.5.3. However, in popular usage, the distinctions are drawn less finely.)

Behaviorally, migration is characterized by persistent, enhanced locomotion in a straightened-out manner, and migrating individuals do not typically respond to stimuli for 'vegetative functions' such as feeding, reproduction, etc. For example, the flight of certain scolytid bark beetles cannot be arrested by their host plant's odor until after they have been flying for many minutes. After long-distance flight, the thresholds for vegetative activities are lowered, and further migration is inhibited.

Insects move around quite a bit, so it is important to distinguish migration from those local movements of varying length and orientation that are concerned with food and mate finding, escape from potential enemies, location of suitable oviposition sites, territorial defense, and other such activities. Such 'appetitive' behaviors may lead to some dispersal, but often no effective displacement occurs at all, despite a good deal of activity. Migration, in contrast, involves a phase in adult life during which directed movement (usually flight activity) dominates over all other forms of behavior. In many insects, such activity is restricted to a short period, after which only appetitive movements occur; in some species, the flight muscles may break down after migration so that no further flight is even possible.

Why do insects migrate? Such a question is more properly two questions. First, the proximate one: what triggers the migratory 'urge' and how is it maintained? Second, the ultimate one: what ecological and/or evolutionary conditions might favor development of a migratory mode of life?

Migration clearly involves more than simply responding to the onset of adverse conditions by escaping to a new habitat. Endocrine changes occur in correlation with particular environmental effects (crowding, food deficiency, short days, etc.), and in turn cause physiological and developmental changes. The insect's behavior, ecology, and genetics all come into play.

3.5.1 Seasonal Migration

Large concentrations of bean aphids appear in central France in early to midsummer every year; over succeeding generations they spread westward and northward, so that by late summer bean aphids have reached high densities as far north and west as Scotland. Bugs in the genus *Dysdercus* are seed predators on many subtropical and tropical plants, including commercial cotton. At the beginning of the tropical dry season, as fruiting begins, the bugs migrate into the plants. As the females begin to feed, they histolyze their wing muscles, develop large numbers of eggs, and reproduce explosively. Then as the dry season progresses and fruiting ends, the absence of moisture and food causes the new generation of bugs to retain their wing muscles, depart and go into diapause until their next dry-season migration begins.

Many examples of insect migration have been described around the world. One set involves the many insects that leave the breeding site, oviposit elsewhere, and die, all in a single season. A second group includes short-lived adults that emigrate and return. For example, many dragonflies depart from ponds to terrestrial feeding sites some distance from water; after the eggs mature, females return to the vicinity of their original breeding site and oviposit. Another category includes longer-lived adults that hibernate or aestivate away from the original breeding site, then return to it the following season.

How can one tell if a flight is truly migratory? The definition of migration should offer an objective and experimental test: during the flight, the insect should not be responsive to stimuli triggering vegetative behavior. The test has seldom been applied, but where it has, there does appear to be a reciprocal interaction between migratory flight and vegetative activities. Stimuli that evoke flight inhibit settling, and stimuli that evoke settling inhibit flight. One example where such migratory–vegetative interaction has been approached experimentally is that of the milkweed bug, *Oncopeltus* (Case Study 3.1).

Case Study 3.1: Migration in the Milkweed Bug, *Oncopeltus*

How can you tell if a flight is truly migratory? The definition of migration should offer an objective and experimental test: during the flight the insect should not be responsive to stimuli triggering vegetative behavior.

The milkweed bug (see Plate 11) is a wide-ranging species occurring from Canada to Central America. It arrives in the northern reaches of its range between spring and early summer. Here, females settle on patches of milkweed, mate, and lays their eggs close to the developing seedpods. The young bugs grow quickly and after a few weeks, they become breeding adults. Throughout the summer the population increases rapidly, but with the shortening days of early autumn, numbers decline as maturing adults begin to leave. Flying south on the prevailing winds, these adults are able to avoid the oncoming winter, while those unable to complete an adult molt before the first severe frost are killed.

Are these bugs truly migrants? In the early 1970s, Hugh Dingle and his colleagues sought to answer this question through detailed field and laboratory investigations. Rearing studies soon confirmed the first criterion—a separation of flight and vegetative activities. Flight activity peaked eight to ten days after the adult molt, whereas oviposition began only after 13–15 days. Flights were also well separated from feeding. A few hours after the adult molts, females entered into a high rate of feeding that, until day seven, lacked periodicity. By day eight, however, a fully developed circadian rhythm was evident. Thereafter, the peak feeding activity for females occurred at the end of the day and proceeded simultaneously with mating. Interestingly, for males the

feeding rate fell markedly after day six to persist at a very low rate for the remainder of life.

Temperature appeared to have a very direct effect upon migration. Raising the temperature from 23° to 27°C, a warmth about optimal for population growth, Dingle found that a lower proportion of the population now exhibited tethered flights of 30 minutes or longer (his operational criterion for migration). This suggested that once the bugs reached a thermally favorable environment, they would tend to settle there.

Laboratory studies clearly indicated that peak flight preceded reproduction. Would prolonging the pre-reproductive period also prolong migration? By altering day length in the laboratory, Dingle knew that he could delay oviposition from 15 to 45 days after the adult molt. Raising bugs under both regimes, he tested comparable groups of females for duration of tethered flight 25 days after adult molt. The early-ovipositing females generally flew for only a few minutes or less. The delayed females, which showed no signs yet of reproductive development, performed like typical migrants. Under field conditions, Dingle reasoned, this phenomenon would have important consequences. One would be that in the autumn females would be capable of migrating for much longer periods, thus improving their chances for escaping the oncoming winter.

In what other ways might a short photoperiod affect migratory behavior? In tethered flights, Dingle compared sets of short-day and long-day bugs of both sexes repeatedly between 8 and 30 days after adult molt. Invariably, a greater proportion of the short-day bugs flew for long periods (at least 30 minutes, usually 2–3 hours). Significantly, the results held true for both sexes. Evidently, in addition to its indirect effect via ovarian development, photoperiod was having a direct effect upon migration as well.

Environmental factors obviously had great importance as determinants of migratory behavior. What about hereditary influence? Under strong selection, Dingle found that he could increase the proportion of migrants of a population of milkweed bugs from 25% to over 60% in one generation. Clearly, migratory capability in *Oncopeltus* could be altered rapidly.

Not just in milkweed bugs, but in a great many insects, migration is associated with an additional photoperiodic response—diapause, discussed earlier in this chapter. Short days in autumn cue an inactivation of the reproductive system and thus permit long flight using energy that otherwise would be channeled to reproduction. Perhaps the best known of these insects is another milkweed-feeder, the monarch butterfly, *Danaus plexippus* (see Plate 3); these long-distance fliers seek out and congregate in sheltered cool locations. Through this behavioral thermoregulation, they conserve the energy reserves they need to tide themselves over the winter diapause portion of their migratory cycles.

Earlier biologists thought migration was probably just a way to escape from one habitat to another more suitable one. On first examination such a simple answer seemed sufficient. Faced with a temporarily unfavorable period or untenable habitat, an insect species could adopt one of two evolutionary strategies. It could migrate first or it could go into immediate diapause where it was already living. If the change in habitat were reversible, as with seasonal changes, diapause in place would be favored. When habitat changes were irregular, migration would have a clear advantage over diapause. A recrystallization of ideas drawing from the fields of physiology, behavior, and population ecology now suggests that migration is not only a means of escape from unfavorable environments, but a positive act of dispersal over all available habitats. Under such a view, insect migrants are more accurately to be viewed as colonizers than as refugees, and migration as an evolved adaptation, not a reaction to current adversity.

Entomologists and government agencies have paid particular attention to some major agricultural pests—particularly several noctuid moth species and various leafhoppers and plant-hoppers—that make round-trip seasonal migrations spanning several generations. Many of these seasonal migrants may have originally found migration adaptive for locating ephemeral habitats induced by rainfall in more tropical parts of their range, but with extensive acreage now under agricultural cultivation, they build up enormous populations that spread far beyond the insects' ancestral range over the temperate zone spring and summer. Late-season migrants are trapped by cold weather and die, because none of these species can diapause, either as adults or juveniles. How can this be adaptive? At first, some researchers speculated that the scenario was a 'Pied Piper' phenomenon, but others argued that such massive losses would result in severe selection against migration. Current evidence suggests the phenomenon of late-season deaths may be overstated. Though many of these migrants do die, weather systems safely bear many other individuals southward to winter breeding areas.

Early studies on insect migration understandably concentrated on the long-distance flight of spectacular insects such as milkweed bugs and butterflies. However, it has become increasingly obvious that migration is a far more widespread phenomenon than previously suspected, including many small species whose movements, relatively speaking, are neither far nor spectacular. In all instances, migration is a distinct behavioral and physiological syndrome closely intertwined with reproductive timing and strategy.

First, migratory flights are limited to a specific stage in the life history, after the cuticle has hardened but before reproduction begins. Second, whether or not the males are in accompaniment, migration always involves the female sex, and migrant females are generally sexually immature and thus have a high reproductive value or expected contribution to population growth (a high r, see Chapter 9). Most migration correlates strongly with age (Fig. 3.9). That is, it occurs prior to egg development, and while the development of the flight system is maximized, that of the reproductive system is minimized, a phenomenon that results in migration occurring chiefly in young female adults. In the 1960s, C. G. Johnson, a leader in the development of migration theory, termed this the *oogenesis-flight syndrome*. Third, migratory flight
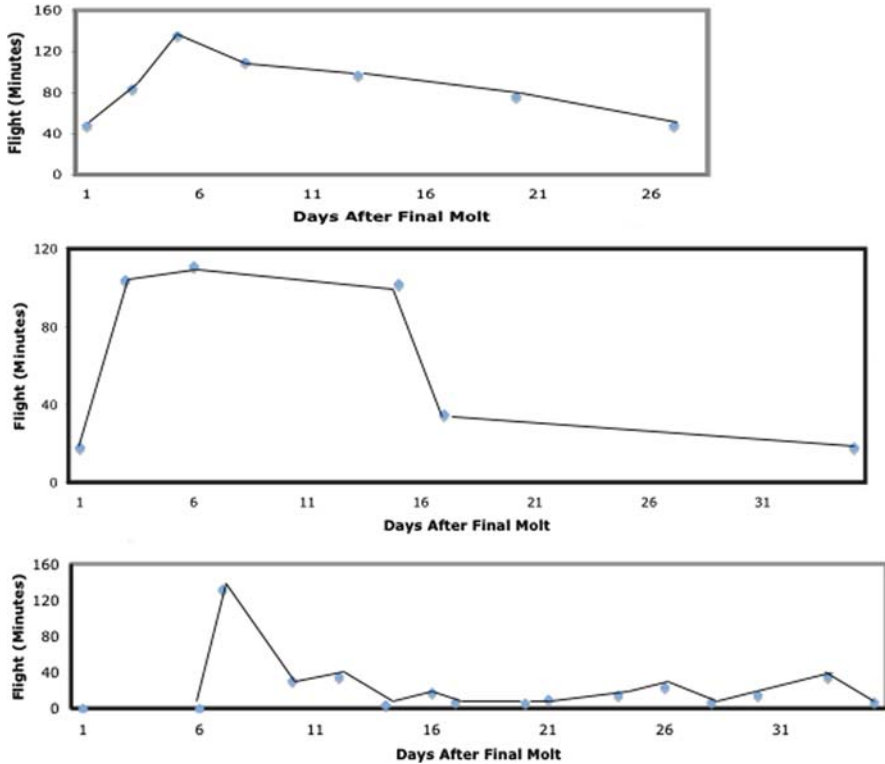
Fig. 3.9 **Making trade-offs**. Duration of tethered flight as a function of age in three insects: (*top*) the frit fly, *Oscinella frit*, (*middle*) the fruit fly, *Drosophila funebris*, and (*bottom*) the milkweed bug, *Oncopeltus fasciatus*. The decline in flight occurs concurrently with an increase in reproduction (the oogenesis-flight syndrome). Similar effects have been demonstrated in a wide range of insects, including bugs, flies, mosquitoes, aphids, moths, grasshoppers, and beetles

is segregated by time of day (or night) from various non-migratory activities. As a result, circadian cycles, migration, and ontogeny interact. The conditions that produce delayed reproduction and adult diapause, such as short days, may also induce migration. Migrants also are often similar to diapausing adults in having immature ovaries and hypertrophied fat bodies. In fact, in many species, migratory flight appears to actually accelerate subsequent reproductive activity.

As with everything, additional studies of the oogenesis-flight syndrome have shown the situation to be more complex than initially envisioned. Migration and reproduction are not totally mutually exclusive, and many permutations of the syndrome have come to light. However, the oogenesis-flight relationship has guided a whole field of studies into the physiological activity that underlies these behaviors, a syndrome that involves hormones, metabolic pathways, and the actions of the nervous system.

3.5.2 Migration Under Ephemeral Conditions

In the arid northern subtropics and tropics of Australia, *Heliothis* moths breed fol-
lowing rainfall; if their productivity is high on the new vegetation, they soon become
large populations that move southward on the winds to agricultural areas.

Environments change, whether viewed over time or over space. Ecological suc-
cession occurs, local climate varies, and the surroundings that once were favorable
are suddenly no longer so. The impermanence of a habitat may result also from
seasonal or irregular climatic changes or simply from the ephemeral nature of the
habitat (such as flowers, fungi, carrion, etc.). In other cases, the insect's require-
ments may change at different life stages, so different habitats would be needed;
acridid grasshoppers, for example, have different requirements for feeding and for
oviposition.

There is clearly a strong relationship between ephemeral habitats and an
increased incidence of migration, and evolutionary biologists have studied this rela-
tionship extensively from many different theoretical and mathematical perspectives.
The central thesis of their models is simply that migration evolves to keep pace
with changing habitat structure. Models based on statistical probabilities have been
expanded in various ways to incorporate factors such as the costs or risks of migra-
tion, carrying capacities, and population growth rates. In general, one can say that
developing such theories has proven easier than gathering extensive empirical data
to test them.

Seasonality places such a major imprint upon the environment that it is no sur-
prise to find examples of insect migration that are strongly tied to seasonal cues.
Likewise, habitats such as plant communities in early successional stages and small
or shallow bodies of water are relatively temporary, but their changes can be antici-
pated with some reliability. In other cases, environmental change is less predictable,
requiring more flexibility in the physiology and behavior of organisms that would
exploit it. For example, temperate and tropical forests are a very 'patchy' and
ephemeral environment for those bark beetles and weevils that require trees of a
particular species and in just the right condition.

Patches of new plant growth in the world's arid regions are even more ephemeral
and unpredictable. Although the rainfall upon which they depend is seasonally
correlated, it is also scarce and unpredictable both in its timing and in its geogra-
phy. As theory would predict, migration is common among desert and dry-country
organisms. However, these migratory behaviors look quite different from seasonal
movements of insects such as the milkweed beetle and the monarch butterfly.
Particularly in tropical and subtropical arid regions, it is common to find cases of
migration that appear nomadic and opportunistic. Sometimes, at first glance it is not
even clear whether such movements represent true migration or simply extended
foraging in search of scattered food. One of the paradoxes of migration, however,
is that for an organism to respond appropriately to environmental change, in most
cases it must alter its physiology. This cannot be done instantaneously, so it would
be highly advantageous to have some way to anticipate changes that will occur.
When the environment is unpredictable, how can this be done?

The complexities of migratory behavior are well illustrated by the group of grasshoppers collectively known as locusts. Five species cause the most crop damage, and these have been the focus of most studies of locust biology. To varying degrees, all show an extreme response to increased population densities called *gregarization*. Each species occurs in two different races (phases) that are biologically and morphologically distinct (see Plate 4). The sedentary or solitary phase, colored inconspicuously green, gray, or reddish, is choosy about its food. The swarm-forming migratory phase, marked with contrasting colors and longer wings, devours any and all plants. In the desert locust *Schistocerca gregaria*, the differences in the two forms are so great that they were considered separate species until 1921 when Boris Uvarov, a major pioneer in acridoid biology, demonstrated that the two forms were a single species and developed a theory that explained the phenomenon, now referred to as *phase polyphenism*. The term means a change in morphology and behavior caused by density effects. (Whereas a 'polymorphism' involves genetic differences, a 'polyphenism' involves differences that are environmental in origin.)

The most conspicuous differences between *Schistocerca* locust phases occur in their behavior. Which phase is present in the locust population depends upon how crowded they, and their parents, have been. Previously uncrowded locusts live quietly, tend to repel one another and tend to remain upon clumps of vegetation. Hoppers that have been continuously crowded, however, are very active, strongly attract one another, and dodge clumps of vegetation, being arrested only briefly even by food plants. In its early stages, either phase can be formed from the other without intervening generations. For example, insects of the solitary phase may transform into migratory individuals if placed with swarm-forming companions.

Differences begin to show up as early as the second instar, when the nymphs begin to exhibit mutual attraction and form up into bands that can contain many thousands to millions of individuals. Then the still wingless nymphs begin to march; the mass pattering of their feet is clearly audible as they travel, often downwind but also in response to the direction of the sun. Before eclosing to adulthood, the band may move tens of kilometers, stopping only at intervals when hunger demands.

With the winged adult swarms, locust migratory behavior reaches its peak. At first sight, a migratory swarm appears to be a vast army flying single-mindedly toward a fixed goal. However, photographic analysis has shown that in the swarm as a whole the locusts are randomly oriented toward one another. Such randomness, in combination with disruption from air turbulence, would be expected to lead to dispersal of the swarm, were it not for a striking phenomenon. All the locusts at the edges of the swarm orient toward the body of the swarm, and those at the back and sides actively rejoin the swarm, probably responding to both visual, auditory, and chemical cues.

Feeding by large swarms can strip vegetation down to bare earth, and during years when major outbreaks occur, an area of approximately 20% of the earth's land surface can be affected. Because of this extreme economic importance, the relationship between meterologic factors and locust swarming has been the object of a great deal of research. About 60 years ago, R.C. Rainey developed a pioneering

model that related locust outbreaks and weather patterns (particularly those around the Intertropical Convergence Zone) for the desert locust, *Schistocerca gregaria.* During the locust plague years of 1954–1955, Rainey's theories were put to the test in a large international effort that monitored locust populations on the ground and followed swarms by aircraft over much of the northern two-thirds of the African continent. Results appeared to confirm the theory's predictions, and for decades this theory was established dogma.

Later reexamination of the data, combined with studies of other species, considerably complicated the picture and cast some doubt whether the Inter-Tropical Convergence Zone was involved at all. Rainey's theory relied heavily on observations of gregarious swarms carried passively along during the day by winds at different heights. A major discovery, confirmed by radar studies, was that solitary locusts fly about at night, often for longer distances than gregarious locusts do. Radar also showed that even when the wind was blowing strongly enough to carry them along, these night-fliers exhibited considerable mutual alignment and collective orientation. In other words, they were navigating (see below).

These discoveries changed the entire scientific view of locust migration. It now appears that most large-scale migration takes place by single individuals migrating at night, not by swarms moving across the countryside by day. In all locusts and grasshoppers that have been studied, swarms have been found to function more as *extended foraging groups* than as migratory groups.. The rolling swarm so visible to an outside observer actually occurs from the movement of feeding individuals. At the leading edge of the swarm, locusts settle and feed. This reduces the vegetation available to those locusts that are behind them, so these latter individuals pass over this area, settle into a new leading edge, and feed. Most recently, it also has been found that some locust species help this movement along by nipping at the abdomens of the locusts in front of them, and escaping from others approaching their own rear end.

Although the details of the swarming-foraging and individually migratory aspects of locust life cycles will continue to be debated, most scientists agree that the system provides a very effective way to exploit ephemeral habitats in arid to semi-arid regions. Not surprisingly, a number of other insects take the same approach to the problem, in the process making themselves major agricultural pests in drier regions around the world. This includes several moths in the family Noctuidae, particularly in the genera *Heliothis*, *Helicoverpa*, and *Spodoptera*. Interestingly, large-scale mark-recapture, radar tracking, and detailed laboratory studies have confirmed that *Spodoptera* armyworms do disperse in a pattern that is closely associated with rainfall occurring with the passage of the Inter-Tropical Convergence Zone.

3.5.3 Dispersal and Navigation

Scelionid wasps ride upon the backs of female grasshoppers; ultimately, those tiny parasites will oviposit upon the grasshopper's eggs. Tropical leafcutter ants are the

original suburban commuters; day after day they travel hundreds of meters back and forth along trails that extend both horizontally along the forest floor and vertically into the canopy. Every spring, vast numbers of insects are transported by winds up through the Mississippi Valley into upper midwestern agricultural regions of the United States and Canada.

Dispersal—movement away from one's place of birth or from centers of population density—is part of the life cycle of almost every living thing, and unsurprisingly it occurs by a wide variety of methods. Dispersal may be random or directed, passive or active. Young individuals quite commonly leave the area in which they were born. Usually such dispersal occurs either passively or under the juvenile's own volition, but in some cases dispersal may be encouraged by the indifferent or even hostile behavior of their parents or nest mates. As a result, through time all populations have a tendency to spread out spatially. Many different mechanisms may be involved, from relatively simple responses to gradients of certain environmental factors, to various active or passive dispersal mechanisms associated with the search for a mate or food.

The distinction between passive and active dispersal is made mainly for convenience; in reality a continuum often exists between them. For example, a *Pemphigus* aphid, which lives on the roots of the sea aster growing in salt marshes, is photonegative for most of its life. However, first instar nymphs are photopositive, climbing up the sea asters until they set themselves adrift on the rising tide. Sea breezes send them scudding across open water to be deposited at low tide on another mud bank where they seek out and colonize new plants. Upon arrival, as a result of their waterborne dispersal experiences they reverse their reaction to light and become photonegative. In another example, female gypsy moths are unable to fly, so natural dispersal of this well-known pest occurs primarily through young larvae being blown on their silken threads by wind. (A similar mechanism, *ballooning*, is employed by many newly hatched spiderlings.) However, gypsy moth larvae vary in their dispersal propensity, and the behavior of first instar larvae depends on several variables such larval density, food availability, and their mother's nutritional status.

Many flightless insects are transported by others, a phenomenon known as *phoresy*. Human bot flies will attach their eggs to the legs and body of mosquitoes, in this way transporting them to a human host for hatching and larval development. Some Trichoptera larvae undergo their development within gelatinous capsules upon the bodies of chironomid midges. Tiny wingless Mallophaga attach themselves to the bodies of the hippoboscid flies which parasitize their bird hosts, in this manner being carried from one host to another (Fig. 3.10). A great variety of mites ride upon beetles, ants, and other insects; the insects are probably not injured unless the numbers of mites become excessive. In several groups of wasps, a unique type of phoretic dispersal has independently evolved on more than one occasion. All cases involve parasitic females that have become so highly modified for tunneling into the soil or food that they have permanently lost their wings. During copulation the genitalia in these species lock together, so that the males carry the smaller females about, suspended in this way, for considerable periods of time. This phenomenon,
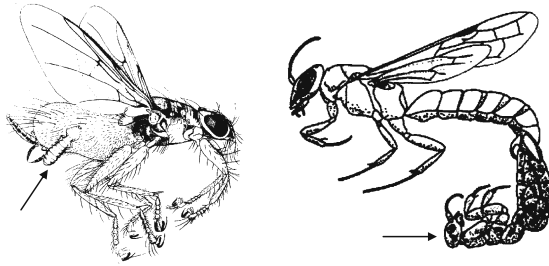
Fig. 3.10 Hitching a ride. Two examples of insect phoresy. (*left*) Feather lice firmly attach their mandibles to the abdomen of hippoboscid flies, obtaining transport to new bird hosts; it is not unusual to find 20 lice (*arrow*) upon a single fly. (*right*) Phoretic copulation in a parasitic wasp, *Dimorphothynnus haemorrhoidalis* (Tiphiidae). The male both inseminates and disperses the smaller, short-legged wingless female (*arrow*), often carrying her to sources of nectar or honeydew and in some cases actually feeding her by regurgitation

termed *phoretic copulation*, allows adaptation for a burrowing life combined with effective dispersal of inseminated females into areas where new populations of hosts may be discovered.

When wind, currents, or other organisms can move an insect to a suitable habitat, little active orientation is necessary. However, many migrants cover very long distances and/or must find very precise locations for breeding, feeding, or diapause (Fig. 3.11). For these species, accurate *navigation*, the act of moving through a place or along a route, becomes a major life task. As with so many other major life tasks, navigation generally uses multiple cues and these cues serve as backups to each other. It is postulated that each species recognizes some sort of cue hierarchy. (However, even for such well-studied organisms as birds, there is no consensus for any organism as to exactly what the hierarchy might be.)

Complex navigation is often divided into three general categories. The first is *piloting*, which is considered to be the ability to use fixed known reference points ('landmarks') to orient or navigate. The second is *compass orientation*, directional ability without reference to a particular origin or destination; in essence, the insect does not know where it is, but only what direction it is heading. The third is *true navigation*, the complex ability to move toward a particular goal in completely unfamiliar territory without sensory contact with that goal. It is important to recognize, however, that these categories are for human convenience; they do not necessarily reflect increasing levels of complexity or the order in which the capabilities evolved. Even though a number of common themes seem to apply across migration systems and taxa, there are simply too few data to make such sweeping generalizations. Navigation, particularly across long distances and/or lengthy time frames, often appears so impressive that humans have been reluctant to ascribe it to simple processes. However, a few detailed studies have shown that quite simple mechanisms such as wind transport can result in surprisingly precise results.

To many researchers, true navigation implies that an organism possesses an internal 'cognitive map' that represents the geometric relations among points in the
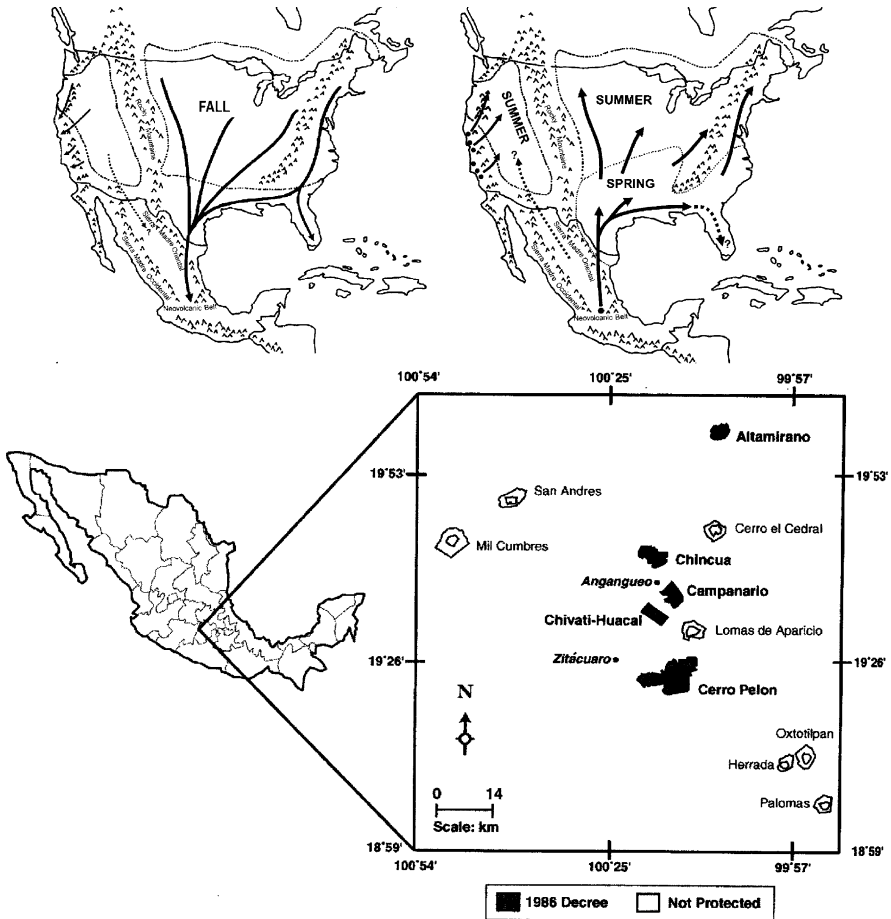
Fig. 3.11 Migrating monarchs. (*above*) The fall, spring and summer migratory routes of North American populations of the monarch, *Danaus plexippus*. Fall migrations take the butterflies to congregation sites in coastal California and central Mexico; marked individuals have been documented to fly over 2000 miles during the fall migration to Mexico. (*below*) The exact destination in Mexico was unknown prior to 1976; since then, at least 22 overwintering aggregation sites have been reported in stands of mature oyamel (*Abies religiosa*) trees in Mexico's trans-volcanic belt at altitudes between 2700 and 3600 m. Since 1986 several of these forest areas (shaded) are now legally protected in the Monarch Butterfly Biosphere Reserve

environment. To humans, 'map' implies visual cues. However, given the importance of chemistry in other aspects of insects' lives (see Chapter 6), such a map for many migrating insects might well be chemically based instead, operating analogously to the ways that homing salmon use the odor structure of water masses to move from the ocean into river mouths.

Some migrants travel by day, others by night, and the sky provides potential guidance at both times. For insects, day travel is by far better studied. At its simplest use, a day-flying insect could just orient to the sun's brightness, and move toward it without correcting for the sun's movement during the day. Even the elegant navigation of the monarch butterfly has a component of this type; because the butterflies do not start flying until they have warmed up, following the sun's path takes them in a southwestward orientation during their fall migration. However, additional precision may rely upon other factors (Fig. 3.12).

In 1911 while studying desert ants in Tunisia, Felix Santschi demonstrated insect sun-compass orientation for the first time. Using mirrors, he altered the sun's apparent direction as viewed by ants and showed that they would change direction at the same angle as the displacement of the sun. Others have since shown that insects can compensate for the movement of the sun across the sky. Time-compensation adds more accuracy to sun-compass orientation; this requires that the insect have an internal timing method or biological clock. Such a system also has been demonstrated for monarchs.

Finally, in addition to information provided by its position and movement, the sun provides information via the plane of polarization of light or the e-vector. Some insects clearly use both the position of the sun and patterns of polarized light, as has been shown in elegant detail for the honey bee. Mechanisms for detecting e-vector
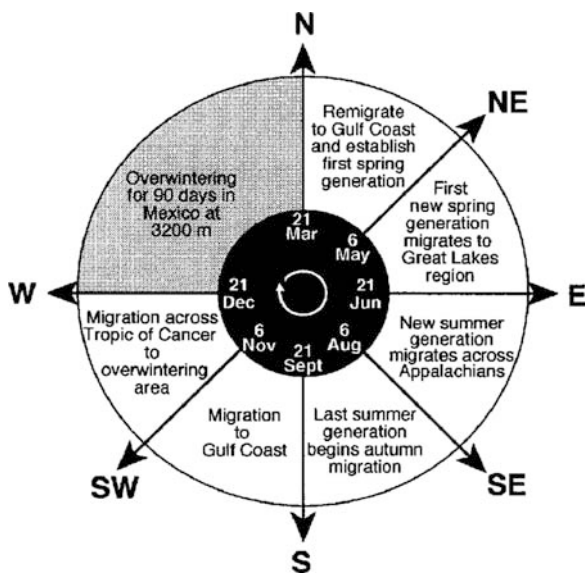
Fig. 3.12 Shifting direction. The rotational orientation hypothesis holds that monarch butterfly orientation shifts clockwise at a rate of 1 degree per day throughout the year for all generations of the annual migratory cycle. The spring equinox at overwintering sites apparently triggers northward migration from Mexico. As time goes on, the orientation of subsequent generations shifts as shown. Once the last generation reaches the overwintering sites, migration is repressed, but the internal migratory clock keeps running
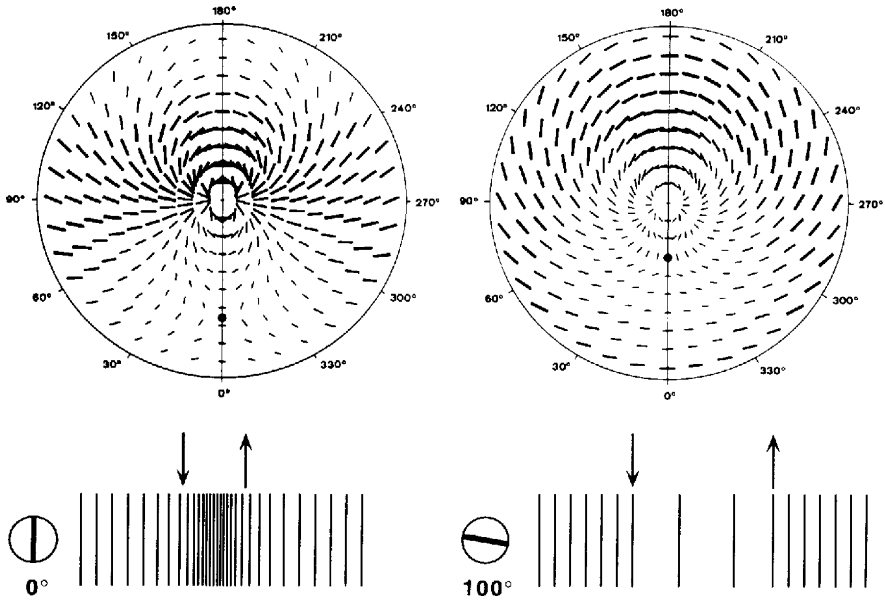
Fig. 3.13 Polarizing cues. Two representations of the e-vector sky or plane of polarization pattern of light with the sun in different positions above the horizon (24° left and 60° right) represented by the *black dot* on the axis. Orientation of each black bar gives the e-vector direction for that bar, and bar width indicates degree of polarization. Below each is the pattern of an optic interneuron firing response obtained from a cricket exposed to changes in the polarization of incoming light. *Arrows* indicate onset and end of the light stimulus

information have been well established in ants, bees, crickets and other insects. Scanning the sky, the insect matches a small patch of polarization detectors in a specialized portion of the retina to the distribution of the e-vector pattern in the sky (Fig. 3.13); the firing of receptor interneurons speeds up or slows down, depending on the degree of polarization.

Although they operate at different scales, both navigational cues and positional cues are intertwined elements essential to spatial adjustment. Every information source that is available—from infrared and magnetic waves and planes of light polarization to visible landmarks of the earth, sea, and sky—is used somewhere. We'll be returning to these in following chapters in different contexts.

Chapter 4
Foraging and Feeding

4.1 Introduction

Gypsy moth larvae defoliate vast areas of forest across Europe, northern Africa, and North America, feeding on over 50 tree species and reaching densities of tens of thousands of individuals per hectare. South American phorid flies lay their eggs on fire ants, and the grub that hatches invades the ant's head, consuming the brain; ultimately the ant's head falls off and a new fly emerges. Bed bugs live only with humans, and do poorly when fed other kinds of blood.

Much of the financial and social support enjoyed by entomologists derives from the negative impact that some insects cause by feeding upon human food plants, fiber sources, stored foods, waste products, farm animals, and even upon humans themselves. In turn, the propensity of other insects to feed upon man's pests has made them noticeable allies. For the insects themselves, finding and consuming food while simultaneously avoiding becoming food for other organisms are two of life's most essential behaviors. The former is the focus of this chapter; the latter will be the subject of Chapter 5.

Let's begin with an overview of foraging and feeding to put things in context. First, a note on vocabulary: Purists would say that *foraging* is the preferred collective term for all the behaviors involved in obtaining food, whereas *feeding* should be used more narrowly for the actual act of consuming that food. As such, feeding research generally is directed toward proximate factors, the 'how' questions that examine ways in which behaviors are directly produced and regulated. Foraging research tends to concentrate more on questions of ultimate causation. Simplistically, one could call these 'why' questions. In practice, the terms feeding and foraging are often used interchangeably, and in the end of course a complete picture involves understanding both proximate and ultimate factors whenever possible.

One popular way to sort feeding habits is by principal nutrition source, e.g., plant, animal, carrion, dung, etc. It provides a convenient way to describe individuals or species, but the larger the taxonomic group one attempts to apply it to, the less useful such a simple scheme becomes. Important exceptions occur in most taxa. Furthermore, many insects that appear to feed on one type of food upon closer scrutiny may be found to be entirely dependent upon another. For example
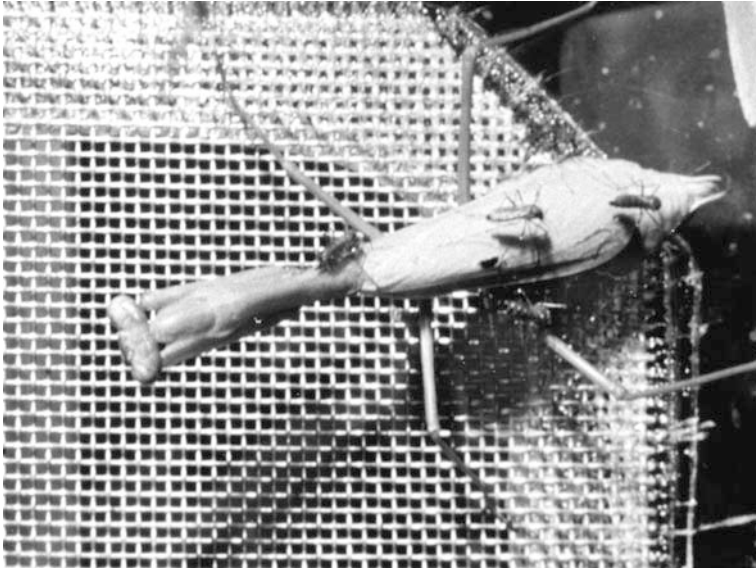
Fig. 4.1 Defying easy classification. Mosquito feeding habits differ with life stage and sex. Here, female *Aedes* mosquitoes feed on an adult mantis; most of their feeding punctures are through intersegmental membranes. The extent of such invertebrate blood feeding by mosquitoes in nature remains to be documented, but these laboratory females were able to develop fertile eggs in the same manner as vertebrate blood-fed individuals

although most people associate *Drosophila* fruit flies with decaying organic matter such as overripe bananas, their larvae are actually eating, not the fruit itself, but microorganisms associated with the decay.

Feeding behaviors also can be partitioned in various ways throughout a species' life; many species feed at different trophic levels at different stages in their life cycles. For example, mosquito larvae feed upon plankton and suspended organic matter. Additional partitioning arises from sexual differences; adult females suck vertebrate and invertebrate blood (Fig. 4.1) but males feed only on nectar. For a surprisingly large proportion of insects, partitioning can be so extreme that entire life stages do not feed at all—e.g., the pupa stage of holometabolous species. Insects such as the silk moths, bot flies, and mayflies do not feed at all as adults. In such cases, the larva acts as a rapidly growing 'feeding machine,' storing huge quantities of reserves for adult life.

Another broad way to classify insect feeding habits is by selectivity. How choosy are insects about their diet? Some insects accept a wide variety of foods (*polyphagy*), a fact that often makes them significant pests. Migratory locusts, carpet beetles, and cockroaches are familiar examples. Generalist feeders are especially likely to adapt rapidly to new crop varieties, including transgenic crops, and to insecticides. It is said that over 500 insect species targeted by crop protection strategies are now resistant to a variety of insecticides.

However, most insect species accept only a limited range of foods and usually prefer one or two (*oligophagy*). Often this is reflected in the common name they are given. Tobacco hornworm moth larvae, for example, feed on various solanaceous plants but prefer tobacco or tomato. Just as most insects are herbivores, so also most herbivorous insects are food specialists, feeding on closely related plant species (or sometimes just a single species). It is generally assumed that chemical or physical differences among plants select for insect host-specificity. The supposition is that physiological costs impose trade-offs among adaptations to different plant characteristics, but only a few genetic and physiological studies provide strong explicit support for this hypothesis. Host specificity also might be favored by other advantages such as use of specific plants as mating/aggregation sites, more efficient host-finding, or better defense through such means as sequestering host-produced toxic compounds.

Some insects take their choosiness to the extreme and exhibit strict specificity to one food, often a single host (*monophagy*). Monophagous specialists occur in almost every insect group. For example, certain leaf-mining caterpillars and gall insects can develop successfully on only one species of host plant. Parasitic species also tend to show a high degree of host specificity.

Like other organisms, insects need the appropriate balance of proteins and carbohydrates. Can insects 'choose' to balance their diet? Under laboratory conditions, both locusts and caterpillars have been able to select foods that provide the appropriate balance, but the composition of these foods was artificially extreme. It remains to be shown whether insects can and do fine-tune their choices when feeding on natural food with much smaller deficiencies.

Regardless of an insect's food choice and the way it is classified, the ability to forage successfully resolves into a remarkably constant chain of behaviors, each link of which facilitates the next: (1) food habitat location; (2) food finding; (3) food recognition; (4) food acceptance; and (5) food suitability. (For some parasitic species, a sixth link—host regulation—may operate as the parasite accelerates, retards, or otherwise modifies the host's physiological development.) This chain can involve any or all of the senses, but the chemical sensory systems predominate. Consider the bee wolf, *Philanthus triangulum*, which stalks honey bees that it captures, stings, paralyzes, and carries back to its nest. As the pioneering ethologist Niko Tinbergen described it:

> A hunting female of this species flies from flower to flower in search of a bee. In this phase she is entirely indifferent to the scent of bees; a concealed bee, or even a score of them put out of sight into an open tube so that the odor escaping from this is clearly discernible even for the human nose, fails to attract her attention. Any visual stimulus supplied by a moving object of approximately the right size, whether it be a small fly, a large bumblebee, or a honey bee, releases the first reaction. The wasp at once turns her head to the quarry and takes a position at about 10–15 cm to leeward of it, hovering in the air like a syrphid fly. Experiments with dummies show that from now on the wasp is very susceptible to bee scent. Dummies that do not have bee-odor are at once abandoned, but those dummies that have the right scent release the second reaction of the chain. This second reaction is a flash-like leap to seize the bee. The third reaction, the actual delivery of the sting, cannot be released by these simple dummies and is probably dependent on new stimuli, probably of a tactile nature.

4.1.1 Food Recognition and Acceptance

Larvae of potato beetles react to the presence or absence of alkaloids that occur in close relatives of the potato, but if their palps and antennae, which carry the olfactory receptors, are removed the larvae will eat substances positively harmful to them. Adult tsetse flies are drawn to their host by odors associated with animal breath, urine, or skin secretions; final orientation is visual, but flies that have seen a potential host and landed on it will begin to probe and feed only in response to the host's body heat, followed by formation of a blood pool at the bite. The polyphagous chalcid wasp, *Trichogramma evanescens*, parasitizes the eggs of more than 180 insect species; oviposition requires only that the object be firm enough to walk upon, protrude from the surface, fall within certain size limits, and have no dimension greater than four times any other. Odor, color, and surface texture are irrelevant, but one important distinction is made. The little wasp will not oviposit in eggs that have already been parasitized by another wasp, unless they are washed to remove the smell the previous female has left behind.

On what specific basis does an insect recognize that an item is food? Or decide to accept it? These questions have immense practical interest, and since the 1940s a great deal of research has been directed toward answering them. In the process, two schools of thought arose. Some scientists proposed that feeding was a simple matter of the presence or absence of certain plant chemicals. Roughly equivalent to 'flavors,' these compounds had no obvious direct nutritional value but appeared to be acting as classical behavioral releasers (see Chapter 2), so they were called *token stimuli.* Other scientists disagreed with this interpretation. Token stimuli might be important in the initial discrimination of different plant species, they argued, but factors more closely related to nutrition must mediate finer decisions such as the discrimination of leaves of different ages. Thus, food preference was a two-step or 'dual discrimination' process. When an insect showed food preferences, it relied upon stimuli that were more closely related to nutrition than to flavor.

Parts of both of these two theories now seem correct, as will become apparent in more detail in Section 4.3. As with the potato beetle, nutritionally nonessential (or even toxic) compounds may exercise an important influence as feeding stimulants. The most nearly universal is certainly sucrose, which is an effective stimulus for most insects. Nutritionally, many monophagous feeders have become physiologically incapable of surviving away from their usual host, and will respond only to a stimulus that is species specific to their hosts; for some plant-eaters, this may even be a substance originally evolved to repel herbivores. Polyphagous insects, on the other hand, show such a broad responsiveness that they may respond directly to nutrients without the intervention of a mediating chemical stimulus; any apparent choice they exhibit is likely to be based on selective rejection due to repellent substances. One useful experimental technique for sorting out the relative importance of plant chemical constituents is the 'feeding preference test' in which the insect is given a choice of different food combinations; the amount of feeding is used as the measure (Fig. 4.2).
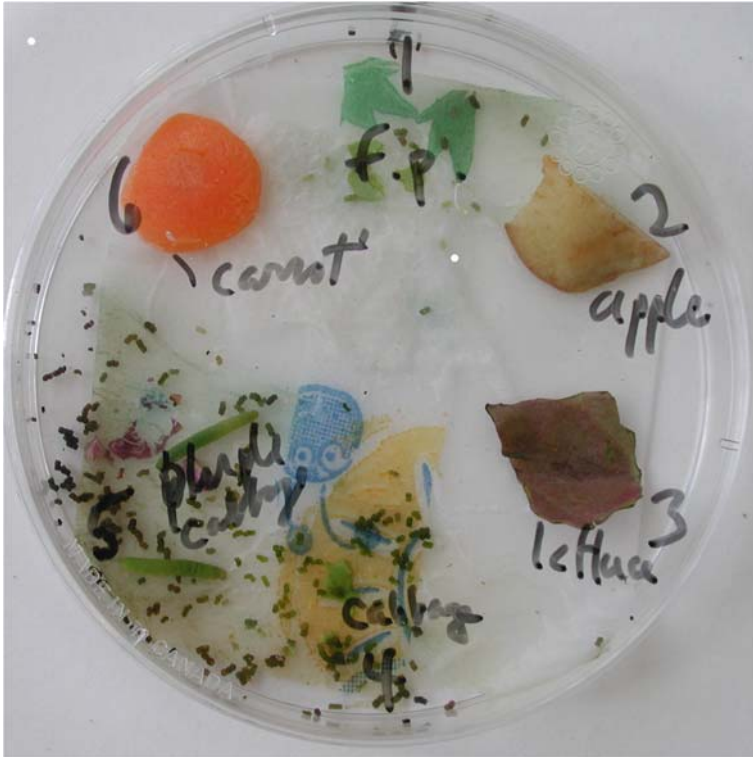
Fig. 4.2   Determining insect food preferences. A simple smorgasbord of potential foods (clockwise from 12 o'clock are fresh pieces of *Brassica rapa* leaf, apple, lettuce leaf, white cabbage, purple cabbage, and carrot) was offered in a petri dish with two *Pieris rapae* caterpillars released at the center. Two hours later relative feeding damage, readily apparent visually, may be quantified by comparing the food weights before and after exposure to the caterpillars. With modification a similar technique can also be used to assay the relative importance of various plant products by incorporating chemicals to be tested in standard agar discs made with powdered leaves

It should be noted that well-designed laboratory experiments that concern feeding behavior have many factors to take into consideration, including the age of the insect, its previous experience, and its nutritional needs. For example, phytophagous insects generally eat more in the middle of a developmental stage, and they generally eat more in the light than in the dark.

Some (and probably most) insects also become less selective if they experience a long period without food, and for some species, 'long' may be shorter than some laboratory researchers realize. In one study of the red locust *Nomadacris septem-fasciata*, gut samples were obtained at short intervals all through the locusts' adult lives; when the temperature was 30°C or above, their foreguts became more than half empty within an hour.

Many insects that are deprived of food will sample items they would otherwise reject. In general, grasshoppers were once considered to be unselective in their choice of foods. In newer observations, several grasshopper species have shown an increasingly wider acceptance of a range of host plants with increasing length of food deprivation. Sometimes this may signal a simple need for water rather than for nutrients. A well-hydrated locust will move away from a piece of wet filter paper, but a dehydrated one will attempt to eat it.

Despite voluminous records of individual insect–plant and parasite–host relationships, a deeper understanding of the evolution of insect diet selection has been difficult to gain. For example, why are some insects monophagous and others polyphagous? A feasible explanation is found in the *congruency hypothesis* advanced by Vincent Dethier. Both feeder and food are continually evolving against a background of multiple pressures—the plant, prey or host by synthesizing different chemicals, the insect by developing different sensory and central decision-making capabilities. Specific changes occur in both organisms as a result of random mutations. Congruency, or match between food source on one hand and insect as feeder on the other, occurs whenever these two independently mutating systems interact in such a way that formerly non-attracting chemicals now stimulate feeding. Sometimes, the change may be in the insect, resulting in the addition, subtraction, or substitution of capabilities. For example, insect neural changes may cause formerly neutral chemicals to become attractive or repellents to be no longer detected. At other times, various chemicals may arise by mutation in the plant, prey, or host.

For phytophagous insects, little information exists upon which to test the congruency hypothesis, although a number of documented cases of sudden irreversible shifts in insect feeding habits suggest that it is not unreasonable. It provides explanations for a number of previously puzzling phenomena, such as why some plants such as ferns have feeding deterrents even though they evolved long before phytophagous insects did. The theory also explains why shifts in diet may occur in any direction, including from polyphagy to monophagy, and why some apparently suitable plants are not eaten.

At the same time, like any model, the congruency hypothesis presents an oversimplified view. The model assumes reproductive isolation of the new mutant and that mutations represent quantum jumps rather than intermediate states. It ignores ecological factors. For example, the host plant or animal is not only a source of food; often it equally may be a place to live. Thus, for a new feeding habit to be established, the host need not necessarily be better nutritionally. For many insects, plant selection is selection of a whole community—a microclimate, a shelter, a set of predators and diseases. The picture at any given moment must be one of dynamic equilibrium, and feeding must be viewed as a compromise between nutritional and ecological optima.

Feeding habits also reflect only a subset of the choices that could potentially be made, because for a plant and insect to interact they must be in contact with one other. This has been graphically illustrated by introduced pest species throughout the world, enthusiastically munching upon certain plants not formerly available to

them. Nor does accessibility require that it be the pest that is introduced; a striking example is the Colorado potato beetle. This native American insect fed upon weedy scrub until humans introduced the potato into its world; with this new opportunity, the beetle population evolved to prefer potatoes over native hosts.

4.1.2 Regulation of Feeding

Preying mantises will consume a relatively constant number of house flies each day when flies are continually available. Blowflies will maintain a relatively constant daily food intake at a constant sugar concentration; if the concentration is decreased, daily intake increases, and vice versa. In fact, most insects will feed to a point and then stop. What causes a feeding insect to finally stop eating? What determines the timing—how long and how often—of feeding?

One of the most thoroughly studied cases of feeding regulation involves *Phormia regina*, a blowfly investigated by Vincent Dethier and his associates. The adult blowfly needs only water, carbohydrates, and oxygen for maintenance, receiving all other necessary materials during its larval stage; adult feeding occurs only to provide locomotive energy. Thus, the blowfly offers a simple system for studying two essential aspects of feeding behavior: the nature of the 'on/off' mechanism and the nature of quality control.

The 'on/off' part is relatively straightforward. Blowfly feeding starts when a fly steps on potential food, stimulating taste receptors on its tarsi. These lead to the extension of its tubular mouthparts (proboscis), which thus contact the food solution. At the proboscis tip, a lobe (labellum) has mechano- and chemoreceptive hairs that experience the consistency and taste of the food. The food quality, along with peripheral and central adaptive processes, determines the sucking reaction. Cessation of feeding behavior involves a homeostatic mechanism (Fig. 4.3) so that, in the presence of excess food, a constant amount is ingested per day. As the gut is filled, stretch receptors in the foregut are activated, and their firing inhibits brain input from the external chemoreceptors that elicited feeding. At this stage in feeding regulation, nonnutritive or metabolically useless foods are not distinguished from nutritious ones. A blowfly will, for example, take up the useless sugar fructose and regulate the amount until it dies.

Timing of insect feeding is more complex. In general terms, the length of the period between meals is usually related to the quantity and nature of the previous meal and to the amount of energy expended in the interim. For most insects, feeding occurs at relatively short intervals of minutes or hours. However, some insects, such as certain filter feeders, eat almost continuously. Others, such as some parasites, may feed only at wide intervals of many hours, days, or weeks.

Even long-term changes in feeding behavior such as seasonality may rely on the same basic physiological mechanisms as short-term feeding regulation, however. A good example is provided by the face fly, *Musca autumnalis*, studied by John Stoffolano. During the summer, face flies, which feed upon cattle blood and lay their
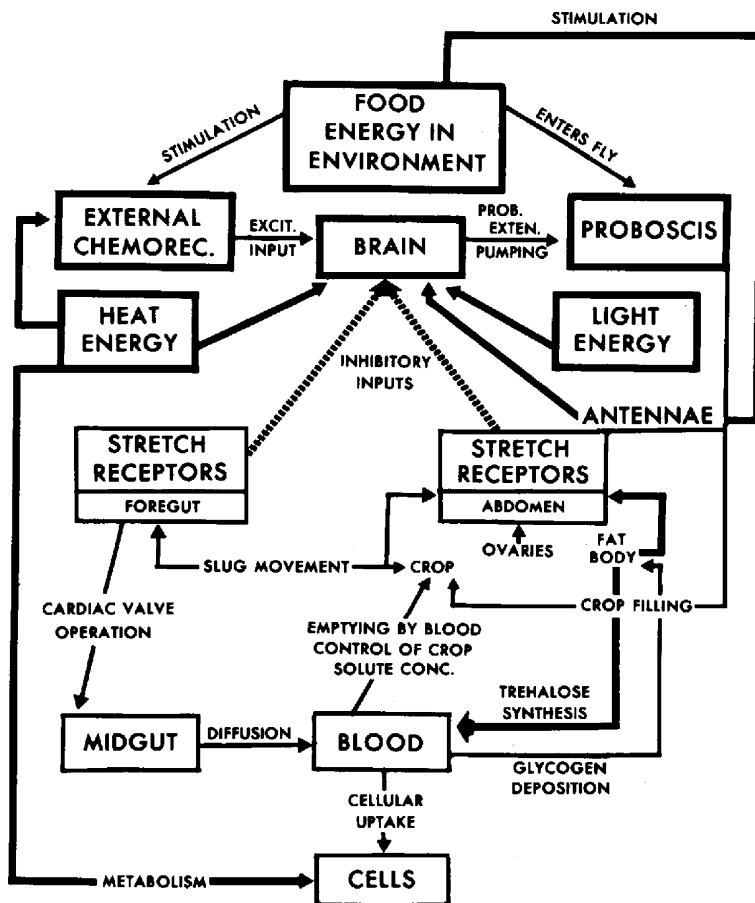
Fig. 4.3   Stopping when full. Metabolic homeostasis in the blowfly, *Phormia regina*: a model system illustrating the interactions of external and internal stimuli and resultant feedback which regulate the physiological aspects of feeding. The actual cessation of food intake is probably mediated through negative feedback from internal receptors. The internal sensing upon which this depends may be based on any of quite a number of variables, such as food bulk and/or gut capacity, level of sensory stimulation, and length of time spent at continuous feeding

eggs in fresh, undisturbed cow manure, go through several generations. Although adult males, which apparently feed on nectar, show their greatest feeding response to glucose, adult female face flies exhibit a cyclical pattern of protein ingestion that increases dramatically when eggs are being matured; they apparently cannot live solely on protein, however. Female face flies respond to both blood and glucose as long as their ovaries are undeveloped. However, as their ovaries begin to swell and act on abdominal stretch receptors, female feeding begins to decline. Fully gravid females do not feed at all. With responsiveness to blood and glucose effectively removed, the lower level of responsiveness to manure they have maintained all along

now asserts itself. In the fall, under the influence of short days and low temperature, the ovaries of the last generation of flies of the season fail to develop. Now face flies of both sexes ignore cattle and feed only on nectar. On this diet and under changed hormonal influences, a face fly's fat body swells and its abdomen distends until abdominal stretch receptors apparently respond with impulses to the central nervous system, nullifying the sensory input from tarsal receptors. Feeding stops. But gradually through the winter, fat is utilized; the fat bodies shrink and the crop gradually empties. Spring marks the end of this developmental arrest. Flies then feed on nectar until cattle are put to pasture.

Among plant-eating insects, feeding periodicity is also common. One important evolutionary reason undoubtedly is that a plant is not a homogeneous chemical entity. Rather, it is a heterogeneous, ever-changing microchemical environment. Important plant constituents such as carbohydrates, fats, proteins, minerals, alkaloids and essential oils vary with a number of factors, such as time of day and season, plant growth stage and tissue, climatic and soil conditions, etc. For example, consider the seasonal changes that occur in oak leaves. New leaves contain relatively more protein, water, and sucrose and less tannin than older leaves. As tannin increases, protein availability is reduced until its decline becomes a limiting factor for most herbivores. Not surprisingly, most lepidopteran larvae attacking oaks feed early in the season on new foliage; by so doing, they make the best use of available protein and avoid most of the toxic tannins that slow growth rates and reduce fecundity. Plants also show shorter-term cycles, the most familiar example of which is the diurnal rhythm of nectar production and flower opening in many plants. Honey bees, apparently able to remember not only the location where food is available but the time of day at which this occurs, continue to gather only during the previously learned hour.

Environmental variables are also important in the establishment and maintenance of feeding periodicity, and it would be a mistake to underestimate their effect. For example, most ants are more active at some times of day (or temperature and light ranges) than at others. Many ant species in temperate climates forage throughout the day, but in hotter lands some regularly stop feeding for a midday break. Many others forage only at night; 54 out of 58 species of ants living in the Sahara are nocturnal. The effect of such foraging rhythms, of course, is to confine the outside activity of the ants to times when temperature and humidity are least harmful and/or to when their food is most easily obtained. It is sometimes difficult to determine the degree to which an insect's foraging rhythm depends upon internal biological clocks, however. For example, leaf-cutting ants, *Atta cephalotes*, normally collect leaves all day, beginning early in the morning. Shading their nest entrance between 5:30 a.m. and 6:00 a.m. will delay the time of appearance of the first workers, but no amount of light before 5:30 a.m. will make foraging start. Some internal clock is apparently responsible for bringing the workers to the nest entrance to inspect for light. At the same time, many studies have shown that when ants are fed regularly at the same time for three to five days, they learn to search for food at that time on succeeding days. This implies that ants in the wild would learn to forage when food was most plentiful. Thus generalizations must be made quite cautiously. Probably the daily

foraging activity of most insect species is the complex result of minute-to-minute conditions, an internal rhythm itself partly dependent on past conditions, and, in the case of social species, the individual past experience of the colony members.

4.2 Foraging Strategies

In olfactometer tests the wasp *Diaretiella,* a parasitoid of cabbage aphids, is attracted to collard leaves; wind tunnel experiments show that it reacts to sinigrin by walking or flying upwind. The ichneumonid wasp *Pimpla ruficollis* is a parasitoid of the European pine shoot moth, but for the first few weeks of adult life it is repelled by the odor of pine; only when a female is ready to oviposit does she find pine odors attractive and return to the forest where her host is located. The aquatic larva of many chironomid flies constructs silken tubes with a conical catch-net spun across the lumen of the tube; periodically the larva devours its catch-net with adhering debris that has been swept into the tube by the water currents.

Procuring and recognizing food are items of overwhelming importance on the life agenda of all insects, whether they live by scavenging, chewing or sucking upon plants, or capturing and/or parasitizing prey. Might it be possible not just to catalogue foraging and other behaviors but actually to predict them? In 1966, Robert MacArthur and Eric Pianka hypothesized a concept that came to be called *optimal foraging theory*. First, because of natural selection animals should evolve ways of maximizing their food intake (benefit) while minimizing time and energy expended (cost). Second, whenever several roughly equivalent patterns of behavior are available to an animal population, the pattern with the most favorable cost-benefit ratio should eventually defeat other less efficient patterns and come to prevail. For convenience, MacArthur and Pianka viewed these patterns of behavior as though each pattern was equivalent to using a different 'strategy'; the term does not imply conscious intent, but something like a general set of 'rules for behaving' that in the animal's evolutionary history has usually resulted in a particular outcome.

From its inception, optimal foraging theory showed promise of being a powerful theory, in that its predictions could be tested quantitatively. Factors presumed to underlie particular foraging decisions could be identified, and one could measure cost-benefit ratios in the currency of calories of food taken in and energy spent. MacArthur and Pianka, and others following them, identified a cost-benefit ratio for many foraging behaviors. Their studies showed that animals are not perfectly adapted in terms of cost-benefit ratio, but that they come reasonably close, given certain imperfections in their sensory and information-processing systems.

As this theory came to be invoked to cover virtually all behavior, its name changed to simply *optimality theory*. The idea that animal behaviors can be viewed in terms of a cost-benefit ratio has been an extremely important breakthrough in evolutionary theory. Today, optimality theory plays a major role in many research studies on feeding and foraging (see Section 4.2.2).

Feeding does not occur in a behavioral vacuum, however; animals balance many different needs for overall efficiency in satisfying fitness requirements. For example,

a generally favorable cost-benefit ratio has to include not only the need for food but also the need to escape from predators and the need to reproduce effectively. And what about situations where insects compete with other insects for the same limited resource? In the real world, a decision-making animal often must consider the behavior of others. In 1974, John Maynard Smith elaborated upon optimality theory to predict optimal outcomes when individuals interact with one another. Borrowing from economic theory, he applied *game theory* to explain how animals develop a strategy that considers competitors' behaviors. Equivalent to coaching strategies in a competitive sport, game theory predicts that an individual will choose different strategies in proportion to their relative effectiveness against choices made by opponents.

4.2.1 Herbivory

Plant eaters comprise almost half of the world's insect species today; they occur in about one-third of the major insect groups, including some of the most numerically successful ones such as the Lepidoptera. Fossil evidence indicates that terrestrial arthropods have been consuming plants for at least 400 million years, and studies of a range of ecosystems demonstrate that insects consume more plant mass than all vertebrate herbivores combined. Even the vast ungulate herds of the African savannas are estimated to be responsible for only 15–35% of the herbivory there, with insects causing 10–75%.

Herbivory (also called phytophagy or simply plant-feeding) most commonly involves feeding upon foliage, but one can also find sap feeders, root feeders, seed feeders, and, in the case of woody plants, bark feeders. (In fact, with the exception of coal there is hardly a source of organic carbon not used to some extent by some insects.) To these directly phytophagous species may be added the complex of insects that feed on the rotting debris below the plants and even the opportunists that partake of the sugary honeydew excreted by the sap feeders. Each of these species in turn serves as a potential host for one or more parasitic insects that may in turn be attacked by their own specific enemies, called hyperparasites. Thus, even a single plant species can form the base of a complex food web (Fig. 4.4).

Herbivory is such an important part of insect behavior that it keeps cropping up in different contexts. Thus, for example, in Section 4.2.6, we'll consider those special cases in which insects can be said to be farmers, rather than hunter-gatherers. In Section 4.3, we'll be returning to the subject of herbivory from the perspective of insect-plant coevolution.

4.2.2 Active Search

Blood-sucking Diptera can be attracted with CO_2. Phytophagous aphids come to light of longer wavelengths, especially yellows and greens. Dragonfly larvae often stalk, then snap at, nearby moving objects within certain size limits; hungry preying mantises behave in a similar fashion.

Fig. 4.4 Life is seldom simple! Food web associated with cabbage plants in Minnesota. Herbivore species include 11 leaf feeders, 10 sap feeders, and 4 root feeders. Other trophic levels were less thoroughly studied, but included at least 21 detritivores, 79 honeydew feeders, and 85 predatory, parasitic, or hyperparasitic carnivores

'If you want dinner, go find it!' For by far the majority of insects, food location involves some manner of active search. Plant-feeding insects (if not hatched on their host) may find their hosts by seeking appropriate habitats, by increased activity that maximizes their chances of encountering a plant, by completely random activity halted by strong arrestant properties of the plant, or by attraction to a plant from a distance by smell or vision or both. Predatory insects, on the other hand, are usually tuned to movement, which is probably the most widely shared characteristic of potential prey; parasites often cue in to by-products of their hosts' feeding activity such as frass (see Chapter 2).

Because active search for food requires energy expenditure and time involvement, one would expect selection to favor behaviors that increase its efficiency. Optimality theory predicts that when food is mobile, it is advantageous to catch more food in less time, to catch larger food items in the same time required to take smaller ones, and to avoid chasing food or hosts likely to escape or prove unsatisfactory for some other reason. The variety of means by which such ends have been approached is nearly limitless.

What of those species like gall midges, in which the mother oviposits directly on or in the plant, or like parasitic wasps that oviposit on an animal host? Locating food would appear to be no crisis for these species, because the young are literally surrounded by it, but in actuality the burden of food location has simply been shifted to another life stage.

When food is unevenly distributed, organisms must develop ways to locate and identify the richest clumps, or patches, of that food. Studies first done with birds but probably applicable to most searching foragers show that optimal foraging has two phases. When they first locate a food source, many animals spent the first few minutes in a 'sampling phase' that looks like random wandering though several patches. Then, in what is called the 'exploitation phase' they spent most of their time foraging in the richest patch.

Under natural conditions, however, food density and condition are often in a state of flux. Consequently, a useful strategy is to sample food availability and condition periodically to keep up with current conditions. In the case of nectar feeders, the amount of food that can be obtained from any one flower is rather limited, and for maximal efficiency one might expect bees, for example, to be able to exploit new food resources as they become available and to differentiate between more and less rewarding flowers in bloom at any one time. Studying bumblebees in the 1970s, Berndt Heinrich performed some of the first direct analyses of insect foraging behaviors in terms of caloric costs and benefits. He confirmed that bumblebees generally collect nectar from several different plants during a foraging trip, spending most of their time on the richest flowers while simultaneously hedging their bets by investing some energy in less productive species. By experimentally enriching some of these 'minor' flowers with sugar syrup, Heinrich demonstrated that an individual forager immediately will switch from its previously most preferred flower and adopt the fortified flower for as long as the sugar syrup is added. (Nectar is far more than just sugar water, however. It contains considerable quantities of various amino acids that are nutritionally essential to adult insects unable to synthesize them.)

Exploiting a food uses it up, of course. Imagine a ladybug beetle on an aphid-infested plant. At first it can eat voraciously, but as it feeds, fewer and fewer aphids remain and they become progressively more scattered. The rate at which the beetle takes in food slows down progressively. By comparison other patches begin to look more attractive, but there are potential costs to moving on, such as the loss of time and energy and the possibility of predation during travel. Might it be possible to predict how long a forager should stay in the dwindling food patch versus striking out to find a new one? This question led Eric Charnov to develop an optimality model that generated a result known as the *marginal value theorem*. He based his model on a concept called the marginal rate of food intake, defined as the rate of food intake associated with the next food item in the forager's current patch.

The marginal value theorem makes clear testable predictions that—as for other optimality models—can be presented in mathematical, algebraic, and graphical forms (Fig. 4.5). In non-mathematical terms, one prediction is that a forager should stay in a patch until its marginal rate of food intake there is equal to that of the average rate of food intake across all available patches, i.e. keep feeding until you could, on average, do just as well somewhere else (after accounting for the costs you must pay to get there). A second, related prediction is that the greater the time or energy it would take to get to another patch, the longer a forager should stay in the current one, i.e. travel costs increase with longer distance, shifting the balance. A third prediction is perhaps less obvious. If the patches in an area are already of
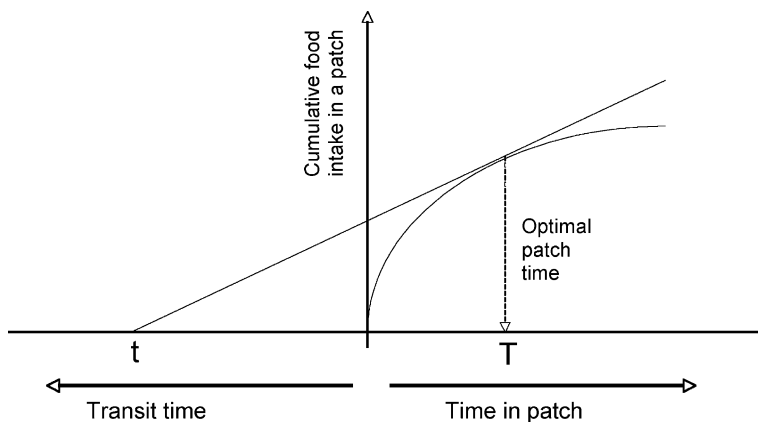
Fig. 4.5 Foraging optimally. The marginal value theorem allows one to predict how long an animal should continue to feed at a particular location (food patch) based on cumulative food intake. For example, it might be applied to bees visiting patches of flowers for nectar. A simple graphical solution is depicted here. First, generate a *curve* that represents the cumulative food obtained over time from an average food patch. Initially when food is abundant the curve rises rapidly; later as food is depleted it levels off. Next, quantify the travel time between food patches and determine an average travel time (t). Starting at point t, draw a *line* to the right that is tangent to the cumulative food gain curve. From the point of tangency, drop a line to the x-axis. The intersection of that line with the x-axis gives the predicted optimal time (T) for the forager to remain in the patch, optimizing benefit/cost ratio

generally poor quality when the forager enters one, it actually will stay longer than if it were foraging in an environment full of more profitable patches. This is because in a poor patch, it takes longer to accumulate the amount of energy needed to make up for the travel costs associated with a move.

In some cases, researchers have been able to gain insights into the nature of the selective forces acting upon a selected insect species by building models for various alternative foraging decisions and comparing the predictions of each model with its observed behavior. For both practical and theoretical reasons, a major focus of insect research on marginal value theorem concepts has been with parasitoid wasps, which lay their eggs on insect hosts that are distributed in discrete patches in the environment. Many of these parasitoid-host systems lend themselves easily to laboratory manipulations of pertinent factors such as host quality and host and parasite density. Applied ecologists have hoped to gain information that could inform biological control measures; population ecologists have seen these insects as a way to explore the dynamics of victim-enemy relationships.

Models such as those provided by optimality theory and the marginal value theorem should be seen for what they are: not some sort of inviolate truths, but instead, valuable research tools. Rarely has there been a perfect quantitative fit between model predictions and empirical test results. Still, their use has yielded valuable insights and sometimes has led in unexpected directions. For example, optimal host selection models predict that when an insect has its choice of two foods or hosts of different potential values, the choices it makes between them depend on its encounter rate with the more profitable species. If the insect's encounter rate with the more profitable species is above some threshold value, the less profitable species should always be ignored; if encounters with the more profitable species are below this value, the less profitable one should always be attacked.

Studies with a braconid parasitoid *Asobara tabida* that attacks *Drosophila* show both the ways such studies work, and the potential pitfalls involved with laboratory experiments that purport to represent natural field behavior. At the high population densities typical of most laboratory experiments, *Asobara* is selective when offered the choice between two host species that differ in survival probability for its offspring; it also avoids superparasitism. However, as is probably true for most insects, encounter rates under natural conditions are much lower. When *Asobara* encounters only one host or less per hour, the wasp always accepts either host and also superparasitizes.

Prey-catching wasps show a relatively constant host stinging sequence that appears to be genetically programmed rather than learned; in all known cases, the first sting is directed at ganglia involved in locomotion and defense, in particular paralyzing the prey's legs, which might otherwise be used as powerful defensive weapons. Then the prey is transported back to the nest in various ways, often with considerable effort. However, the wasp *Ampulex compressa* has evolved an efficient alternative, *zombification*; its cockroach prey (usually *Periplaneta americana*) follows it home like a submissive dog on a leash.

To accomplish this feat, *Ampulex* relies upon two injections of venom. The first, delivered into the thorax, transiently paralyzes the roach's prothoracic legs. The

second, given very precisely into the neck, targets the cerebral ganglia. In response, rather than fleeing, the roach stays put, frantically grooming itself, while the wasp cuts the roach's antennae with its mandibles and feeds on its hemolymph. Then *Ampulex* grabs one of the roach's antennal stumps and, walking backward, leads the unprotesting roach back to a pre-selected burrow for oviposition. The stung roach follows the wasp inside and lethargically waits while the wasp glues an egg to its cuticle, then exits and closes the burrow entrance with small pebbles. For days, while the egg hatches and the larva feeds, the roach remains alive but passive; it only dies after the pupa finally becomes ensconced in its abdomen.

Researchers have become quite interested in the proximate mechanisms involved in zombification. To resolve whether the venom is injected directly into the central nervous system or simply diffuses in from the hemolymph, Frederic Libersat and colleagues injected *Ampulex* with a mixture of carbon-14-radiolabeled amino acids; they found that the radioactive signal was positioned in the central nervous system so precisely that they compared it to the most advanced stereotactic administration of drugs.

How can a small change in one particular brain center, protein, or gene lead to such a dramatic effect? In most cases the mechanisms that underly such a dramatic behavioral change are unknown. In a first step toward an answer, D. G. Biron and colleagues have been examining the observed behavioral changes in the insect host using *proteomics*. A rather young discipline, proteomics can be defined as the qualitative and quantitative comparison of proteomes (genome operating systems) under different conditions to unravel biological processes. Because it allows one to study the host-parasite interaction at the genetic level precisely in the midst of the manipulative process, the technique appears very promising as a tool for exploring the proximate mechanisms responsible for host manipulation.

4.2.3 Trapping and Ambush

The bola spider twirls a sticky ball of silk from a silken thread. Moths approach the swinging ball, drawn by an impregnated attractant, and become stuck to it, whereupon the spider retrieves its catch and consumes it. Little zorapterans, members of one of the smallest and most poorly known insect orders, live in decayed logs and sawdust piles; they feed primarily on fungal hyphae and spores but are not adverse to an occasional meal of nematodes, mites, or springtails should one of these creatures pass by. Some preying mantid species are exquisitely camouflaged as leaves; an unsuspecting herbivore that approaches is quickly snatched and consumed.

Remaining relatively motionless to trap incoming food is less common than moving about to search for it, but a sit-and-wait strategy has many advantages, both reducing searching energy expenses and allowing an insect to engage in other concurrent activities such as environmental monitoring for mates and/or territorial intruders. Ambush is the most common lay-in-wait strategy, and it can be extremely effective when employed by an agile predator. The grand masters of lay-in-wait are undoubtedly the spiders, whose evolutionary repertoire includes not only web
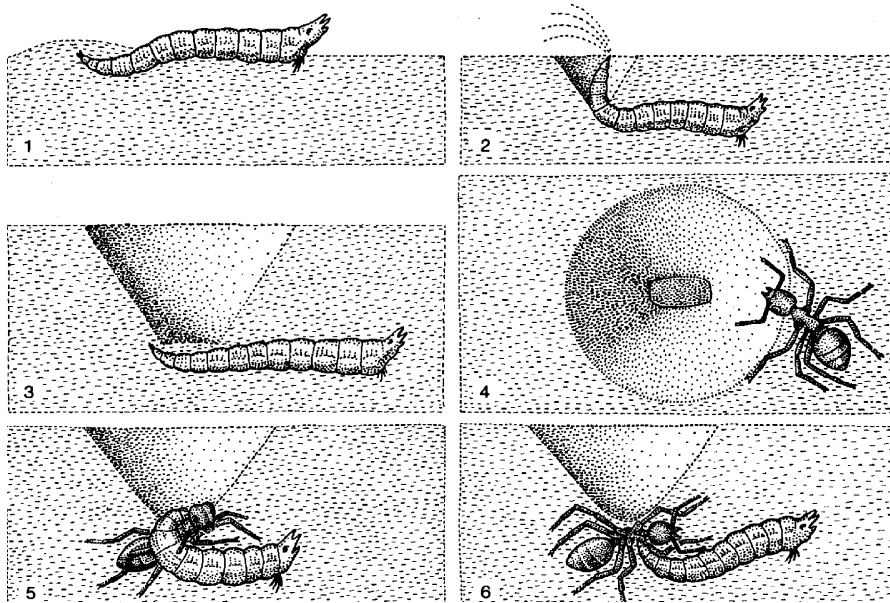
Fig. 4.6 Trapping supper. Ambush by the worm-lion larva, *Vermileo comstocki*. In frames (1) and (2), the larva makes a pit; then it hides at the base of the pit (3). An approaching ant (4) slides into the pit, where it is seized and paralyzed (5). Hauled under the surface of the sand, the ant's body fluids are sucked out by the worm lion (6)

weaving but also quite a wide range of other ambush methods. In a similar vein, many predatory insects such as tiger beetles, ant lions, and worm lions construct devices such as pits or snares that increase the probability of locating and capturing prey (Fig. 4.6). Considerable time and energy are often invested in the building and maintenance of such devices. However, they can result in a good return in food which otherwise would be so widely dispersed as to be uneconomical to wait for and perhaps difficult to catch as well.

Lures can improve the odds that dinner will appear. Certain assassin bugs have forelegs covered with hairs that exude small droplets of a highly viscous substance that looks like dew; when the assassin bug spots small, fast-moving prey such as fruit flies, it raises its forelegs and holds them parallel to the ground. Flies attracted to the 'dew' become entrapped and quickly are consumed. The Javan bug, *Ptilocerus*, has a tuft of bright-red hairs on its body, marking the spot where a gland opens beneath the abdomen; secretions from this gland are very attractive to ants. However, after partaking of these secretions, an ant collapses, apparently from narcotic action, whereupon the bug pierces the ant through the neck and promptly sucks it dry.

Attracting prey often involves some sort of deceit or false sensory message. Certain Malaysian preying mantids greatly resemble flowers; unsuspecting prey attracted visually to these 'blossoms' become a quick meal. Similarly, female *Photuris* fireflies flash false coded messages to sexually lure unrelated males,

which are then eaten. The predatory larvae of many green lacewings have the habit of covering themselves with camouflaging debris of one type or another; in the case of *Chrysopa slossonae*, this disguise allows access to the woolly aphids that are its sole diet without alerting the aphids' ant guards. These behaviors are described as *aggressive mimicry*; despite the superficial similarity in terminology, however, they are quite different from the classical types of mimicry treated in Chapter 5.

Obviously, a lie-in-wait strategy requires that the food itself be mobile. Usually this implies a diet upon animal prey. However, when wind or water currents exist, small plants and microorganisms may become an important diet item for lie-in-wait food gatherers. Trichoptera larvae of the family Hydropsychidae use nets spun with their silk glands to capture drifting food particles in streams. These feeding nets sometimes have an exceedingly fine mesh, allowing the caddisfly larvae to graze upon fine particulate organic matter, phytoplankton, and bacteria strained out of the moving water. The evolution of hydropsychid larvae reveals a tendency toward more complicated larval feeding structures and smaller capture-net mesh size. In some species, plant detritus may comprise more than half of the diet of younger instar individuals.

4.2.4 Parasites and Parasitoids

Little wasps in the genus *Copidosoma,* which lay their eggs in the eggs and young larvae of noctuid moths, regularly produce brood of over 2,000 young. Tsetse flies have been dubbed the world's least specific bloodsucker; they will apparently feed indiscriminately upon any vertebrate they encounter. The wasp *Ichneumon eumerus* attacks the caterpillars of *Maculinea rebeli* that live inside the brood chambers of ant nests; to reach them, the wasp releases chemicals that cause the ants to lock into combat, leaving the caterpillars defenseless and available for oviposition.

Organisms that feed upon a host that they do not kill are termed *parasites*. Examples include mosquitoes, lice, bed bugs, fleas, and the many other insects that feed on humans and other animals that often have significant health and medical impacts. Haematophagy or the utilization of blood as food occurs in six insect orders. The order Diptera has the largest number of haematophagous species and includes both ectoparasitic forms that feed from the animal's body surface and endoparasitic forms that feed from within. Distinctions can be drawn even more finely, as for example between ectoparasites that stay permanently on their hosts and those that are off their hosts except when feeding, or between ectoparasites that are the most to the least host-specific with regard to both their host location and host preference patterns.

Parasitism is a major life style, occurring in so many of the world's organisms that it deserves, and has, coverage in textbooks of its own. Here, we will restrict mention to some of the relatively unusual insects that are external and internal parasites of other insects. Their parasitism can sometimes have enormous effects on the behavior of their hosts.

First, however, a distinction must be made between the true parasites and another much larger group of insects that live at the expense of another insect (host) that is always consumed and dies as a result. Members of this group (which includes the so-called 'parasitic' Hymenoptera and some Diptera and Coleoptera) are termed *parasitoids*, and like true parasites they may feed either externally (ectoparasitoids) (Fig. 4.7) or internally (endoparasitoids). Predators also consume their prey, of course, but parasitoids require only a single host individual to complete their development; predators generally require more than one prey. Most parasitoids are parasitic only in the larval stage, being free-living as an adult, but in the real world exceptions to strict categorization are not unusual.

Parasitoids may be solitary or gregarious in their development. Some paralyze their host and develop rapidly, a situation that differs only slightly from predation. Others manipulate host physiology in ways that permit the host to continue to grow and develop after the parasitoid lays its eggs; meanwhile parasitoid development may be concurrently delayed until the host becomes sufficiently large enough to sustain it.

Studies of parasitoid-host interactions are fundamental for implementing biological control of pest insects. A large body of published literature addresses aspects of parasitoid biology for a wide range of species. Some of these are discussed elsewhere in this book, in contexts as varied as enemies of solitary wasps, host finding and learning host odors, foraging strategies, host marking, courtship, and as a selective force in parental care.

In considering parasites and parasitoids, one once again is faced with a choice of viewpoints. Whereas many researchers study the proximate mechanisms involved in such behaviors as predation and parasitism (such as the zombification already

Fig. 4.7   Growing up together. *Melittobia digitata*, a gregariously developing ectoparasitoid, attacks the prepupa of various solitary bees and wasps. The female wasp oviposits up to several hundred eggs; upon hatching, they develop rapidly and completely consume the host

mentioned), others are particularly interested in parasitism's ultimate evolutionary context. What is the best way to interpret changes—particularly behavioral changes—observed in a parasitized host?

It would probably be rare to find a parasite that had absolutely no effect on the behavior of its host. However, simple changes such as a host becoming less active are generally just considered to be straightforward byproducts of the infection. Complex aberrant behaviors are a different story. They seem to beg for an evolutionary explanation. Are these changes in behavior simply a side effect of infection? Alternatively, might they be host adaptations that reduce pathological consequences but have little (or only accidental) adaptive value for the parasite? Or perhaps they represent manipulation by the parasite for its own purposes?

One who has searched most intently for an answer to these questions is Laura Beani of the University of Florence. Her work involves a social paper wasp *Polistes dominulus*, a strepsipteran parasite *Xenos vesparum*, and the concept of adaptive manipulation. *Adaptive manipulation* includes any alterations in host behavior that increase a parasite's 'inclusive fitness' (see Chapter 10); thus, it includes not only direct changes like those that improve the probability of the parasite being transmitted but also indirect changes that improve the host's fitness and thus in the process, its own.

The normal behavior of paper wasps is particularly well-studied. In brief, mated females emerge each spring to start new nests. At first, they must feed and care for their young by themselves, but as their offspring become adults, they join their mother in feeding and caring for subsequent young and in expanding and defending the nest.

Fewer people know of the Strepsiptera, an order of insects related to the beetles with only about 600 species. The early stage larvae and the short-lived adult males are free-living, but most of a strepsipteran's life is spent as an endoparasite in other insects (see Plate 6). The first-instar larva (called a triungulin) enters a host, usually in its abdominal region. Once inside, they induce the host's tissue to produce an internal pouch-like structure that protects them from the host's immune defenses as they feed and grow. Though the parasites do not feed directly on their host's body organs, they do greatly reduce their nutrient intake. Sometimes over 30 of these parasites may be found on one host, though three or four is far more common; when several are present, they may occupy up to 90% of the abdominal volume of their hosts.

For most of the period of infection, no external signs of the parasites are visible. However, after pupation, adult males leave the host body, and their sclerotized cephalothecae remain behind as a visible sign of this 'stylopization'. (Stylopidae is the best-known strepsipteran family.) Females, however, have no wings or legs. They remain inside, with their heads barely protruding from the host abdomen. Their odor attracts males that mate by rupturing the female's brood canal opening, which lies between the head and prothorax. Each mated female later produces many thousands of triungulin larvae that emerge from the brood opening on her head and disperse to continue the cycle.

Strepsiptera attack many kinds of insects in at least seven different orders, with hymenopterans being one of their more preferred hosts. It should be noted in passing that communal and social insect colonies must present a particularly appealing target for parasites, given their high density of potential hosts of a similar genotype. However, successfully breaking through these social defenses is generally so difficult that colonies have been called 'factory fortresses'. Studies of social wasps have suggested that nest aspects such as multiple comb construction and nest envelopes may have evolved in part to provide some defense against parasitoids and predators. Behavior is also important; for example, in Chapter 1 we discussed honey bee defense against brood diseases.

Every aspect of Strepsiptera that has been studied has proven to be highly unusual in some aspect, from their bizarre and complex life cycles to their genome, which is one of the smallest known for any insect, although the size of the entire *18S* ribosomal DNA sequence is among the biggest, containing a number of unique expansion segments. No aspect, however, is more unusual than the many ways in which these parasites alter the morphology, physiology, and behavior of their hosts.

Striking changes in host morphology are often evident even before adults become visible. The parasites' presence may change the color and shape of the host's abdomen. In many host species, both male and female become sterile, having been effectively castrated by their parasites. Females of solitary bees often have their pollen collecting baskets greatly reduced, and the sting is also often reduced in size. In males, the copulatory apparatus is often greatly reduced. Male and female hosts often appear to have acquired some appearances of the opposite sex.

Behavioral changes also occur. In ants, unhealthy workers become diurnal, abandon their nests, and climb high on grasses and bushes. When a *Stylops* female is releasing larvae, her normally slow-flying *Andrena* bee host will suddenly race from flower to flower, dragging her abdomen through the stamens and spreading triungulins that other foraging bees will take into their crops, becoming vectors for infection.

It was with this background in mind that Laura Beani and William Hamilton watched an aggregation of *Polistes* behaving strangely in the surroundings of her house in Italy. It looked like an overwintering aggregation (see Plate 5) but it was too early in the season. At Hamilton's urging, Beani began to investigate their unusual behavior. From her own inspection and previous observations by others, she was able to piece together a remarkable story. The wasps in the aggregation were parasitized by the strepsipteran *Xenos vesparum*, and their strange behavior was part of an even bigger picture of aberrant acts that spanned the seasons.

After overwintering, affected *Polistes* females did not form a stable association with healthy nest foundresses; they showed no inclination to nest or to act as helpers. However, some made unusual short-range 'migrations' from one nest to another. Resting on the nest combs, they were occasionally attacked by the nest's owners, but usually they were just ignored.

In the summer, wasps hung around listlessly in unusual aggregations like those Hamilton and Beani had observed; these were always away from the nest, often at lekking or pre-hibernant sites. The groups were initially and mostly formed by workers, not sexuals, and though aggregations might persist for days, individual turnover rates were high.

When Beani artificially infected wasps with strepsipterans and moved the wasps into large cages in the laboratory, these infected workers deserted the colony early. Though they were of no help at the nest, they were not evicted by healthy wasps, but left to their own volition. When she caged naturally parasitized and unparasitized wasps together, the stylopized wasps hung out sluggishly in the corners, ignored by the healthy ones, and they lived a long time, unusual since workers normally die and do not overwinter.

What does all this mean? It appears that the *Xenos/Polistes* interaction represents a case of adaptive manipulation. How might such diverse alterations enhance parasite success? By castrating its hosts, *Xeno*s shifts the host's resource allocations from reproductive organs to energy reserves that can directly benefit the parasite. By causing infected female wasps to cluster in groups while healthy gynes scatter to occupy good nesting sites in early spring, triungulin-laden overwintered females essentially wait within an aposematically defended herd until healthy wasp larvae are available to be parasitized. Likewise, the high turnover rate in the strange summer aggregations can be explained by the fact that these are mate-encounter sites for the parasite, not for the castrated hosts.

If only for curiosity, one must, however, return to a proximate-mechanism question. How do the parasites do this? In *Polistes*, normal worker behavior is known to depend on juvenile hormone. The stylopization syndrome resembles the pre-hibernation physiological state of overwintering wasps, when they are in a diapause ovarian state that can be broken by applying juvenile hormone. Studies have shown that the strepsipterans alter juvenile hormone production, not the wasps' sensitivity to the hormone, by their infection. Strepsipterans are the only parasitoids that cause a host's life span to be lengthened to allow for the parasitoid's life cycle completion.

What about looking at the wasps' behavior from a colony perspective? Some earlier observers, noting how infected workers leave their nest to aggregate, suggested that this nest desertion could be interpreted as an 'altruistic act' (see Chapter 10) because it reduces the infection of kin. However, only wasps carrying *Xenos* females with triungulins are vectors for the next generation; these have never been found in these aggregations.

4.2.5 Theft and Kleptoparasitism

When the fly-hunting solitary wasp, *Stictia heros*, returns to her burrow with prey, another female *Stictia* often knocks her to the ground and retrieves the dropped fly for herself. Among honeybees, the large honey store is a magnet to foraging conspecifics; weakly defended colonies are highly susceptible to raids. Many dung beetles, known as rollers, are noted for collecting feces into spheres that

are used as a food source or placed in brood chambers; these dung balls must be rapidly moved away from their source, because other dung beetles will abscond with them.

Individuals of the same species usually feed on the same type of food in much the same way, and even the diets of other closely related species may not differ by much. This may not cause much problem in situations where food is abundant and evenly distributed. (Why put out the energy to fight when there is nothing additional to be gained by winning?) However, animals that live on patchily distributed foods can experience considerable competition and even overt aggression. When competition is intraspecific, it sometimes leads to the establishment of social hierarchies and/or territoriality, systems that reduce the expression of aggression between group members.

When competition is between members of different species, extreme conflicts are expected. These conflicts exemplify the well-known ecological *competitive exclusion principle*: no two species can coexist in the same locale and utilize the same resources at the same time. The less successful competitor will either be driven to extinction or be forced to modify its feeding pattern. Modification is probably the more common outcome. An insect species may switch to a slightly different type of food, feed at a different time of day or night, or forage in a slightly different area. As a result, such competition promotes evolutionary divergence in food choice and feeding patterns.

Cuckoo bees and cuckoo wasps deposit their eggs in the nests of other bees and wasps. These insects are normally referred to as *kleptoparasites*, sometimes spelled cleptoparasites. (Their counterparts the cuckoo birds are a special case of kleptoparasitism known as 'brood parasites' because the immature parasite is fed directly by the adult of the host and raised as the host's offspring; this situation often occurs in birds but is almost unknown among insects.)

In the broadest sense, both parasites and kleptoparasites can be thought of as predatory thieves. Parasitism is a type of thievery in which one organism attacks another, stealing its energy stores and sometimes its life. In contrast, a kleptoparasite attacks the host's young not primarily as food but rather to free up the host's food store for its own offspring. In many cases kleptoparasitism probably began with simple prey stealing, such as the brigandage reported often among solitary wasps. Many kleptoparasites are closely related to their hosts and appear to have shared a recent common ancestry. Several species of a spider wasp, *Ceropales*, enter the nest burrow of close relatives after the rightful owner has prepared and stocked the hole with paralyzed spiders and laid an egg; inside the burrow, they lay a cleverly concealed egg of their own upon the stored prey (Fig. 4.8). Some *Ceropales* species substitute their own egg after eating the host egg themselves; others leave the host egg for their own young to eat.

Theft can be a great strategy when it works. Small flies that look superficially like house flies (see Fig. 1.14) are among the most abundant parasites of solitary wasps. Each of the several genera involved has its particular method of attack, but all of them produce eggs that hatch just before they are laid. These young maggots attack and destroy the wasp's egg or larva, but the maggots develop primarily upon
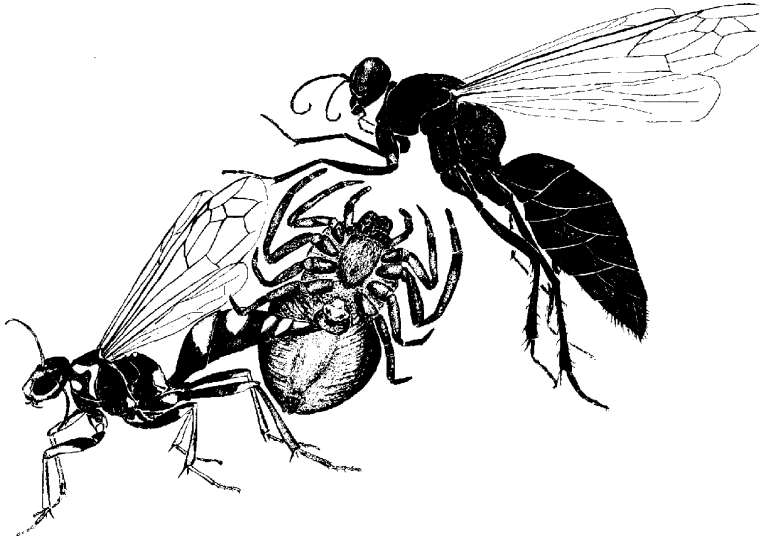
Fig. 4.8 Hiding the baby. The kleptoparasitic Australian spider wasp *Ceropales ligea* (*left*) hides its eggs in the book lungs of the spider prey used by its host, the wasp *Elaphrosyron socius* (*right*). Oviposition occurs very rapidly when the wasp briefly drops the spider in order to clear the entrance to her nest burrow

the prey in the cell. Being 'food thieves,' the flies are not at all host-specific and will attack species in several solitary wasp families indiscriminately if they are in the proper ecological location.

There is no free ride, however, and anticipated victims often fight against such theft. Many kleptoparasites have become armored in various ways, apparently as an adaptation for deflecting the bites and stings of their intended hosts. For example, the exoskeleton of cuckoo wasps (Chrysididae) is very hard and coarsely punctured (see Plate 7); when disturbed or threatened, these wasps curl into a small tight ball that is nearly impenetrable and difficult to grasp.

4.2.6 Insect Agriculture

Leaf-cutting attine ants of the New World have entered into partnership with various species of fungi that do not occur outside of their nests. A nest-founding queen has a blind pouch off her pharynx in which to carry a small fungal mass to inoculate the garden in her newly established nest. The fungus will serve as the colony's primary and probably sole food source; these ants are unable to feed directly upon cellulose. Under the ants' care the fungus flourishes in the underground nest chambers, but if ants are denied access to this garden, it rapidly deteriorates. The leaf cutters file out along well-defined trails to cut leaves, flowers, and stems to be transported to the nest, where each will be cleaned and scraped, then chewed into a small pulpy mash with salivary secretions. As the ants insert it into the fungus garden, they cover the

mash with a transplant of several tufts of fungal mycelium and one or more drops of fecal 'fertilizer.' This fecal material contains significant quantities of all 21 natural amino acids, a nutrient supplement of considerable importance, as well as providing the fungus with a proteolytic enzyme that breaks polypeptides in the leafy mass into forms that are usable by the fungus. The ants have even evolved a means to protect their food source from destruction, transporting and cultivating a crust of *Streptomyces* bacteria that produce antibiotics against serious bacterial parasites of the fungus.

This example is classic, but not alone—mutualistic feeding arrangements such as this are relatively common. Termites, ants, and beetles appear to have become fungiculturists by different evolutionary routes (Fig. 4.9). In termites it is believed that fungi were an important food source before cultivation, and fungiculture arose when the termites developed an ability to manipulate fungal growth in their nests. In contrast, ancestral beetles may have begun as vectors for fungal spores, as many non-fungus-feeding relatives of ambrosia beetles still are now. It is not clear which of these evolutionary pathways might have given rise to fungiculture in ants.

The parallels with farming have intrigued observers for centuries. Other examples involve plants and 'livestock' such as aphids. Cornfield ants (*Lasius* spp.) gather eggs of the corn root aphid, *Anuraphis*, in the fall and take them home for the winter. All winter the ants solicitously move the eggs about the nest, keeping them at appropriate temperature and humidity. When the aphid eggs hatch in the spring, the ants place the young aphids near weed roots to feed. Later in the season, these solicitous caretakers move their aphid herd to corn roots, dispersing them around the cornfield where their feeding can cause considerable damage.

Many insects have a symbiotic relationship with microorganisms. Sometimes, as in this leaf-cutting ant example, the microsymbionts live outside the insect's body, though they may be temporarily stored in special organs of ectodermal origin for purposes of dissemination. A special type of ectosymbiotic relationship occurs among some of the wood-inhabiting insects—the ambrosia beetles, wood wasps of the families Siricidae and Xiphydriidae, and some bark-feeding bark beetles. Sometimes, the fungus is eaten together with wood particles; in the most impressive cases the insects feed upon their fungus alone.

Ambrosia beetles generally have an extremely wide host range but tend to occur as secondary insects on diseased trees or felled logs. Each species is symbiotically associated with one or more specific fungi indispensable for the development of its brood. Identification of fungal symbionts is a difficult matter because they do not produce fruiting bodies; however, it appears that the true ambrosia fungi are highly specialized forms that cannot grow in the host plant in the absence of the symbiotic insect. In return, the fungus provides a rich and available food containing important vitamins for the insect and its larvae. How is fungus transmitted from an old tree or log to a new one? Early workers thought spores were simply carried in the beetle's gut or upon its integument. It now appears, however, that certain specialized organs of variable location and structure but usually confined to one sex are involved. They serve to protect the fungi from desiccation, provide secretions
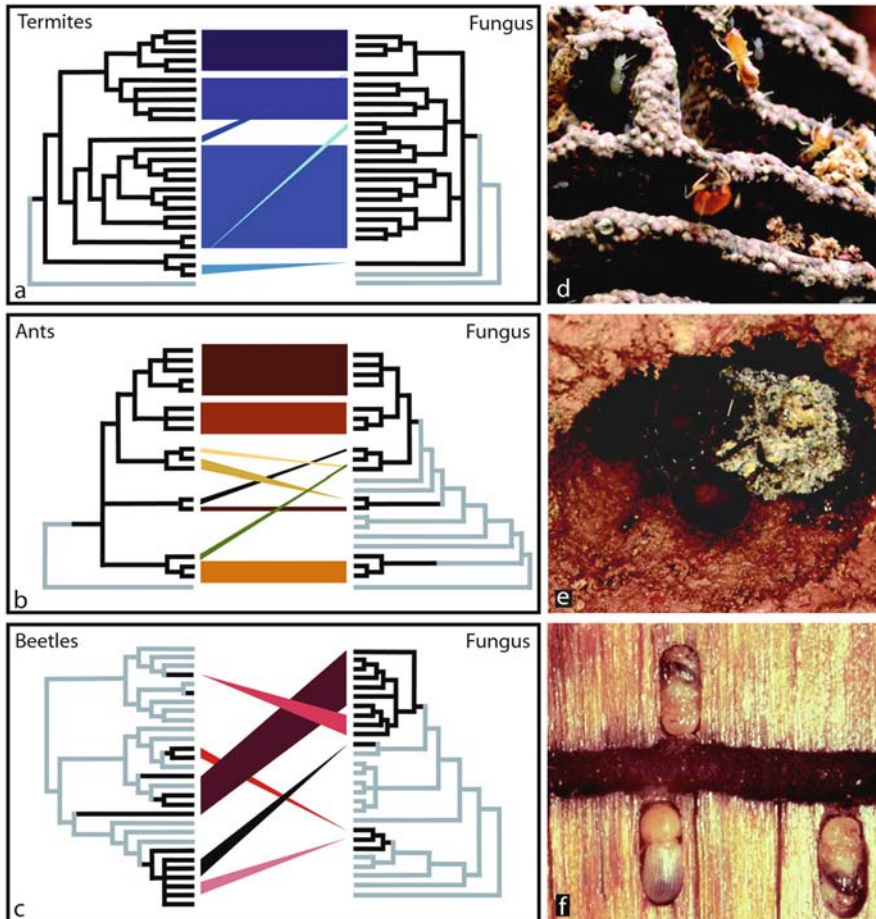
Fig. 4.9   Farming fungus. Comparison of the patterns of evolutionary diversification in three major groups of fungus-farming insects—termites, ants, and ambrosia beetles—and their cultivated fungi food. In the left cladograms, farmer lineages are shown in *black* and non-farmer lineages in *gray*; in the right cladograms, fungal cultivar lineages are shown in *black* and non-cultivated feral fungi in *gray*. Photos depict typical examples of each group: (**d**) *Macrotermes bellicosus* fungal garden grown on walls of termite fecal pellets; (**e**) *Atta cephalotes* queen resting on her incipient fungal garden; (**f**) *Trypodendron lineatum* gallery with brood niches showing the black ambrosia fungus lining the walls

necessary for germination and arthrospore formation, and ensure the mechanical dissemination of the fungus on the tunnel walls.

Wood wasps (Siricidae) also attack weakened trees or freshly cut logs. However, their symbiosis with wood-inhabiting fungi is entirely different from ambrosia cultivation. Only the larvae bore in the wood, but larval development may last two or three years. During their adult stage, wood wasps are on the wing. Female wasps possess intersegmental pouches at the base of the ventral parts of their stingers; during oviposition, symbionts are pushed out with the egg.

Whereas some insects live mutualistically with ectosymbionts, more often the mutualism takes the form of an internal symbiosis, with the microorganism living within one of several organs inside the insect's body. Most of these *endosymbionts* of insects are microscopic. Their discovery dates back to the nineteenth century, but initially their existence as independent living beings was difficult to comprehend, and they were variously described as sporozoa, yeasts, metabolic products, and yolk spheres.

Partnering with endosymbionts has enabled insects to feed on a wide range of nutritionally incomplete and/or indigestible matter. The first, and the most numerous, category of endosymbiotic hosts includes insects that suck sap, which is rich in carbohydrates but poor in protein—scale insects, leaf lice, and aleurodid and psyllid 'flies.' Among the bugs (Hemiptera), predaceous forms possess no symbionts, but those such as stink bugs (Pentatomidae) that have switched over to plant juice for nourishment have symbionts. Blood-suckers are a second important host category. All insects that suck vertebrate blood for the whole of their lives have symbionts; this includes the bed bugs and their relatives. Vertebrate blood is deficient in certain vitamins that the symbionts can synthesize. Mosquitoes are a familiar exception; they need no symbionts because they suck blood only as adults and have a bacteria-rich nourishment at their disposal during earlier developmental stages. A third group of insects with symbionts includes species that feed on cellulose-rich substrates: most famously termites. Symbionts also occur among that small group of insects whose whole life is spent on keratin-containing food, the feather lice.

Endosymbionts pose an interesting problem for their hosts—they must be rigidly retained, but they also must be passed on to offspring. Varied arrangements have arisen for housing them; these are species specific in both origin and development. Depending upon the location of these guests within their host, these include oral uptake of symbionts by young brood, smearing of eggs with symbionts, or infection of eggs or embryos before laying.

4.2.7 Nest Symbionts: Becoming a House Pet

The nests of social insects provide living quarters for a diversity of creatures besides those building them. Like our own homes despite our efforts to keep them clean, insect nests are besieged by everything from cockroaches to flies. In addition to these uninvited guests, some social insects purposely keep guests of other species in their nests, much as we keep various pets.

Depending on their hosts' identity, such symbionts or *symphiles* are referred to as termitophiles, mellittophiles, etc. A particularly impressive range of vertebrate and invertebrate species can be associated with long-lived termite and ant nests, in particular, including organisms as diverse as microorganisms, plants, insects, amphibians, reptiles, and mammals. In the case of species that live in the nests of others of their own kind, the term 'inquiline' is used (see Chapter 10).

Fig. 4.10 Begging like an ant. Larva of *Atemeles* beetle being fed by regurgitation from a worker *Formica* ant. When the beetle larva secretes a chemical from a row of paired glands along the sides of its abdomen, ants respond by intensively grooming the larva. In response, the beetle larva rears up and attempts to make mouth-to-mouth contact with the ant

Nest guests are particularly frequent in the ants, where all manner of organisms have specialized as myrmecophiles, literally, 'ant lovers.' Many bristletails (Thysanura), for example, live with ants. Feasting on debris, food scraps, and even ant corpses within their common dwelling, these bristletails reward the ants with a 'tidy house' in turn for being inadvertently fed by their ant hosts. When army ants emigrate, bristletails may be seen running in the column or riding along upon ant larvae and booty.

Beetles are also common in the nests of social insects. Sometimes, acting as scavengers they appear to be ignored by the nest owners. In other cases, the ants not only tolerate the interlopers but feed, groom, and rear their guests, as happens with *Atemeles* rove beetles (Fig. 4.10; see Case Study 4.1).

In many cases, even when their intruders eat the host ants' young, they are treated cordially. For example, *Formica sanguinea* ants avidly seek out beetle larvae of *Lomechusa strumosa*, even though the latter usually destroy the whole population of the ant hill. William Morton Wheeler expressed the puzzle well when he stated:

Were we to behave in an analogous manner we should live in a truly Alice-in-Wonderland society. We should delight in keeping porcupines, alligators, lobsters, etc., in our homes, insist on their sitting down to the table with us and feed them so solicitously with spoon victuals that our children would either perish of neglect or grow up as hopeless rhachitics.

Case Study 4.1: Myrmecophily in the Rove Beetle, *Atemeles*

How do nest symbionts gain such acceptance? Clues are apparent in the case of one well-studied example.

Among the beetle family Staphylinidae a number of myrmecophilous relationships have evolved. Some of these beetles only live along ant food-gathering trails or at ant garbage dumps outside the nest. Others live within the nest's outer chambers, but a select number have penetrated all the way inside the brood chambers. Of this last group, one well-known example is *Atemeles pubicollis*, a European rove beetle that spends its larval stage within the nest of the mound-making wood ants, *Formica polyctena*. In examining their behavior in some detail, Bert Hölldobler unraveled much of the communicative behavior between host and symbiont.

Watching the behavior of ants encountering *Atemeles* larvae, Hölldobler noticed that brood-tending ants respond to *Atemeles* by grooming them intensely. Might the ants be imbibing something from the larval cuticle? Hölldobler ran experiments with radioactive tracers, and confirmed that some sort of chemical signal was passing between the ants and the larvae. To determine its action, he variably coated large numbers of beetle larvae with shellac, then placed them at the nest entrance. As long as at least one body segment was left unpainted, the ants carried larvae into the nest and adopted them. When the entire larva was covered, however, the ants either ignored it or deposited it in the garbage dump. Hölldobler washed some beetle larvae with acetone; ants dumped most of these 'deodorized' larvae as well. Then he made filter paper dummies soaked with the acetone 'bath water' and left them at the nest entrance; like real larvae, many were carried into the nest. Paper dummies soaked with fresh acetone, however, were either ignored or carried to the dump.

Hölldobler turned his attention to a second puzzling behavior. Within the brood chambers, adult ants scurry about feeding their young. When an adult ant's antennae or mouthparts touch an *Atemeles* larva, the latter rears up and attempts to contact the ant's head. When the attempt is successful, the ant regurgitates a droplet of food (see Fig. 4.10). It appeared that the beetle larvae were imitating the behavior of ant larvae. Wondering how the beetle's success rate compared with that of the ant larvae, Hölldobler gave the ants food labeled with radioactive sodium phosphate. In a mixed brood of beetle and ant larvae, the beetles obtained significantly more than their proportionate share of food. Apparently, they were more intense as beggars than were the ant larvae. As if this were not enough, the predacious beetle larvae actually ate small ant larvae, as well. How could the ant colony survive such intense competition and predation? Observation provided the answer—the beetle larvae were not only predacious but cannibalistic. Unable to distinguish their fellow larvae from ant larvae, they cut down their own population ruthlessly, whereas ant

larvae did not. Thus, the brood chambers soon contained clusters of ant larvae but only a few scattered beetle larvae.

Further studies revealed even more behavioral complexity. *Atemeles* beetles, it turns out, have not one but two ant homes: a summer woodland domicile with *Formica* and a winter grassland one with *Myrmica*. After the beetle larvae have pupated and eclosed in their original home, they beg for one final, ample food supply. Drumming rapidly with their antennae upon an ant to attract its attention, they touch the ant's mouthparts with their own maxillae and forelegs; since this mechanical signal is quite similar to that used by ants among themselves, the ant responds by regurgitating food. Now fully fed, the adult staphylinids begin to migrate out of the nest. Guided primarily by light and odor, the beetles move into open grasslands and find *Myrmica* nests. When a staphylinid encounters one, it wanders around until it encounters an ant worker. Going through a brief ritual, the beetle moves in, carried by its host right into the brood chamber. Although the beetles are now adult, they are still sexually immature. Within these latter nests, they continue to be fed until sexual maturity the following spring, at which time they return to *Formica* nests to mate and lay eggs.

To penetrate *Myrmica* nests, *Atemeles* must adopt a new set of skills and a second language. Hölldobler again suspected chemical cues, because as the guest and host first encounter one another, the beetle antennates the ant lightly, then raises its abdomen toward its host. In response, the ant licks the tip of the beetle's abdomen, seeming to grow calmer in the process, then moves on to the side of the abdomen. Finally, the beetle lowers its abdomen. The ant then grasps bristles around the beetle's sides and carries its tightly curled guest inside. True to prediction, Hölldobler found two types of glands and secretions (see Fig. 4.11). At the tip of the abdomen, 'appeasement glands' produce a partially proteinaceous secretion that apparently suppresses aggressive behavior in the ant. Along the sides, a series of 'adoption glands' produces a chemical necessary if the ants are to welcome the beetle in. Apparently, this odor mimics the odor of members of the ant species.

Chemistry plays a large role in the acceptance of adult *Atemeles* (see Case Study 4.1), but this is not unusual. For example, 'appeasement glands' (Fig. 4.11) turn out to be fairly widespread among the better-integrated myrmecophiles including many of the ant nest beetles and lycaenid butterfly caterpillars. They are of a number of novel forms (including glandular hairs) and exist in different locations. Many types of glands aid in mediating myrmecophily, and appeasement devices are just one of a syndrome of changes in morphology and behavior that social symbionts belonging to various insect groups have independently undergone. Three are worth special mention.
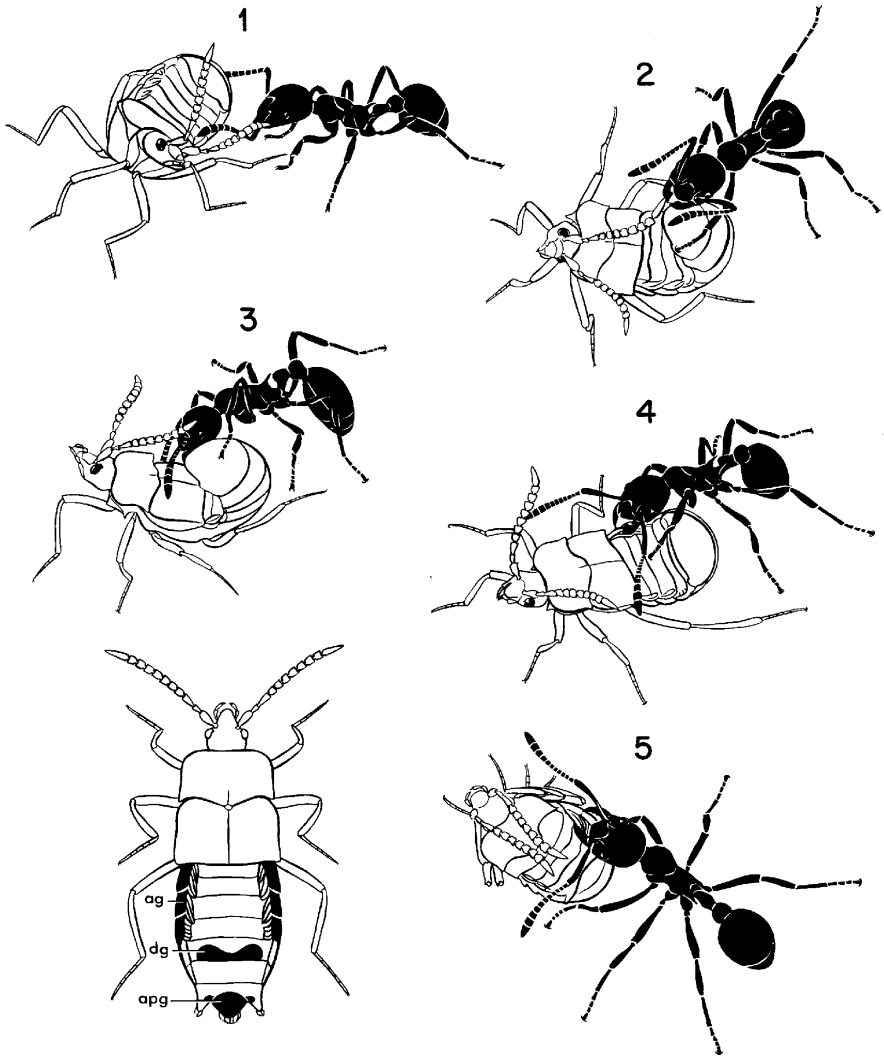
Fig. 4.11 Getting adopted. Adult *Atemeles* beetles' entry into nests of *Myrmica* ants is largely chemically mediated. Encountering a potential host and worker, the beetle presents the tip of its abdomen and taps the ant lightly with its antennae (**1**). The ant responds by licking the abdomen, ingesting an 'appeasement' chemical from the 'appeasement gland' that apparently serves to suppress the ant's normally aggressive behavior toward intruders (**2**). Next, the ant licks the sides of the beetle's abdomen where it obtains an 'adoption' secretion (**3, 4**) that releases its brood-carrying behavior. It picks up the tightly curled beetle and carries it into the nest brood chamber (**5**) where the beetle now has access to the ant's brood

First, many symphiles look very much like their hosts. Commensal staphylinids, in particular, strikingly resemble ants, with a slender body form, antlike 'petiole,' and even body sculpturing and color (Fig. 4.12); this antlike appearance is found almost nowhere else in this large family of beetles. Early investigators working from
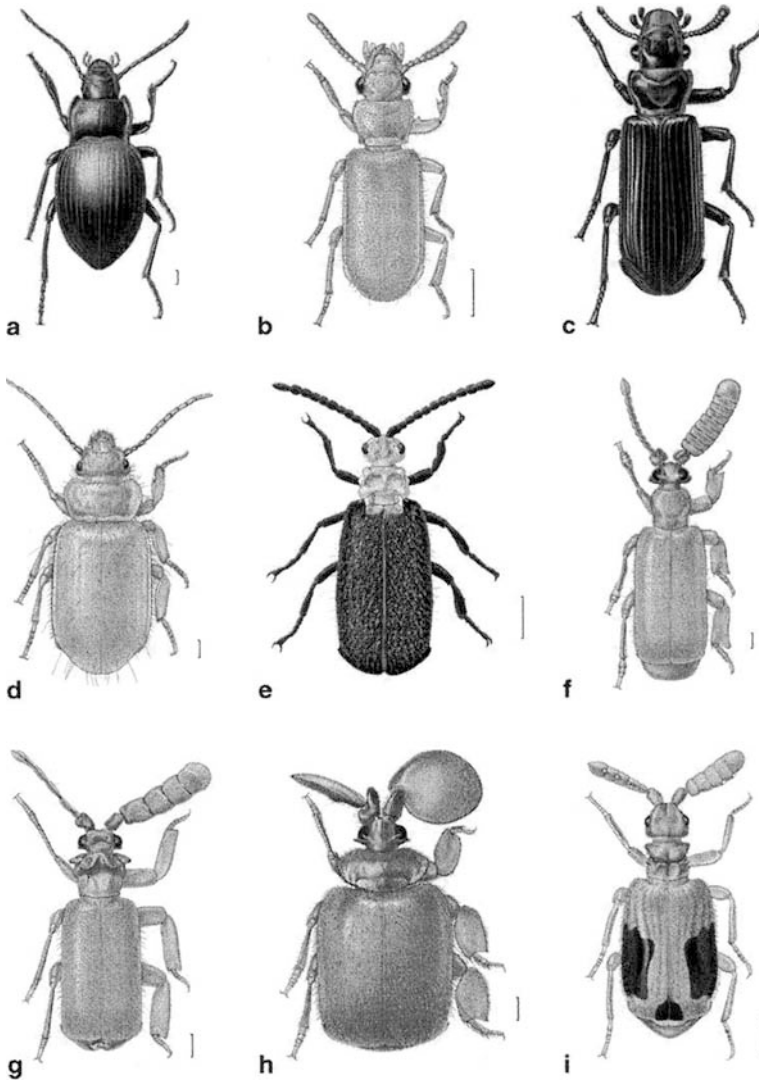
Fig. 4.12 The habits of ant nest beetles (Carabidae: Paussinae) range from free-living and predatory to obligatory myrmecophily, and these differences are reflected in their morphology. All these beetles are displayed here with the right legs and antennae at their broadest view and the left extremities at their narrowest view. Scale bar, 1 mm

museum specimens believed that the antlike body form of the symphiles was tactile mimicry to deceive their host ants and that color was visual mimicry to deceive birds and other predators that attack marching ant columns. However, for ants chemical identification is paramount; if an ant's surface odor is disturbed even slightly, other workers will immediately attack it, even though its morphology has not changed.

Therefore, it seems unlikely that such mimicry is tactile and directed toward ants. Current thought is that predators watching ant columns for edible morsels have been the selection agents for both the color and morphological mimicry.

A second adaptation characteristic of many unrelated symphiles is *physogastry*, a condition in which the abdomen is greatly enlarged, particularly in its membranous parts. Physogastry appears to be one of the major ways in which termitophiles, particularly among Coleoptera and Diptera, mimic their hosts. To human eyes, such swelling often makes them superficially resemble termites, but the question of whether physogastry is a primarily visual or primarily chemical adaptation is difficult to answer because direct study of termites and termitophiles poses problems. Termitophiles are extremely delicate, and it is usually necessary to crack open the termite nest to reach them and then make one's observations under quite artificial laboratory conditions. In at least some cases, there appears to be a mutual exchange of exudates between termites and termitophiles, and histological studies of some termitophiles demonstrate the existence of various abdominal glands and pores. Whether termitophiles and their exudates are beneficial to termites is unknown, but it is clear that termitophiles depend on their hosts. Most physogastric species have such rudimentary mouthparts that they could no longer feed themselves and such a heavy dependence on the controlled temperature and humidity of the termite nest that they do not live long if they are removed from it.

A third morphological adaptation of many termitophiles and myrmecophiles is a limuloid (teardrop-shaped) body. Generally, it is assumed that this body form has arisen for defense because it would be difficult for an ant or termite to grasp the smoothly streamlined dorsum. However, actual field observations of limuloid symphiles are even scarcer than those of physogastric species.

Termites, ants and other social Hymenoptera all care for their larvae progressively and exhibit fundamentally similar ways of communicating; no really great differences exist in colony size or in length or stability of colony life. However, specialized symphiles are almost unknown in nests of the social bees and wasps. The few mites, beetles, and flies that live as scavengers and brood commensals are quite generalized in form and behavior by comparison with symbionts of ants and termites. Most are probably either attacked by their hosts or treated indifferently. Why this difference? Probably the most plausible explanation centers around nest structure, location, and feeding habits. Ants and termites live in relatively open systems rich in refuse. Many chambers and galleries go unguarded from time to time, and the nest interiors are generally made of material not too different from the immediate environment—soil and rotting vegetable matter. Furthermore, young are reared clustered in groups. Social wasps and bees, in contrast, 'run a tight ship' and construct compact (and often tightly sealed) nests, typically in arboreal locations. Thick envelopes of carton or wax pose formidable obstacles; nest entrances, often narrow and tightly guarded, may also be lined with sticky substances and/or repellants. Young are reared individually in specially constructed cells that make it more difficult for a symbiont to conceal itself. Furthermore, rubbish inside is usually sparse; even when detritus occurs, workers simply heave most of it out the nest entrance.

4.3 Coevolution and the Arms Race

Caterpillars of tropical heliconiine butterflies feed on particular species of toxic *Passiflora* vines; some *Passiflora* produce tiny structures that mimic *Heliconius* eggs and thus fool visiting butterflies into avoiding 'further' oviposition. Oak trees produce high levels of tannins in their leaves that chelate nitrogenous compounds; gypsy moth caterpillars maintain a gut pH so high that it inhibits chelation, allowing them to feed on the leaves with impunity.

How did such systems come about? Paleoentomologists say the earliest insects were small, wingless creatures that lived and fed chiefly in moist forest floor litter, a mode of life still continued by the bristletails and springtails today. However, various insects also grazed on the nutritious spores from sporangia on the tips of plant branches. Over evolutionary time, as plants became vascularized and grew to greater heights, insects followed, as crawling, jumping, and finally flying forms arose. Seed plants evolved; seed-eating insects followed. Hard seed coats developed; insects found ways to tunnel into them. When the first flowering plants appeared early in the Mesozoic Period, an almost limitless new food source became available. Insects were quick to take advantage of it, and a rapid evolutionary radiation occurred.

When two or more populations, species, or genomes interact in this way, impinging so closely upon each other that each acts as a strong selective force on the other's evolution and causes direct, genetically based changes, the reciprocal stepwise adjustments that occur are called coadaptation or, more commonly, *coevolution*. These interactions cover a broad range of scenarios—including competition between species, mutualism, mimicry, or such 'consumer/victim' exchanges as predator/prey, herbivore/plant, or parasite/host relationships. Thus, even though it can be difficult to prove that true coevolution has occurred in a particular case under observation, the concept has broad explanatory power and intellectual appeal. Detailed coverage of coevolution is beyond the scope of this book, but a brief introduction to the topic is justified because insect feeding has figured so prominently in coevolution research.

Evidence such as Australia's dramatic control of adventive prickly pear cactus by an introduced cactus-feeding moth demonstrates that insect herbivory at least has the potential to act as a powerful selective agent on plants. Likewise, outbreaks of agricultural and forest pests emphasize the selective potential of insect feeding. That the challenge of herbivores should be regarded as a *major* selective pressure in plant evolution was first explicitly emphasized in the mid-1960s by Paul Ehrlich and Peter Raven. In the years since, the plant/herbivore aspect of coevolution has emerged as a major interdisciplinary focus. Plant species have been likened to islands defended by chemical, mechanical, and biological barriers, penetration of which may allow an insect species to exploit a new 'adaptive zone.' Presumably, the metabolic costs of maintaining these barriers and the depredations of those species that have overcome and even exploited them are more than offset by the general degree of protection these defenses provide against other potential herbivores and pathogens. (One's meat is another's poison.)

According to coevolutionary theory, a succession of defenses against herbivores is produced in a stepwise fashion by a particular plant species. At each step, some herbivores go extinct, while others circumvent the botanical innovations, forcing the plant to evolve further deterrents. Through time, the process may be regarded as a series of filters or doors through which the plant and remaining successful herbivore taxa are alternately released for flurries of adaptive radiation. This process is often called 'escape and radiate' coevolution.

Cospeciation as a result of reciprocal interactions between two interacting species, a process called *pairwise coevolution*, has received a great deal of research attention. However, in coevolution as in war, battles are often waged simultaneously on several fronts. Diffuse or *guild speciation* occurs when the genetic change in at least one species affects its interaction with two or more other species. For example, early season attack by flea beetles makes sumac plants more susceptible to stem-boring cerambycid beetles; developing resistance to the former would also reduce the impact of the latter. On the other hand, some cucumber genotypes have evolved high levels of the chemical cucurbitacin. This chemical helps them resist attacks by mites, but concurrently the plants become more attractive to cucumber beetles.

4.3.1 Attack, Defense, and Counterattack

Potato plants are members of the Solanaceae, a family of plants whose species are often rich in alkaloids with effects that range from mildly irritating to fatal in small quantities. Yet consider the common potato beetle, *Leptinotarsa decemlineata*. Although the mother beetle actively chooses a site for egg laying, the larvae do not usually begin feeding near the place of hatching. Instead, they begin searching, guided mainly by vision, until they encounter a potato plant; at this point, they begin randomly biting the substrate over which they are walking. Close-range olfactory stimuli from the plant are attractive to the larvae. If the proper smells are present, they clip off any hairs on the plant surface and pierce the epidermis. Tasting the potato plant, they finally decide whether to reject it or begin feeding.

Despite a common misconception, coevolution does not necessarily enhance mutual harmony or promote stable coexistence of species. Obtaining, maintaining and protecting an energy pool is the major preoccupation of every individual in any species. Sharing this energy with organisms of other species is evolutionarily maladaptive unless one gains, or expects to gain, at least indirect benefit in return. Therefore, an insect should protect its own energy pool against other would-be consumers and at the same time try to break through the defenses of other species, particularly those at a lower trophic level, to take advantage of a lucrative potential energy source. For each species, this results in a more or less continual battle of attack and defense or counterattack, waged over the ultimate trophy of enough energy for successful reproduction.

Plants likewise seek to protect themselves, often by chemical means, but many insects turn this around and use it to their own advantage. Odor normally mediates

the first steps in herbivory, determining whether the insect detects the plant as a potential host for sampling and whether it takes the first bite. Removing or blocking olfactory organs in a variety of insects leads to acceptance of non-host plants otherwise treated as inedible.

Considerable experimental and observational evidence confirms that a particular subset of plant chemicals are utilized by insects as distinctive cues to identify and discriminate among their host plants for feeding and breeding. They include alkaloids, terpenoids, essential oils, and quinones. Terpenoids are particularly widely represented. The lower molecular weight representatives include highly volatile compounds that function as floral scents that attract pollinators. Those with higher molecular weights include plant resins, cardiac glycosides, and saponines that are typically distasteful or toxic to herbivores.

Because these chemicals, which are of almost universal occurrence in plants, included a diverse array that were not known to have any function in plant growth or metabolism, early researchers called them 'secondary substances'. One view held that they were either metabolic by-products (waste products) or metabolic precursors needed for some as yet unknown physiological functions. Another school contended that such metabolically expensive 'curiosities,' which are often produced in large quantities, have a *primary* significance to the plant as defensive substances, and to label them as 'secondary' was in a sense an ironic injustice.

From the 1950s on, evidence has rapidly accumulated in favor of the latter interpretation. Some authorities prefer the term 'plant natural products' for this reason. However, the term 'natural product' also has come to mean a chemical compound or substance produced in nature that has a pharmacological or biological activity of potential use in pharmaceutical drug discovery and drug design. Many of the secondary substances do in fact fit this definition, but others do not (at least yet). At present, *secondary plant metabolites (SPMs)* seems to be the preferred name for these chemicals. The term 'secondary' distinguishes them from 'primary' metabolites, the removal of which results in immediate death to the organism. Sometimes, elimination of a secondary plant metabolite may have no apparent effect at all, but more often closer study reveals that removal can impair long-term survivability or fecundity.

Whatever one chooses to call them, to an insect these chemicals function widely as signals of edibility, either by their presence or by their absence. Even though they may differ widely in other respects, the food plants of a particular insect species, genus, or even family often share similar secondary plant metabolites. The concentration of these chemicals often differs in various parts of the plant in ways that seem to correlate with the need to protect them from attack. For example, the natural insecticide pyrethrin is concentrated in flower heads, which seems logical because protecting future seeds would seem more important to a plant than protecting individual leaves.

Some of the best SPM examples occur in the cabbage family Cruciferae, which includes many garden vegetables from turnips and radishes to broccoli and kale. The pungent smell and tastes of cruciferous plants are due to mustard oil glucosides, particularly sinigrin, that cause most insects to consider them inedible. However, for

some species, the reverse is true; experimental studies show that sinigrin acts as a feeding stimulant for the turnip aphid and the cabbage aphid, and these species consider plants inedible that lack the chemical. (Interestingly, inedible does not always equate to non-nutritious. When leaves of 10 non-host plant species were treated with sinigrin, aphids readily fed upon them all; five of the plant species turned out to be nutritionally adequate to support the growth and development of at least one generation of aphids.)

Producing strong chemicals is a knife that cuts two ways, however. Plant defensive compounds can substantially reduce herbivore feeding, but these compounds may be energetically expensive to produce, and their production competes with the production of other necessary compounds and tissues. Moreover, insects also identify plants by their chemical fingerprints, and many have come to use plant volatiles for their own purposes. One way in which plants can balance the tradeoff is to produce two groups of chemical defenses. One is a chemical fingerprint made up of constitutive defenses that are always present; it tends to consist primarily of relatively unspecific but generally effective compounds. If and when actual damage occurs, however, these general compounds are joined by inducible defenses that are more specific to particular types of injury. Bark beetles on pine trees provide a classic example. During the initial beetle assault, the trees produce pitch, a gummy terpenoid-containing mix that prevents bark penetration and seals wounds. However, if the beetles successfully break through the bark, the tree produces more complex phenols that can kill the beetle and cause lesions to form in the tissues surrounding the wound.

Other herbivores steal the plant's chemical defenses for protection against their own enemies. The relatively inert exoskeleton provides an ideal site for passive storage of toxic compounds. A famous example is the monarch butterfly whose larvae sequester vertebrate heart poisons from their milkweed host plant; later, stored in the butterflies' wings, the chemicals confer protection from many birds. Some go well beyond passive defense. Some sawfly larvae that feed upon foliage of coniferous trees store the resinous defensive chemicals in diverticular pouches in their foreguts and regurgitate the fluid to repel predators. Likewise, some coccinellid beetles store plant toxins derived from their prey in their hemolymph, and can bleed the toxic fluid reflexively from their leg joints. We'll return to this subject in Chapters 5 and 6.

Still other insects use secondary plant metabolites for sexual communication. Some male nymphalid butterflies congregate to feed at the dead shoots of plants containing dehydropyrrolizine alkaloids and then biochemically modify the ingested alkaloids to produce chemicals used during courtship. Many moths similarly have an intricate relationship with plant chemistry. Likewise, virgin female polyphemus moths will not begin their sexual call unless stimulated by *trans*-2-hexenal which emanates from leaves of their host plant, oak. (In other tree species, the activity of this chemical is apparently masked by other odors.)

Insect responses to plant chemicals take many forms (Table 4.1), but generally can be divided into two categories: immediate and delayed reactions. So far, we have concentrated on immediate responses, which are basically behavioral. Now,

Table 4.1 Some ways that plant-produced chemicals may affect plant-eating insects

Chemical actions	Insect's response
Repellents	Oriented movements away from source
Attractants	Oriented movements toward the source
Arrestants	Aggregation at source
Stimulants	Enhanced feeding, mating, or oviposition
Deterrents, suppressants	Inhibition of feeding, mating, or oviposition after attraction to source
Phytohormones	Developmental anomalies; failure to molt or metamorphose properly
Growth regulators	Changes in growth and/or development
Toxins	Sickness or sometimes death
Nutrients	Reduced fecundity and longevity
Sterilants	Incapacitated reproductive system (none presently reported)

let's briefly consider delayed reactions, which are largely physiological and include developmental anomalies, toxicity effects, and hormonal changes.

Insect development and reproduction are governed primarily by two hormones—molting hormone (ecdysone) and juvenile hormone. A large number of plants produce their own version of these hormones. Some of these analogues are extremely potent; plant-produced ecdysones have been identified that are as much as 20 times more active than the ecdysones produced by the insects themselves. These hormone mimics are highly disruptive to insect development, typically preventing maturation or producing imperfect and sterile adults. They can function as potent deterrents and anti-feeding agents, sometimes even at dosages strikingly lower than expected. (As might be expected, however, some insects have evolved enzymes capable of detoxifying such compounds.)

Research is finding that many ferns and gymnosperms produce ecdysone analogues. There is a common myth that ginkgo trees and ferns are free from insect attack; as survivors of relatively ancient plant groups, they are said to have outlived all their enemies. As with all myths, there is a kernel of truth. Chemical analysis of ginkgo leaves has confirmed that the leaves are highly acidic and inhibitory to insect feeding. The 'bullet-proof' reputation of ferns has not held up as well. A number of common and widespread ferns are almost insect-free because they produce high phytoecdysone concentrations, but other fern species quite commonly suffer attacks from insects that range from bark beetles to Lepidoptera larvae (Fig. 4.13).

Certain plants also have mimicked that other major insect hormone class, the juvenile hormones. A well-known example is the so-called 'paper factor' story. The setting for this episode was the Harvard University laboratory of Carol M. Williams in 1964, when Karl Slàma came from Czechoslovakia to spend a year and brought along his favorite laboratory insect, the native European fire bug, *Pyrrhocoris apterus*. Very soon it became clear that cultures of *Pyrrhocoris* were not faring well in William's laboratory. Instead of metamorphosing into adults at the end of the fifth instar, the fire bugs molted to an extra larval stage to form giant sixth
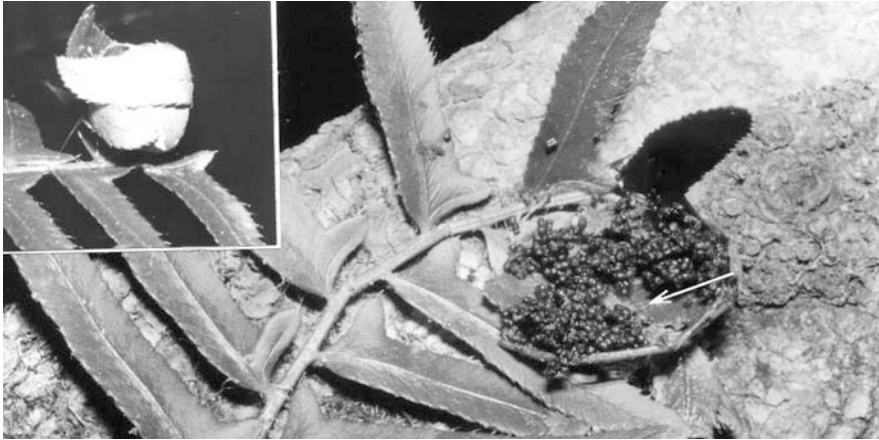
Fig. 4.13 Feeding on ferns. Christmas fern frond, knotted (corner insert) at the tip as a result of feeding by a *Herpetogramma aeglealis* (Pyralidae) moth larva (*arrow*). The larva notches the stem so that it coils, but leaves the vascular bundles of the rhachis intact. No one yet knows whether this is an adaptation to avoid plant-produced ecdysones

instar nymphs, which ultimately died without becoming sexually mature. Every precaution had been taken to eliminate all sources of hormone contamination from the culture containers, yet the problem seemed to be clearly of a hormonal nature. Baffled, Slàma and Williams undertook a systematic analysis of every item in the bug's culture environment, searching for evidence of suspected juvenile hormone. By a process of elimination the culprit was at last found—the paper toweling used to line the cage floors. When the researchers substituted the filter paper that Sláma had always used in Prague, the bugs again developed normally. Further detective work traced the origin of the hormone to paper pulp derived from the Balsam fir (*Abies balsamea*), a principal pulp tree indigenous to North America. This bit of serendipity was the first indication of the existence of juvenile hormonal materials occurring naturally in plants. As with ecdysone, juvenile hormone analogs have since turned up in a diverse array of plants.

Whereas ferns and gymnosperms reply primarily on insect hormone analogues and terpenoids for defense, angiosperms more commonly produce alkaloids, phenols, and many other compounds. In fact, just as it is often said that 'no two snowflakes are alike,' many scientists postulate that each plant species has a unique 'chemical fingerprint' conferred by its own mix of secondary plant metabolites.

Plants also produce analogues of essential amino acids; over 300 of these are known, primarily from legume seeds. These are potent defenses against insect feeding, because proteins constructed with these analogues are toxic, interfering with many physiological processes. A particularly potent group of these analogues are the alkaloids, which have been identified from about 20 percent of higher plant families. Used with extreme medical care, many of these (such as atropine, belladonna, digitalis, strychnine) are familiar pharmaceuticals, but even at relatively low concentrations they are highly toxic and teratogenic.

Not all plant defenses are chemical, of course. An arsenal of spines, thorns, pubescences, and tough cuticles characterizes many plants from cactus to acacias. Such structural features of plant surfaces have long been assumed to confer a certain measure of resistance to herbivore attack, and their prevalence seems to bear testimony to the intensity of herbivore pressure. (However, some may have arisen in response to other selective pressures; for example, the waxy texture of succulent leaves undoubtedly helps to prevent desiccation.)

Physical barriers can be very effective. Female cereal leaf beetles lay significantly more eggs on smooth-leaved strains of wheat than on strains with leaves covered in dense, fine hairs; furthermore, larval survival is much lower on densely pubescent plants. Various morphological traits of the bean family (Leguminosae)—including such devices as flaky-surfaced pods that scale off eggs, gummy sap, and pods that explode when penetrated—lower the success of bruchid weevils attempting to oviposit in or on the seed pods. The foliage of many species of Neotropical passion flower vines is eaten by larvae of flashy heliconiine butterflies. However, when vines of one species, *Passiflora adenopoda,* were exposed to *Heliconius* attack in the laboratory, no feeding damage occurred. In fact, the larvae that had been placed on the plants were found dead and desiccated by the next day, even though other *Passiflora* species in the laboratory were heavily eaten. The cause of the immunity of *P. adenopoda* was traced to the cloak of hooked trichomes (hairs) that cover the plant's surface. Scanning electron micrographs verified their defensive function—the trichomes made numerous puncture wounds in the larval integument, immobilizing the larvae and causing them to starve to death.

When they occur together, mechanical deterrents and chemical ones provide considerable plant defense against feeding, but as always, some insects have turned the tables. Camphorweed (*Heterotheca psammophila)*, a common roadside plant of the American southwest, has leaves, stems and buds covered with tiny glandular hairs which produce droplets of aromatic resin that effectively deter most insect feeding. However, the female of a reduviid bug *Apiomerus* spends hours harvesting these droplets, which she then uses to fasten her eggs into a resin-covered cluster. The resin, a complex mixture of terpenes, deters ants and other egg-eating insects and may protect the eggs from microbial pathogens as well.

4.3.2 Employing Mercenaries for Protection

One of the stranger types of defense employed by plants against herbivores uses other organisms as a front guard or standing army. These mercenaries are paid, in turn, through benefits they receive from the plant. Mutualistic relationships between organisms are widespread. Some of the best illustrations may be found among the ants, many of which have become specifically adapted to live upon certain plants. One of the best known is that between ants and a diverse assortment of sap-sucking plant bugs that excrete sugary drips of semi-processed phloem sap called 'honeydew' as they feed. Various ants exploit the concentrated food bonanza in such a

systematic fashion that some early naturalists likened it to cattle farming. In return for the aphids' honeydew—produced not only passively during feeding but also on demand in response to stroking by the ant—the aphids receive protection from their predators and other services (see Plate 10). These ant-aphid protection systems are generally very well integrated. For example, when ants are exposed to artificial sources of the green peach aphid's alarm odor, they respond aggressively. Ants guarding *Prociphilus* will even readily attack a human finger that approaches their wooly aphid flock.

In a very real sense, plant-ants may be regarded as analogous to the secondary compounds found in the foliage of most plants, the primary defense of their plant against herbivores, as was illustrated by Daniel Janzen's studies of acacia bushes and the ants that guard them (see Plate 8 and Case Study 4.2). Many other ant–plant relationships have been noted both before and since Janzen's work. Each will require the same sort of detailed investigation in order to understand the dynamics and evolutionary adaptations on the part of the participants before they can be truly termed mutualisms. One of these is the interaction between *Cecropia* plants and certain species of *Azteca* ants throughout Central America; like the acacia, *Cecropia* produces glycogen-rich food bodies (trichilia or Müllerian bodies) that are harvested by its ants. Another is a 'parasite', *Pseudomyrmex nigropilosa,* that Janzen later discovered; this ant harvests the resources of the swollen-thorn acacias but it does not protect the acacia, attack foreign objects, or clean debris from the foliage.

Case Study 4.2: Coevolution of Acacias and Their Ants, *Pseudomyrmex*

The mutualism between plant ants and ant plants is highly coevolved and costs each contributor a substantial energy outlay, but each participant also derives considerable benefits.

In disturbed areas in the lowlands of Mexico and Central America, a common shrubby tree is the bull's horn acacia, *Acacia cornigera*, so named for the pair of swollen, hornlike thorns that occur at the base of most of its leaves. A rapidly growing woody plant that cannot tolerate shading, it quickly springs forth as sucker growth from old rootstocks in pastures, along roadsides and in natural disturbance sites such as riverbanks and arroyos. Close examination of the plants reveals that they crawl with small *Pseudomyrmex ferruginea* ants, which pour forth from holes in the thorns whenever the acacia is touched (see Plate 8). In the 1800s the naturalist Thomas Belt had discovered a similar relationship between an ant and acacia in Nicaragua and noted that the ends of each leaf segment were modified into peculiar little oval structures. These 'Beltian bodies' seldom survived long, because the ants cut them off and either ate them or fed them to their young. Subsequent studies have shown that they

have an unusually high food value for foliar tissue, on the order of yeast in quantity and quality of nutrients.

Following Belt's discovery there was a great deal of armchair speculation on the exact nature of the relationship between ant acacias and acacia ants. The ants clearly depended upon the acacias because most acacia ant species had been recorded only from living ant acacias. But did the acacias benefit from the presence of the ants? Two viewpoints persisted: one stated that the ants were merely exploiting the acacia, while the other regarded the relationship as a true symbiosis. This question became the focus of intensive eastern Mexican field studies by Daniel Janzen.

One of Janzen's early observations was that these acacias were commonly left untouched in pastures with cows and other domestic animals. From a local farmer, he borrowed a pet native deer that was thought not to have had any previous experience with *A. cornigera*. When he offered it foliage that had been cleaned of all ants, the deer ate the foliage readily, including some of the thorns. After several days of feeding the deer unoccupied foliage, Janzen offered a branch complete with some very agitated ant workers. As the deer began to eat the foliage, ants ran onto its face and stung; immediately the deer stopped feeding and withdrew to clean them off. Similar simple experiments with cows and burros—animals that may have had previous experience with *A. cornigera*—gave results that did not differ materially but suggested additionally that these herbivores may have learned to recognize the alarm odor of the ants and learned to avoid contact with the plant.

The survival of the bull's horn acacia is dependent upon rapid growth so as to remain unshaded. Thus, Janzen began to examine the relative growth and development of occupied versus unoccupied shoots of *A. cornigera* by treating selected shoots with an insecticide. A number of striking differences emerged. First, the frequency and extent of phytophagous insect damage was greatly increased in shoots from which ants were removed; this resulted in a great lowering of the growth rate of the shoots. In contrast, ant-occupied shoots remained virtually free of phytophagous insects because the latter were quickly attacked and removed from the shoot by worker ants. At least 40 species of insects fed on unoccupied shoots of *A. cornigera*, but only eight species attacked occupied acacia shoots, and even the cumulative sum of their feeding was not serious. During the rainy season, phytophagous insect activity increased greatly, and the differential growth rates of occupied versus unoccupied shoots became even more striking. Unoccupied shoots showed almost no growth, but occupied shoots grew vigorously. Because of their slow growth rate, surrounding vegetation quickly shaded the unoccupied acacias, and this further slowed their growth. Many unoccupied shoots simply died.

Data from experimental plots also confirmed another observation that Janzen had made, namely that occupied shoots were almost always free of

living vines even though the acacia plant appeared ideal for the support of vine growth. Whenever foreign vegetation contacted the acacia plant, the ants would maul it and chew off the growing tips. In this way they prevented vines and lateral branches of neighboring plants from growing into the canopy of occupied *A. cornigera*. Unoccupied acacias, in contrast, accumulated heavy masses of vines during the rainy season. Vegetation-mauling activity of worker ants also resulted in a bare circle on the ground around the base of the shoot. Janzen felt that this behavior was of significance in protecting the shoot from fires as well as in lowering the incidence of phytophagous insects reaching the shoot. Even when the shoot was killed by fire, suckers from protected rootstock in the bare basal circle quickly sprouted and were immediately colonized by the mature ant colony, giving the new shoot an immediate competitive advantage in the post-fire succession.

Based on these data and observation of occasional naturally unoccupied acacias, Janzen concluded that a shoot of *A. cornigera* must be occupied by a colony of *P. ferruginea* for a substantial part of its life to produce seeds and become a part of the reproductive population. Because of the interdependence of the ant and acacia for normal population development, the interaction between them could properly be called obligatory mutualism.

4.3.3 The Tommy Tucker Syndrome: Food in Return for Services

'Little Tommy Tucker sang for his supper ...' Mother Goose may have been on to something. Many insects transport pollen and/or seeds in return for food or other rewards. Violets, for example, reward ants for collecting their seeds by incorporating lipid-rich compounds (elaiosomes) into them that are highly attractive. In the previous section we discussed coevolution in the context of plant defense. However, this is only one part of a much broader coevolutionary picture that has been particularly well studied in the context of pollination.

Pollination in its most basic sense is simply the transfer of pollen from the male sex organ (anther) to the receptive portion of the female sex organ (stigma) in flowering plants. If the transfer is successful, it leads to fertilization and seed production, and the plant reproduces. This process often involves some external vector, usually wind, water, or animals. Authorities are in general agreement that the first insects to become anthophilous, or pollen-loving, were the Coleoptera; even today, most simply rummage around in flowers, destroying some flowers by feeding on them but in the process managing to pollinate others. Pollination apparently appeared next in the Diptera, but fly pollination is understudied and probably also underrated. With the development of pollination habits in Lepidoptera, highly mutualistic associations began to become quite common, reaching their culmination in the Hymenoptera,

especially among the bees. Today, while many insect taxa visit flowers and thus cannot be dismissed as pollination agents, members of these four largest insect orders still are pollination biology's major players.

Many flowering plants provide primary rewards—including nectar, pollen, lipid secretions, food bodies, scents, resins, and nest building materials—that attract pollinating insects and keep them returning. In addition, most insect-pollinated flowers also produce sensory cues—including odors, colors, shapes, textures, and tastes—that distinguish their own flowers from other species and make it easier for an insect to find more of their own flower type. For most flowering plants, this step is crucial for pollination success because they are self-incompatible.

Have plants tailored these cues to attract certain pollinators and exclude others? The concept remains controversial. Patterns certainly exist. A typical flower pollinated by a night-flying hawk moth (see Plate 42) is white and has a strong sweet fragrance; a typical flower pollinated by day-flying butterflies is red and has very little odor. Particularly among tropical flowering plants, these signals are often combined into patterns that some scientists have recognized as *pollination syndromes* related to the type of pollen vector. However, it is also true that rather than a single pollinator type, many flowers are visited by 'guilds' that include diverse insect taxa, and the composition of these guilds may change over time. Furthermore, just because an insect is an apparent guild member and visits a
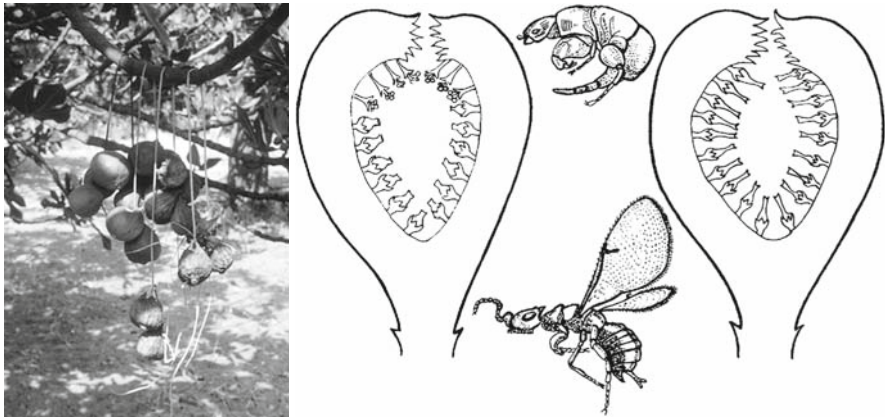
Fig. 4.14   Pollinating figs. (*left*) Caprification in an orchard in Greece involves hanging bunches of 'goat figs' from tree branches. Pollination by the wasps that develop from these inedible fruits is necessary to produce a mature edible fig crop. (*right*) Not all figs require fig wasps for pollination, but among those that do, the fruits come in two types; compare the internal flower structure of the 'goat figs' at the left and the edible fig on the right. Fig wasps develop in the ovule of the short-necked female flowers that pack the inside of goat figs. Before dispersing, newly emerged winged females (*middle bottom*) mate with wingless males (*middle top*) and collect pollen from the male flowers that cluster around the upper end of the goat fig. When the females find the new crop of fruit, they enter the figs and thus pollinate them, but inside these edible figs the flower necks are too long for their ovipositors to reach the flower ovaries. Thus, they cannot lay eggs or rear offspring in the figs' edible generation

flower does not always mean it is actually an effective pollinator of that plant. For these reasons, some pollination biologists see little conceptual value in pollination syndromes.

Because pollination is so closely tied to reproductive behavior, not just of the plants but of the insects as well, this subject will come up again in Chapter 9. For now, let us consider an example of the extreme forms that pollination mutualism can take—the relationship between fig wasps (Agaonidae) and their fig plant hosts (Fig. 4.14).

Although the Smyrna fig story has received the most attention (see Case Study 4.3), figs actually include about 850 species of woody trees, shrubs, vines, and epiphytes, most of which are native throughout the tropics. The fruits of many species are edible and serve as important food resources for wildlife. Most tropical *Ficus* species bear several crops of syconia through the year, with short- and long-necked female flowers and male flowers in the same syconium. Because the female flowers are receptive several months before the male flowers release pollen, they require wasp pollination between synchronized syconia of the same or different species.

Case Study 4.3: Mutualism Between Fig Trees and the Wasp, *Blastophaga*

The most delicious figs require tiny symbiotic wasps to pollinate their minute flowers. The relationship is so perfectly timed and intricate that if one partner should die out, the other would inevitably follow.

Although European honey bees were valued co-travelers to the New World for their honey production, one of the first insects introduced into North America specifically to pollinate a crop came to southern California in 1899 to help with a problem—whereas common figs had been grown successfully in the American Southeast and Mexico for two to three hundred years, the choice cultivar called the Smyrna fig consistently failed to produce a crop. The trees grew well, but immature figs simply dropped off rather than ripening. Why? Farmers were puzzled until they realized that the trees were missing an essential pollinator that was not native to California. However, they could not merely import the wasp, because the mutualism was very complex.

What we call a fig is actually a *syconium*, a specially adapted involuted group of multiple flowers, rather like an almost-closed jug with flowers lining the inside. The flowers cannot be seen unless the fig is cut open; doing so reveals the flowers as fleshy 'threads' that each bear a single seed inside. There are many kinds of figs, but only one, *Ficus carica,* is cultivated on a commercial scale. Its ancestors arose long ago in Asia Minor; some archeologists say fig trees were cultivated before cereal grains were domesticated. Wild populations of this tree include both male trees and female trees. Early authors

thought they were different species; a key to understanding this complex system came with the realization that they are actually two natural sexual forms of the same species, and that the two flower sexes develop asynchronously. A second breakthrough was the realization that these Old World fig trees house a tiny wasp, *Blastophaga psenes*, that is vital to their reproduction.

Male Old World fig trees actually bear both staminate and pistillate flowers, but they produce fruits that contain only wasps and pollen. Generally not eaten by humans, the fruits were named 'caprifigs' because they were commonly fed to goats. Male trees produce three crops of inedible seedless figs per year that maintain the pollinating wasps—profichi that produce abundant pollen and ripen in early summer; mammoni that have short-style flowers and ripen in the fall; and mamme with long-style flowers that overwinter on the tree and ripen in spring. Within the profichi, female flowers develop first; their shape is modified in a way that makes egg-laying easy for dispersing female *Blastophaga* wasps that push their way through a tiny pore into them. Soon afterwards, the pore closes, and the syconium becomes virtually impervious to insect entry. In response to oviposition, the flowers swell like tiny galls, each nourishing a developing wasp larva that feeds safely inside.

As the profichi reach maturity, so do the young male and female wasps within. Wingless males chew holes in the sides of their nursery chambers, escape, find females still imprisoned in adjoining chambers, chew into these, and quickly mate. Pollen-bearing male flowers in the profichi are now also mature; to leave the fig where they were born, females wasps must pass through a ring of these male flowers surrounding the fig's entrance, becoming well dusted with pollen.

Female trees, by contrast, produce only one or two crops: a parthenocarpic (seedless) breba crop that ripens in early summer and a main crop that ripens from late summer to fall. Though the figs on female trees also have flowers of both sexes, the male flower parts fail to develop. Breba figs are never pollinated because they develop before male profichi ripen on nearby male trees. Main crop figs may become pollinated or not, depending whether they receive pollen via pollen-loaded *B. psenes* wasps from nearby mature profichi. (Commercially cultivated fig tree types differ in their production of breba figs and their need for pollination.)

As the female wasps emerge from caprifigs and begin to search for new immature syconia in which to oviposit, they encounter an evolutionary surprise—the fig trees are now producing not profichi, but edible figs that have only large numbers of female flowers with long-necked styles. Ovipositing in these is all but impossible, but in their repeated vain attempts to do so, the female fig wasps successfully pollinate what will become edible figs. Some fig wasps find still another type of small, inedible figs on the tree's uppermost branches. These 'mamme' or mother figs contain only short-styled female

flowers in which the female wasps can oviposit successfully. Young male and female wasp larvae hibernate within, to begin the profichi–fichi–mamme cycle anew the following spring. The delicious Smyrna and Calimyrna figs are a dead-end for the pollinating fig wasps, however.

As a result of this understanding of the fig/fig wasp mutualism (see Fig. 4.14), Calimyrna figs are now grown successfully throughout California's hot San Joaquin Valley. Every June, visitors see a most unusual sight— thousands of acres of fig orchards 'decorated' with small brown or white paper bags stapled to the lower limbs. Inside each bag is a caprifig branch with pollen-bearing profichi, picked prior to emergence of its associated fig wasps. Although wasp-bearing caprifig trees have become naturalized in moist riverbeds and creeks in California, they are kept at some distance from orchards. Controlling the pollination process using only the bagged caprifigs is important, for if too many wasps pollinate an edible fig, it splits open and has no commercial value.

Typically, only one wasp species is capable of fertilizing the flowers of each species of fig. Therefore, plantings of fig species outside their native range results in effectively sterile individuals. It should be noted, however, that the common fig cultivars grown in home gardens in southern and western North America require no pollinator. A single dominant mutant gene is responsible for this change; rather than prematurely dropping unpollinated fruits as the Smryna figs do, the common fig trees expressing this gene retain unpollinated developing figs to maturity. The ability to produce sweet fig fruits without the need for male trees that carry symbiotic fig wasps within their syconia is very advantageous to farmers in regions where wild caprifigs and natural pollinator wasps do not occur. However, these fig trees must be propagated by cuttings because they do not produce seeds.

4.4 Feeding as a Communal Activity

Gregarious feeding is characteristic of some herbivores, such as tentworm caterpillars and various sawflies (Fig. 4.15). Courtship feeding, another type of cooperative social feeding between conspecific individuals (see Chapter 9), is also common. It is among the truly social insects, however, that cooperative feeding behaviors are exhibited in their widest scope and variety. In fact, certain social feeding behaviors are more or less unique to the social insects.

4.4.1 Simple Groups and Feeding Aggregations

Larval sawflies, caterpillars, and chrysomelids all have converged on a lifestyle that includes a syndrome of maternal care, larval gregariousness, or both, suggesting to some evolutionary biologists that there might even be something about
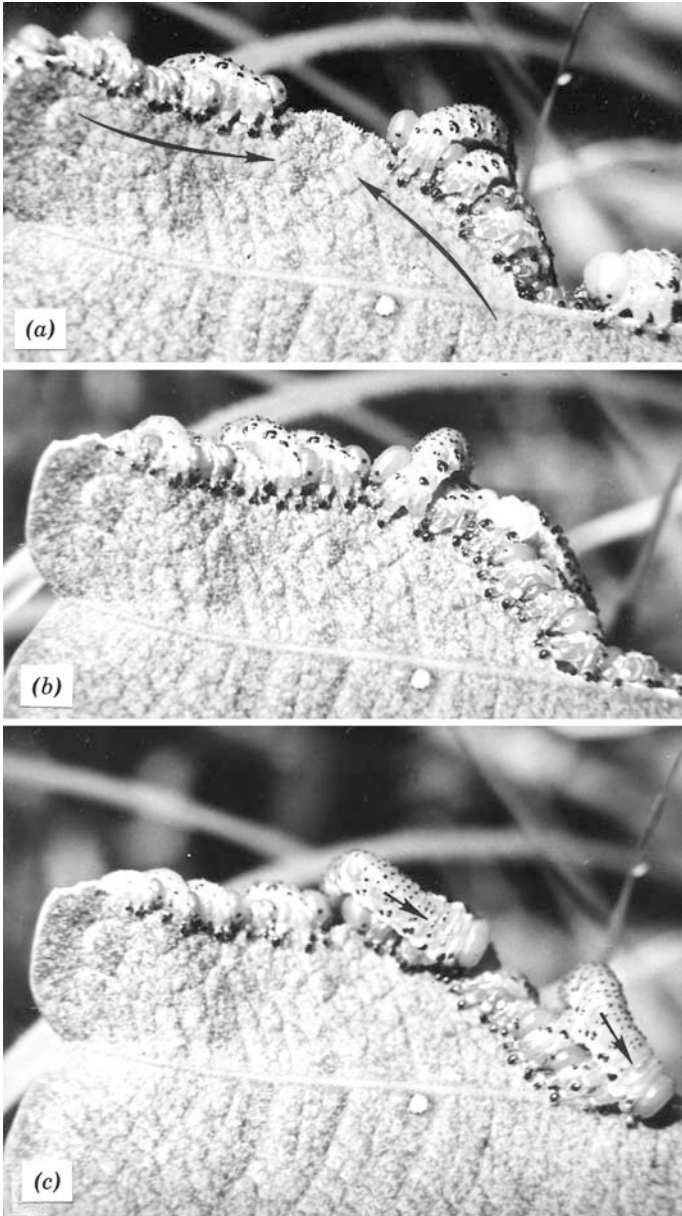
Fig. 4.15 Gregarious feeding. 'Escalator style' feeding by larvae of the Brazilian sawfly, *Themos olfersii*, whose host plant possesses extremely tough leaves. Aligning themselves in two convergent rows, the young larvae use their enormous heads and jaws to gain access to the thick edges of the leaves (*a*). As the larvae feed, the leading individuals are pushed forward until they collide (*b*). Upon collision, the leading larvae retreat to the ends of the rows (*c*) where they cannot readily feed, while others are moved forward for a turn at eating. This process continues for many hours

the nutritional and defensive ecology of exposed leaf feeding that selects for this syndrome.

Gregariousness, the tendency to gather in groups, begins with laying eggs in batches. Often, even the eggs of gregarious species are chemically defended; the tip-off is their bright coloration. It might seem puzzling for vulnerable eggs to be advertised, but advertising is the point. Such eggs are, in fact, packed with unpalatable or even toxic compounds, often in such high doses that a single egg is enough to kill an ant.

All gregarious leaf-feeding species that have been studied are chemically defended as well. There have been relatively few empirical tests of the efficacy of these chemicals against an insect species' known natural enemies, but some suggest that predators are more likely to be deterred than permanently stopped. This may be enough, however, to give prey the statistical advantage necessary to select for the strategy.

Because of these chemical defenses and bright coloration, it is generally assumed that almost all simple feeding groups and feeding aggregations function to improve defensive capabilities. However, increased feeding efficacy may be equally or even more common. One well-studied example involves the imported willow leaf beetle (see Case Study 4.4).

Case Study 4.4: Group Feeding and Cannibalism in the Willow Leaf Beetle, *Plagiodera*

Among some group-feeding larvae, the Dr. Jekyll of better defense and feeding efficiency has a flip side, the Mr. Hyde of cannibalism. What balance of costs and benefits maintains such patently antisocial behavior?

Across eastern North America each spring, females of the willow leaf beetle, *Plagiodera versicolora,* (see Plate 12) emerge from overwintering sites under loose bark and begin laying the first of their two or three clutches of 15–20 eggs. The larvae of this little metallic blue-green chrysomelid complete their development in about two weeks and soon become reproductively active themselves, so that even on a single tree, broods of different generations and ages can be found as the summer progresses. The larvae stay in tight aggregations throughout the first two instars, then gradually become less gregarious as they continue to grow. Like many larvae with a social childhood, *Plagiodera* produce copious chemicals, in this case through paired dorsal glands. They also often assume a 'cycloalexis' formation with their heads facing out, like pioneers circling their wagon train.

Since 1985, Michael Wade and Felix Breden have been thoroughly researching *Plagiodera* group behavior. Their early field studies yielded puzzling results; the first year, larval survivorship showed a significant positive relationship to initial group size. The next year, they could only say that the group size-survivorship relationship varied considerably in space and time.

What was going on? Breden and Wade designed a clever way to address the question. First they located natural *P. versicolora* clusters in the field, and randomly assigned them to group size and duration classes. Then they 'downsized' the aggregations to create replicate groups of various sizes that were followed and collected at various intervals over a week's time. When they analyzed their data, once again survivorship was unaffected by initial group size, but an interesting new relationship surfaced. Larvae gained significantly more weight in larger groups. Thus, Breden and Wade concluded that for this species, the benefit of group living related more to increased feeding efficiency than to increased defense. Careful observation provided the reason. In 1994, Wade described feeding facilitation in this species. Each larva attempts to break through the cuticle of a willow leaf by rocking from side to side as it bears down with its mandibles. When one larva succeeds, others stop their own rocking and move to the break to feed. Larger groups presumably allow more and earlier breaches of the plant's defense.

Gregariousness begins with laying eggs in batches. Imagine the surprise of these observers upon finding that newly emerging *Plagiodera* larvae are intensely cannibalistic for about 24 hours before they switch to become strict vegetarians. At first glance such behavior looked very antisocial and selfish; if it happened frequently enough, it seemed as though it could completely destroy the group. There must be some serious trade-offs in costs and benefits for this cannibalism to persist, they reasoned.

Feeding efficiency might be one benefit. At the end of 24 hours, cannibalistic individuals weighed a very noticeable 14% more than non-cannibalistic larvae in the cluster. Presumably these larger larvae would have an increased chance of early successful leaf penetration, and through their success, other group members' feeding would be facilitated, as well. However, the positive effect of group size on larval survivorship was weakened in groups with cannibals simply because cannibalistic feeding has the obvious effect of reducing group size.

At present, perhaps all that can be conclusively said is that for a non-cannibalistic *P. versicolora* larva, being a group member is clearly advantageous in terms of survival and growth, but that the presence of cannibals in the group can completely undermine these advantages. Interestingly, for a cannibal, the work of Wade and Breden indicates that fitness is not dependent on group size or the percent of cannibals in the group. Rather, it depends on the average larval fitness of everyone in the group, cannibal and non-cannibal alike, plus a personal fitness gain that the cannibal experiences from dining on its siblings.

Like water from a bottomless well, complex and fascinating new questions about *P. versicolor* keep arising. For example, if average survivorship declines in the presence of cannibals but the cannibals themselves do well, is this

an evolutionary equilibrium? To assess selection within and between groups, Breden and Wade have performed a great many field-based experiments in which they manipulated group size and proportion of resident cannibals. Is there a genetic basis for cannibalism? Very possibly; without it, the behavior cannot be subject to selection. Certainly, the species appears to be polymorphic for it; some 41–77% of the colonies exhibit cannibalistic individuals. Are group members closely related? With colleagues Wade and Breden have examined kinship structure, and found that it varies widely among localities and years, due both to multiple mating and to colony merging. Is cannibalism lower in groups consisting of closer kin? This needs further study; if so, it would be consistent with kin selection (see Chapter 10). Do cannibals reproduce more than non-cannibals? This is another key question that needs an answer, because if so, it could provide a strong group selection example (see Chapter 10). Another question that has been raised concerns whether the cannibalism is a simply a carryover of an ancestral trait; the type of comparative study of solitary relatives that would be needed to determine this has yet to be done.

4.4.2 Social Feeding Behaviors

When a social wasp larva is fed by an adult, the larva almost always secretes a droplet of salivary fluid, which the adult imbibes. In many social insects, chemical communication signals are spread through the colony by an exchange of liquids between nest mates. The reciprocal exchange of liquid foods between colony members, a behavior called *trophallaxis*, occurs both between adults and between adults and larvae.

Trophallaxis is highly developed in social insects. It appears to occur generally throughout the eusocial wasps. Among bees and ants, on the other hand, its occurrence is highly variable, apparently determined both by phylogenetic position and ecological constraints. In termites, trophallaxis has multiple functions. Lower termites share both 'stomodeal food' from the salivary glands and crop and 'proctodeal food' from the hindgut. The former is the principal nutrient source for the royal pair and nymphs; the latter, a milky material quite different from feces, contains symbiotic flagellates. These break down the cellulose that the termites are otherwise unable to use as a source of nutrition. With each molting these hindgut symbionts are lost, and the nymphs must acquire new ones. Among the higher termites, the habit of proctodeal trophallaxis has been lost along with dependence on symbiotic flagellates for cellulose digestion. However, the nymphs have become entirely dependent on stomodeal exchanges and no longer even possess functional mandibles.

Since 1918 when entomologist William Morton Wheeler first coined the term for this unilateral or bilateral liquid food exchange, there has been strong dispute over the signal value of these liquids. Some entomologists have even suggested

that the word trophallaxis should be used synonymously with communication because it provides a mechanism for maintaining a colony-specific odor. However, trophallaxis serves more functions than simply communication. The larvae of some vespid wasps, for example, take over certain metabolic functions for the colony through trophallaxis. Receiving proteinaceous food from the adults, they transform it into carbohydrates that are stored and, if required, later returned to the adults. Because the adults are apparently unable to synthesize these essential nutrients, such behavior is critical to colony survival during periods of food shortage, such as rainy periods.

Both prolonged direct observations and radioactive tracer studies have shown that in the majority of social insects trophallaxis allows a material to be distributed throughout a colony with striking rapidity (Fig. 4.16). Trophallaxis is an open system—each individual shares with an unlimited number of nestmates. Although trophallaxis requires both a giver and a receiver, which individual performs which role largely depends upon the state of their crop contents at the moment, and roles can easily be switched. For example, a set of *Formica* ant workers showing predominantly begging behavior can be shifted to predominantly donor behavior simply by feeding them to satiation. Because of this rapid exchange, it has been said that ants have a 'communal stomach'; each worker shares virtually the same diet and is kept informed of the nutritional status of the colony as a whole. Therefore, when an individual worker reacts to feeding stimuli in terms of its own hunger or satiation, in the majority of cases it is also acting in a way that is appropriate for the colony as well.

What are the releasers for a trophallactic exchange? In the honey bee, they appear to be the combination of tactile and olfactory cues provided by a honey bee head with antennae intact. A freshly severed head will elicit either begging or offering; if its antennae are removed, the head is less favored until insertion of imitation wire antennae of the proper length and diameter restores its effectiveness. In addition,
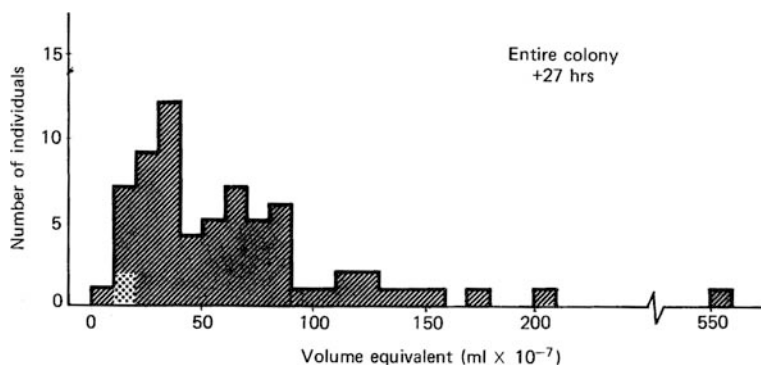
Fig. 4.16 Sharing a 'communal stomach.' *Formica fusca* is an ant species that engages in rapid oral trophallactic exchanges. Within a day after a single worker was fed small amount of honey mixed with radioactive iodide, evidence of the radioactive food was present in varying amounts in every colony member, including the 2 queens (*stippled part*). Over time, the frequency distribution of individual shares of the radioactive food became progressively more normalized

both ants and bees appear to favor larger individuals, with the result that queens, males, and larger workers tend to receive more than they give.

In social wasps, the release of trophallactic behavior is more structured and complex, because dominance relations place severe constraints on food exchange, slowing the rate of food distribution and increasing the variance in crop contents among workers. For example, an inert severed head does not release trophallaxis in *Vespula*; rather, the pair must engage in a very definite pattern of continuous reciprocal antennal signaling. Dominant workers receive more food than they give. The mother queen always receives and seldom ever gives, and virgin queens dominate over their worker sisters. Males, possessing a quite different antennal form, are quite inept at begging and must rely primarily upon surreptitious sips of the regurgitated liquids being passed between others or upon stimulating larvae to give forth salivary secretions.

In the previous section, we considered cannibalism in the context of simple feeding groups; now let's revisit the subject in the context of eusocial insects. All termites studied to date eat their own dead and injured on at least some occasions, a degree of cannibalistic behavior that is far more intense than in any other social insect group. Some *Reticulitermes* termite workers even eat apparently healthy nestmates when grooming is carried too far. If the cuticle of a leg is broken, for example, the leg is eaten, and then the whole termite is consumed. Winged *Coptotermes* reproductives that are unable to leave on a normal nuptial flight are finally killed and eaten by workers. Alien conspecific workers that enter a termite nest are generally disabled, then consumed. Because termite diets under natural conditions are usually low in protein, it is generally believed that this cannibalism functions as a protein-conserving device. Colonies of *Zootermopsis angusticollis*, for example, become intensely cannibalistic when reared on a laboratory diet of pure cellulose, but adding sufficient casein to the diet reduces the cannibalism to almost zero.

Among the social Hymenoptera, cannibalism of adults is rare in some groups, unknown in most. However, a related phenomenon is common—eating immature stages. In ant colonies, for example, injured eggs, larvae, and pupae are quickly consumed. When colonies are starved, workers begin attacking healthy brood as well. Hunger and the degree of such *brood cannibalism* are so precisely related as to suggest that the colony's store of immature stages functions normally as a last ditch emergency food supply to keep the queen and workers alive.

A related phenomenon, widespread in the social Hymenoptera, is egg cannibalism, *oophagy*. In the more primitive social groups, the dominant queen eats the eggs laid by subordinates, thus ensuring that her own progeny will predominate. This exploitive character has been transformed into something quite different among the higher social Hymenoptera, however. In these groups it has become an important form of food exchange between cooperating members of the same colony. Sometimes, oophagy functions like brood cannibalism; once colonies are well under way, if workers are starved the eggs are the first brood stage to be eaten.

In other cases, workers lay eggs that seem designed only to be eaten. Most workers of *Atta* leafcutter ants have rudimentary ovaries that never produce eggs.

However, a few small and medium workers form a retinue around the queen and lay large, flaccid eggs that lack yolk. The eggs are not viable; they serve only to feed the queen. Such *trophic eggs* have been reported in a wide diversity of ants and are apparently laid in enormously varying frequencies among the various ant species. As a rule, however, the more frequent the exchange of trophic eggs, the less frequent the liquid exchange through trophallaxis. Other cases of trophic egg-laying, primarily in which mothers provide non-developing eggs for offspring to eat, have been found not only among social and subsocial insects, but throughout the animal kingdom from amphibians to fish and marine gastropods.

Chapter 5
Defense: A Survival Catalogue

A predator can be a predator more than once, but an individual that becomes a prey item necessarily finds itself in this position once only...

5.1 Introduction

A great variety of moths spend their days resting safely upon tree trunks, so perfectly matching the mottled bark that their very invisibility forms their defense. To repel honey thieves, some stingless social bees erect walls of sticky resin in front of or around the nest entrance, while other species smear a repugnant liquid there. Taking a more active and direct approach, pentatomid bugs earn their common name of 'stink bug' from the odorous, distasteful chemical they discharge when disturbed.

Because herbivory is such a major insect lifestyle, Chapter 4 concentrated upon the evolutionary arms race between herbivorous insects and plants. This chapter will consider the analogous evolutionary battle of wits between insect predators and parasites and their insect prey. Almost all insects face a nearly constant threat of death. A familiar estimate states that a single pair of houseflies is capable of producing 125 billion great-great grandchildren were all their offspring to survive. Obviously this does not occur. When averaged over a span of many years, the hundreds or thousands of eggs a female insect may lay usually result in only a few adults that reproduce again. This high percentage of losses is due to a variety of factors, but a major one is predatory attack.

Defined broadly, *defense* includes all the ways that organisms respond to perceived threats by potential predators, parasites, and microorganisms. Whereas the insect immune system generally provides the ultimate defense against bacteria, viruses, protozoans, and fungi (and backup defenses after parasite attack), behavior and life history strategies provide front-line defenses against assault from macroscopic predators and parasites.

Most past attention focused upon insects as prey of vertebrates, with defense against invertebrates tending to be overlooked or its importance discounted. However, insects are often their own worst enemies. Aphids are preyed upon by a wide variety of insect enemies from adult pemphredonine wasps to coccinellid

beetle larvae, syrphid flies, and lacewings, yet these small, soft-bodied creatures are far from helpless. A formicine ant stumbling into a foreign ant colony is quickly hit with venom spray; the victim responds with much grooming and rubbing of its mouthparts on the ground. The nests of certain tropical social wasps are suspended on a single stalk that is continually treated with secretions from the wasps' abdominal glands; ants are repelled from walking upon treated stalks but otherwise enter and destroy developing brood within the nest. Likewise, relatively little research has accounted for the fact that insects are also continuously under siege by less conspicuous but nonetheless significant microorganisms, such as bacteria, fungi, viruses, nematodes, and parasites. In these contexts, such chemicals may have long-term antagonistic or even antibiotic effects.

The potential predator as an evolutionary force has important implications in every form of defense. For example, in considering color crypsis, the optic system of the predator must be considered. Insects and vertebrates inhabit what amount to two very different spectral and focal worlds, a subject that will receive more attention in Chapter 7. Moreover our own sensory world often differs from that of an insect's vertebrate predator, a fact that can lead human investigators astray. For example, Chapter 8 raises the possibility that many insect 'protest sounds' might actually be vibrational signals intended for conspecifics.

5.2 Defense Messages

Eleodes beetles react to threats by performing a headstand and firing a stinking irritant spray from their abdomens into the faces of their small vertebrate assailants. Some mice have evolved a way of thwarting this defense—quickly grabbing a beetle they stuff its abdomen into the sand and proceed to calmly devour their prey from the head down.

In order to live long enough to reproduce, all animals must eat, and their food choices are limited to materials derived from other life forms. With animal flesh being among the richest food sources in energy and nutrients, not surprisingly a fierce competition has arisen, as organisms strive to eat others without themselves being eaten. Under such severe pressure, selection greatly favors those individuals which are able to reduce the risk of attack or injury with the most effectiveness while simultaneously interfering the least severely with their performance of other necessary activities.

Defense is often complex and multi-modal for the simple reason that no given set of defensive maneuvers is equally effective against all enemies nor equally functional at different life stages. The puss moth caterpillar, *Cerula vinula*, is one of the most elaborate in its defense. When it rests upon a branch it resembles a curled poplar leaf with a blackened margin, even to holding the two prongs of its tail together like a leaf stalk. When a threat appears, however, the caterpillar quickly throws off its passive protection, rearing its head to display the startling crimson front of its prothorax with its two eyespots. Simultaneously, the caterpillar spreads its forked tail, everting red whip-like threads from its ends and flourishing them in

the air. Finally, when the attack persists, the caterpillar forcibly ejects from its prothoracic gland a burning, colorless fluid containing 40% formic acid. The adult puss moth has none of these defense options open to it.

At the same time, certain defense strategies have widespread utility, so evolutionary convergence commonly occurs in various structural and behavioral adaptations. Thus, defensive behaviors have been classified in various ways. One way is to examine each sensory modality in turn; for example, Table 5.1 presents basic types of visually perceived anti-predator adaptations. Another approach to classifying insect defenses is to consider the prey-to-predator message that is implicit in a particular behavior or structural adaptation. Approximately half a dozen such messages will handle the bulk of the variety of insect defenses. Lets examine these and see how, when, and why these defenses have survival benefit.

5.3 Passive Messages

Broadly speaking, insects sort into two non-exclusive categories—passive or active—with respect to adaptations for defense. For example, body coloration is a passive defense that can make an insect either conspicuous like a monarch butterfly or difficult to see like many moths that blend into their background. On the other hand, when an insect aims a shot of acrid chemical upon a potential predator, thwarting the capture attempt, it is active indeed.

Some defenses are completely obvious, always apparent, and carried with an insect as it goes about its daily life. They are sometimes called *primary defenses*. Most of these require no particular special action, and by virtue of always being present, can be considered to be passive messages. Other defenses come into play only after actual contact with a potential enemy. The latter are termed *secondary defenses*; they typically require some type of active response or reaction on the part of the insect, and so can be considered as active messages. However, like nearly all attempts to categorize behaviors, such a dichotomy is not absolute. For example, a passive defense such as camouflage is enhanced by the active behavior of becoming motionless. On the other hand, a noxious chemical may be passively incorporated into body tissues but the predator must actively contact it in order to learn to avoid it.

In the first stages (search and detection) of the predation cycle, a prey's primary defenses are of critical importance. Later in the predation cycle (attack and handling), as a predator actually contacts a potential prey and attempts to ingest it, the stakes are raised for a potential prey. At this point, one or more new forms of active defensive behavior generally are immediately elicited.

5.3.1 Crypsis: 'I'm Not Here!'

A whole series of insect larvae including geometrid moth 'loopers,' noctuid caterpillars, and sawfly larvae have come to resemble pine needles, with alternate stripes of pale and dark green and a resting behavior in a straight line parallel to the needles themselves. Stick insects often resemble the substrate upon which they rest with

Table 5.1 Visually mediated systems of passive defense and their correlates

Adaptation category	Correlated abilities			Predator response
	Morphological	Behavioral	Populational	
I. Crypsis (a) Imitate background	Countershading; disruptive coloration; homochromy; dorsoventral flattening; body flanges; often secondary startle mechanisms	Prolonged immobility; night feeding; correctly orient; select proper background; special poses; dash and freeze or move slowly	Genetic plasticity and/or polymorphism for color forms; low population density; dispersed distribution	Fails to discriminate prey from substrate
(b) Resemble inedible objects	Correct shape, color; finely detailed patterns favored; often have startle mechanisms	As above; rocks, teeters, mimetic poses	Dispersed distribution; low population density	Confuses prey with inedible objects
II. Bizarre forms	Unusual appearance, style, Gestalt; may possess startle mechanisms	Unexpected, unusual and/or startling behaviors	Dispersed distribution; low population density	Fails to see prey as food; startled, lets prey escape
III. Simple aposematism	Weapons (stings, bites, poisons); bold vivid pattern, often red, yellow, orange, black; conspicuous structure	Usually diurnal; may aggregate; conspicuous behavior; warning displays	Clumped distribution; high population density	Learns to recognize prey as distasteful and/or dangerous
IV. Mimicry (a) Müllerian	Same as for III; superficially similar to others in complex	Conspicuous behavior similar to others in complex; may aggregate	Clumped distribution; high population density	Learns Gestalt is distasteful and/or dangerous
(b) Batesian	Conspicuous coloration and/or structure similar to model(s)	Similar to model(s)	Mimetic polymorphisms; low population density; dispersed	Confuses prey with one it has learned to avoid
(c) Wasmannian	Similar to predatory host, at least in releasers; chemical, auditory, tactile mimicry favored	Similar to predatory host that serves as both model and selective agent	Low population density; linked to social insects with large colonies at maturity	Allows prey to approach; is exploited, may become prey itself
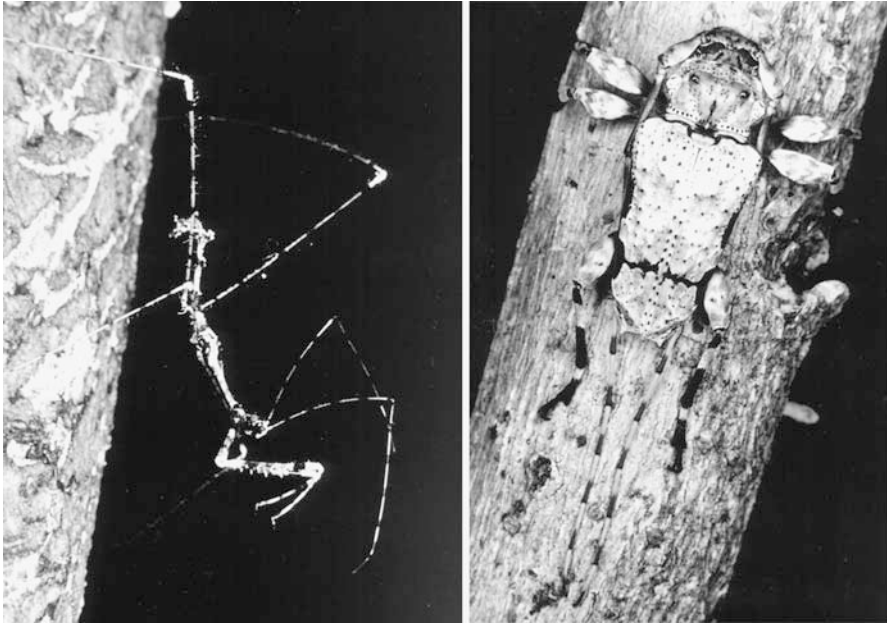
Fig. 5.1 **Disrupting the outline**. (*left*) A threadlike reduviid bug (Emesiinae) from Panama is so thin that it 'disappears' except when viewed from the side. Its banded legs are an example of disruptive coloration that enhances its ability to merge into the background. (*right*) The banding pattern on the antennae and hind legs of this resting Neotropical long-horned beetle (Cerambycidae) create the additional illusion that the beetle is going in the opposite direction

striking accuracy. Katydids may imitate leaves to such an extent as to include copies of blemishes, fungal spots, or bird droppings in addition to reproducing the proper leaf tint and venation.

By far the commonest method by which insects evade potential predation is through camouflage or *crypsis*, that is, by imitating certain environmental background features; a wide variety of diverse unrelated insect groups often have evolved to simulate the same inedible (to a carnivore) object. Crypsis involves at least shape, color, and color pattern (see Plate 14). In some instances it probably also involves scent and sound matching although human sensory apparatus may not be equal to the task of discerning it. To be maximally camouflaged, a cryptic individual also must solve the major problem of body contour. Probably the most widely used solution is disruptive coloration, a visual breaking of the insect's outline so that parts of it appear to fade separately into the background (Fig. 5.1). A second way of minimizing contour cues involves actually or apparently reducing any telltale shadows. This may be accomplished through a dorsoventral flattening, as occurs in many aradid bugs, often in combination with lateral flaps or various irregular body protuberances that bridge the gap between body and substrate.

Of course, even the most exact reproduction will be of little value in concealment without appropriate behavior, such as resting on the proper background in the right

orientation and attitude, moving seldom and/or slowly and in such a manner as to attract as little attention as possible. Thus, properly considered, crypsis is not solely a matter of coloration or morphology but a type of behavior as well. For example, many moths have wing stripings that resemble grooves in bark; those moths with vertical stripes rest on tree trunks with their heads pointed up or down, but horizontally striped moths orient themselves at right angles to the trunk.

Another widely encountered method for eliminating shadows is countershading, that is, a compensatory deepening or lightening of body color to counteract
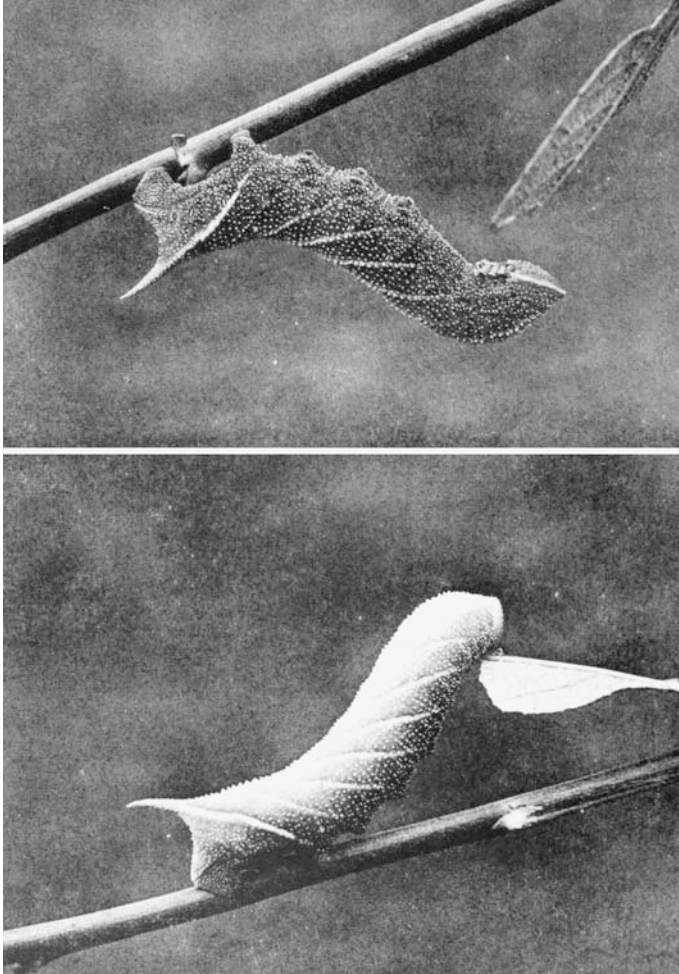
Fig. 5.2   Countershading. Nearly every green caterpillar that rests in the open has color shading that compensates for the shadow on its lower parts, producing an apparent flattening. (*above*) A hornworm caterpillar *(Manduca)* in normal resting position. (*below*) Inverting the caterpillar destroys the illusion, and the addition of countershading to natural shadow makes the caterpillar highly conspicuous

for apparent color changes due to light intensity. Insects that have countershading invariably rest with the darker surface directed toward the light, a behavior critical to the success of countershading (Fig. 5.2). Shadow also may be minimized by proper body alignment. (It has been suggested that many cryptic butterflies perch relative to the sun so that their wings throw the least shadow, but the observation is complicated by the fact that butterflies also control body heat by soaking up or avoiding sunlight.)

Some insect species have the chameleon-like ability to change their color to match temporary backgrounds. By varying the quantities of orange, yellow, and black pigments they form, many locusts can adapt their color from dirty white to yellow, brown, or black; kept for a few days on burnt ground, even adult locusts can darken. Only when the hoppers are kept amid green vegetation and fed with abundant moist food in a very humid atmosphere do bright-green locust hoppers appear. Likewise, certain caterpillars are able to change color and markings to match the background of their varied diets. When they feed upon birch, the larvae of peppered moths are smooth and purplish brown with darker 'lenticels' resembling a birch twig; on oak, however, they are brownish green with markings suitable to these trees. On oak covered with lichen, they become mottled in such a way as to mimic a lichen-covered twig!

Genetic variations in cryptic coloration also occur. One of the most thoroughly studied cases of rapid directional selection in progress involves crypsis in this common English insect, the peppered moth (also sometimes called the salt-and-pepper moth), the subject of Case Study 5.1.

Case Study 5.1: Melanism in the Peppered Moth, *Biston betularia*

What happened to change the color of a little cryptic moth? The research that answered this question has become a classic story in biology textbooks.

Peppered moths, like many others, fly at night and rest quietly by day on the sides of tree trunks. Naturalists of the nineteenth century knew them well and noted that they were usually found on lichen-covered trees and rocks, against which their pale mottled coloring made them practically invisible. Prior to 1845, all museum records of *Biston betularia* were light-colored or 'typical' specimens, but in that year, near the growing industrial center of Manchester, England, one black or 'melanic' moth of that species was captured, so distinctive that it was given the name *B. betularia* f. *carbonaria* (see Fig. 5.3). As the years passed, black individuals turned up with increasing frequency, mainly from the vicinities of industrial towns. By the mid-20th century, the peppered moth population around Manchester consisted of nearly 99% *carbonaria*.

Fig. 5.3   Attracting attention—or not. The peppered moth, *Biston betularia,* and its black form *carbonaria* at rest on a lichen-covered tree trunk in a non-industrial area of England. The typical light form (*upper center*) illustrates the principle of disruptive coloration, but the dark form (*lower center*) shows conspicuous contrast against the same background (see also Plate 13)

Why were melanic moths becoming predominant? In 1952, H. B. D. (Bernard) Kettlewell undertook the first field experiments on the phenomenon. Smoke from the expanding industrialization of England had polluted the surrounding countryside, he noted, killing the epiphytic communities on the trees and blackening tree trunks and the surrounding rocks and ground. It seemed plausible that upon this darkened background the dark moths were better protected from predators, particularly birds, but Kettlewell had little support for this hypothesis. Many entomologists and ornithologists vigorously objected that no one had ever seen any bird eating a *B. betularia* of any color, nor was there any published support for such predation on any of a variety of related cryptic moth species.

Thus, Kettlewell first needed to determine whether in fact birds actually ate peppered moths and whether they did so selectively. Into a large outdoor aviary containing a nesting pair of birds with young, he placed both light and dark tree trunks and boughs of equal surface area. Into the aviary he released ten moths—five melanic and five typical *B. betularia*. Based upon their appearance against these backgrounds at a distance of about two meters, resting moths were classed as 'conspicuous' or 'inconspicuous'.

For the first two hours of the first day, the birds failed to recognize the moths of either form as food. But in the next hour, all five of the 'conspicuous' forms and two of the 'inconspicuous' moths were taken. In a repeat experiment the next day, Kettlewell released 18 moths; 16 were eaten in the

first half hour, leaving only two 'inconspicuous' survivors. Subsequent replications followed the same pattern, suggesting that the birds required a period of contact with the prey before recognition but that after recognition was established, all the moths were under risk of predation. Satisfyingly, the data seemed to indicate that the most conspicuous were preyed upon first.

Encouraged, Kettlewell turned to field experiments in two study sites: a polluted area and an uncontaminated woodland like that which must have prevailed 200 years before. Setting up a camp that included sheds to house some 3,000 *B. betularia* pupae to raise for release, Kettlewell began round-the-clock studies. During the day, he released melanic and typical moths in known numbers, carefully marking each with a paint spot beneath the wings where it could not be seen by a predator. Then he watched wild birds' behavior toward the moths. During the night he operated light traps, capturing the peppered moths of both forms that were attracted to the ultraviolet bulbs. (The use of such a method was essential because of the moths' crypticity. When Kettlewell attempted to visually discover and count his released moths again immediately after their release in an area where his continual presence precluded predation, over a third of the cryptic forms were already 'missing,' that is, so well hidden that they eluded even Kettlewell's experienced eye.)

With help from the prominent ethologist Niko Tinbergen, Kettlewell watched bird predation on the moths, both with binoculars and with a movie camera from behind camouflaged blinds. In this way he was able to document at least five bird species actually selecting and eating the moths, which they did with such alacrity that it is surprising they were not previously observed. More important to his hypothesis, on the majority of occasions all the bird species at both locations took all of the more conspicuous moths before any of the inconspicuous phenotypes. Further proof of the selective advantage of having coloration appropriate to one's background was obtained by recapture of marked moths at night in the light traps. In unpolluted woodland, the survival rate of light moths was about twice that of dark ones, while in soot-darkened woodland the ratio was reversed.

Do moths discriminate among a choice of possible resting substrates? As a pilot study, Kettlewell outfitted a barrel with a lining of alternate black and white stripes of identical texture to eliminate tactile cues. Each night he released three moths of each form into the barrel; in the morning, he recorded their resting positions. Of 110 moths so tested, 65% chose the 'correct' background. However, the artificiality of such tests disturbed Kettlewell, so he selected a number of lichen-covered tree trunks and then carefully removed the bryophytes from one side. Over this denuded half he painted a soot suspension and then placed the trunk upright and covered it with a muslin tent. At the midline of the two sides, he released equal numbers of females of each form and recorded their final resting position. Every one of 31 *carbonaria*

individuals chose the black background; of the light forms, 75% selected the 'correct' background. These highly significant results provide quite conclusive evidence that female *Biston betularia* are able to selectively choose their background with respect to their own coloration, probably through visual cues (see Plate 13).

Several important additional implications arose from Kettlewell's studies. One major revelation was the speed with which evolution can occur at the level of the single gene. Geneticists had previously considered a selective advantage on the order of 0.1% as being 'normal'—Kettlewell illustrated an advantage on the order of 50%! This selection, intense enough to cause a significant change in gene frequency within a single generation, when extended over tens of generations could result in a nearly complete reversal in the favored gene.

In the years since Bernard Kettlewell's study, others have continued to research what is now called 'industrial melanism' in peppered moths, and there has been some evidence that other differences in fitness among the phenotypes that are not directly related to the visual differences in color pattern may also be involved. However, studies continue to support the fundamental finding of a relatively rapid switch in survival of the pale and dark phenotypes in response to corresponding changes in crypsis arising from an altered environment (Fig. 5.3). Interestingly, as Great Britain and other countries in northern Europe have reduced levels of air pollution from soot and gases such as sulfur dioxide, the tree trunks are once more showing their pale bark's true color; in response, the relative fitnesses of the two moth phenotypes are changing again. The fully black form is again becoming more conspicuous and vulnerable to birds, and the now-better-camouflaged light phenotype of the peppered moth is on the increase.

5.3.2 Systemic Defenses: 'I'm Noxious!'

Certain brightly colored tiger moths that fly at night may be captured by bats but rejected by experienced bats because the moth's bodies contain toxic alkaloids obtained as larvae. Aphids that feed on oleander and milkweed similarly gain protection by accumulating host-produced steroids that are toxic to predators. Distasteful lycid beetles are particularly prone to bleed from the wings, which possess swollen, easily ruptured veins.

Although hiding from predators is a common insect defense, another approach is to become noxious, that is, harmful to a predator's life or health. Chemical defenses are common; an insect may smell or taste so bad that predators spit it out, get sick and learn to avoid it, or even die and thus no longer be around to bother it. Many interactions of insects with potential predators involve *allomones* (see Chapter 6)—chemical agents that benefit their producer while (often detrimentally) affecting

another species. Allelochemic defenses are widespread throughout the biological world, but it is among the invertebrates, especially the arthropods, that chemical defense seems to have reached its peak of diversification.

One way to acquire defensive chemicals is to 'borrow' deterrents already present in one's prey or host plants. A classic example is the caterpillars of the monarch butterfly that can feed harmlessly on milkweed plants whose sap contains cardiac glycosides that are potent emetic agents to birds; when they become adult butterflies, the monarchs retain these toxic chemicals in their wing veins. However, depending on a plant's toxic principle can be an evolutionary constraint in its own right. Monarchs raised on cabbage instead of milkweed have no chemical protection.

An alternative is to synthesize one's own anti-predator chemicals. For example, aquatic Hemiptera differ from their terrestrial relatives in producing aromatic instead of straight-chain hydrocarbon defensive compounds. The apparent significance of this difference is that the aromatic compounds are much more repellent to fish.

Like plant chemical defenses, some insect defenses are strictly passive: parts of the insect must be eaten before an effect is felt. However, an insect normally can ill afford to allow body parts to be ingested before a predator learns of its mistake. An individual facing predation would have an obvious advantage were it to have some 'disposable' way to be sufficiently bad tasting or bad feeling for the predator to reject it while leaving the rest of the insect relatively unharmed. For example, a v-shaped notch in the wing of a butterfly is convincing evidence of an avian 'educational experience' allowing the butterfly to survive another day. Like monarchs, many butterfly species incorporate systemic noxious chemicals in their wing tissues.

Some distasteful insects have cuticular outgrowths such as hollow, brittle spines that are easily broken by predators. Many caterpillars have developed a coat of long hairs that render them unacceptable to most predatory birds, but some species gain still further protection by the inclusion of urticating hairs, delicate hollow organs each containing a minute quantity of irritating venom secreted by a gland at their base (Fig. 5.4). These occur in at least eleven lepidopteran families. When brushed against, these fragile hairs break and act like tiny poisoned barbs.

The evolutionary and ecological implications of various systemic chemical defenses can be problematic to explain. Consider the case of the blood and tissues of meloid blister beetles, which contain cantharadin. Long known as Spanish Fly, cantharadin was traditionally but incorrectly reported to have aphrodisiac properties, but the chemical actually is capable of inducing severe systemic effects when ingested. It is present in such quantities in some meloid species that swallowing a single beetle could kill some vertebrates. How can a systemic poison like Spanish Fly be adaptive? It would seem as though no learning could occur if the potential learner is now dead, and the beetle is no better off, being dead as well. And what about the many other cases where noxious effects are delayed—how can a predator be expected to associate a particular feeding event with ill effects that occur so much later? In fact, since toxins require energy in their production or incorporation, their development actually would seem to be disadvantageous.

Fig. 5.4 Stinging caterpillars. (*top*) Feeding group of pine processionary caterpillars (*Thaumetopoea pityocampa*). The short hairs along the dorsal surface contain skin-irritating chemicals. The processionary behavior of this species was subject of a study by J. H. Fabré over a hundred years ago. Fabré attributed the circling to blind instinct, and it is one of his best known insect stories, perhaps because it came to be viewed as a metaphor for mindless living or blindly following a leader. (*below*) The buck moth, *Hemileuca mala*, is another stinging caterpillar. The impressive crowns of urticating spines that adorn each segment (*inset closeup*) can cause severe itching,

Often such questions cannot be answered, if for no other reason than incomplete knowledge of the particular system. Lethal dosages almost certainly depend on the predator involved, a fact often unknown. In still other cases, even if predatory organisms neither die nor discriminate against the causative agent, systemic chemicals may impair vigor or fecundity; any substance that does this to the predators of an area is advantageous to the species that produces the poison.

How can the sacrifice of ingested individuals be justified in adaptive terms? Sometimes the answer may lie within the concept of *altruism* (see Chapter 10), in which the surviving insects are such close kin to those sacrificed that their survival is nearly equivalent genetically to the survival of the sacrificed individual itself. Support may be found in the observation that many poisonous arthropods develop dense, highly localized, and often quite static aggregations, conditions that would be expected to favor a high degree of relatedness. Clonal aphid clusters are an example. Behaviors such as egg placement in one or a few concentrated masses (a common oviposition pattern in butterflies) also probably increase the likelihood of genetic relatedness of adjacent individuals.

Chemical defenses have received so much research attention that before leaving this subject, it is important to reiterate that being noxious is a broader concept than merely being foul-tasting or unpalatable. It can also involve defenses that have no direct connection to chemistry. For example, most people avoid bumblebees because of their stings, and assume that stings are the reason that predators do, also. However, it appears that the tough chitin and hairy bodies of these insects are at least as important, making it necessary for birds to expend great efforts to subdue, tear apart, and swallow them. Naïve young birds have been observed taking as long as 18 minutes to kill, dismember, and eat a single bumblebee; the equivalent handling time for houseflies, mealworms or beetles was a fraction of a minute, even for young birds.

It is also important to note that when it comes to noxiousness, defense and offense are particularly closely linked. Behaviorally, the use of systemic chemical defenses covers a range that overlaps at the active end with forms of assault, the subject of Section 5.4.

5.3.3 Mimicry: 'I'm Someone Else!'

Cerambycid beetles and a host of different flies often resemble ants, bees, or wasps. A larva of the moth *Hemeroplanes* responds to threat by inflating its anterior end to form an excellent representation of a snake's head, then waving it about. The viceroy butterfly, *Limenitis archippus*, sports a color pattern that is completely unlike any of the species to which it is closely related but is very similar to that of monarch butterflies; furthermore, the viceroy has three color forms, each resembling a different species of monarch.

When insects imitate environmental objects such as twigs, leaves, and thorns, scientists call it crypsis or camouflage, but when insects imitate another living organism, scientists call it mimicry. *Mimicry* is the resemblance of one organism (the mimic), usually in color, pattern, form or behavior, to another organism (the model). Butterfly mimics and models have received what is probably more than their fair share of the attention, because numerically Hymenoptera form the most important group of models, and Diptera are said to form the largest group of mimics (particularly due to almost 300 species of mimics in the hoverfly family, Syrphidae).

Mimicry can be likened to a stage performance with a minimum of three actors: two signal senders and one receiver, with the receiver judging the resemblance of the signals from the two senders. In most cases, the resemblance of one organism to another can be considered mimicry only if both organisms are found together. (Migration and long-term associative memory might provide exceptions.) When similar forms are found in different areas, it is more likely to be an example of evolutionary convergence. Although visual mimicry has received the most attention and study, mimicry also may be olfactory, tactile, or auditory. Mimetic signaling is often multimodal, and the particular evolutionary direction it takes in a particular case undoubtedly has been influenced by receivers' sensory ecology. Appropriate behavior is necessary for an effectively functioning system, with mimics acting in ways that enhance their deception.

There are several types of mimicry. Two of the most common types, called Batesian and Müllerian, are related through the important evolutionary dynamics that arise from whether receivers are expected to try to discriminate or generalize on the senders' signals. In other words, are the senders sending dishonest signals or honest ones?

Dishonest signals characterize *Batesian mimicry*, the situation that occurs when a palatable species evolves an appearance similar to that of an unpalatable, venomous, or otherwise protected one (see Plate 15). The phenomenon is named after Henry Walter Bates, a British entomologist who first observed it while traveling in the Amazon in the mid-1800s and proposed that by imitating a model that is unpalatable or dangerous, individuals can gain an increased protection from predators that confuse them with their aposematic model.

For a Batesian mimic, being rare is advantageous; becoming more common increases the probability that a predator will discover that some insects (the mimics) in the complex are palatable and therefore all (mimic and model alike) are worth sampling. Thus, the fitness of Batesian mimics is inversely related to their proportion in the prey community, a situation called negative frequency dependence. It is no surprise that in natural situations Batesian mimic species are as a rule far less common than their models, but when a mimic species is numerous, an interesting phenomenon occurs. Consider, for example, the African swallowtail butterfly, *Papilio dardanus*, the female of which exists in half a dozen different color forms. In different regions of its range, different color assortments appear, and the balance of the percentage of the forms varies as well. In addition, other unrelated butterflies in some of these areas produce mimics with the same coloration. The example is not an isolated one; a great many Batesian mimics are polymorphic.

The establishment of such *mimetic polymorphisms* is relatively easy to explain on theoretical grounds. Because palatable mimics must be less common than their models, a mimetic form can increase in abundance only up to a certain point before losing its advantage. Strong pressure would exist toward development, within part of the population, of mutants resembling other distasteful species. These mimics, too, would show negative frequency dependence, so any new (or rare) mutant resembling still another protected model would be favored. In this way, a complex 'balanced

polymorphism' could be established. By presenting varied appearances, polymorphism also theoretically would reduce the rate at which predators develop a strong search image that improves their ability to capture that particular species. This could be quite advantageous because over time, search image formation results in *apostatic selection*, a situation in which the relative rate of predation rises more rapidly than does the relative rate of encounter.

Some of the best-studied cases of Batesian polymorphism are found among butterflies in the families Papilionidae and Pieridae. In some of these species only the female is mimetic. Negative frequency dependence is given as the usual explanation; by restricting mimicry to one sex, the effective mimetic population size is halved. Why should females be the chosen sex? One suggestion has been that mimicry is more beneficial to them. Female butterflies have less agile flight because of their egg load, and more predictable patterns when searching for oviposition sites. Another is that male wing patterns may be constrained by sexual selection; males might not be able to evolve Batesian mimicry without losing mating opportunities and/or being at a competitive disadvantage with other males. In experiments with North American swallowtail butterflies that have female mimics, painting males mimetically lowered their mating success; it also caused them to lose more fights with other males and therefore to hold lower quality territories.

Different dynamics occur when the mimetic signal is an honest one. Consider the various bees and wasps with their bands of yellow and black, or the tiger stripe butterfly complex of the Neotropics. Situations like these—when two or more relatively unrelated insects that are *all* distasteful or otherwise protected and that share one or more common predators mimic each other's warning signals—are named *Müllerian mimicry*. The advantages of such a system are obvious. When aposematic species converge in appearance, all of them benefit, sharing the number of predatory attacks incurred in the predator's learning process and reducing its confusion and learning time.

Müllerian mimicry runs counter to Batesian mimicry on three important points. First, with Müllerian mimicry there is no bluffing; each warning of unsuitability as prey is absolutely true. Thus, while Batesian mimicry has been likened to a parasitic relationship in which the mimic benefits at the model's expense, Müllerian mimicry is a true mutualism. When German naturalist Fritz Müller first proposed this eponymous concept in 1878, he backed it up by demonstrating mathematically that two unpalatable prey could each benefit from mutual resemblance, and showing that this benefit was biased in favor of the rarer of the two species, to a factor equal to the square of the ratio of the species' abundance. Therefore, unequal population sizes translate into even more unequal benefits. However, even at the extremes, the mimicry is still mutually beneficial. Thus one could say that for a predator the existence of Batesian mimicry complexes is detrimental, because they result in avoidance of 'good' food, but Müllerian mimicry complexes are advantageous to the predator, since they result in pursuit of fewer injurious or unpalatable items.

Second, whereas polymorphism is favored in Batesian mimicry, polymorphism runs contrary to the advantages of the Müllerian system. Because both the warning

prey and the learning predator benefit from a correct interpretation of the signal, rare or new variants within a prey population are at a disadvantage; they will not be recognized as distasteful and thus will suffer higher predation. This selection against rare forms translates into positive frequency-dependent selection. Thus, not surprisingly, most distasteful Müllerian mimics are monomorphic in local populations, with polymorphic forms that bridge narrow hybrid zones between color-pattern races.

Third, as more Müllerian mimics use the same warning signal, the protection given by the signal becomes stronger. Predators generalize more, and the selection for close resemblance appears to be somewhat relaxed. Ultimately it would seem as though there should come to be just one giant mimetic cluster in the entire habitat, but nature seems to behave otherwise. Particularly in the tropics, aposematic insects of similar size and shape usually group into not just one, but several distinct complexes. A 'mosaic mimetic environment' is usually invoked as an explanation— if different mimicry rings occupy different microhabitats and predators do not move between them, then each 'subpopulation' might have different fitness peaks and also be small enough to be particularly sensitive to genetic drift into different color patterns in different patches.

Still, despite these theoretical differences, Batesian and Müllerian mimicry both depend on stimulus generalization by their vertebrate predators, and both are probably labels for extreme cases in what is essentially a mimicry continuum. Within a mimicry complex, for example, some members may be more palatable than others. Should these less protected individuals be considered Müllerian mimics for which selection for bad taste has been relaxed? Or are they Batesian mimics that have subsequently evolved (or are in the process of evolving) a bad taste? Such questions are nearly impossible to resolve. In another example, certain mimetic cerambycid beetles often feed upon the distasteful lycid beetles that serve as their models. Such mimics might be alternatively Batesian or Müllerian, depending upon how recently they had fed upon a lycid.

Although Batesian and Müllerian mimicry receive most of the attention, other types of mimicry are also documented and classified by a number of different names. One of the better known is *aggressive mimicry*. James E. Lloyd's investigation of female fireflies of the genus *Photuris* revealed they emit the same light signals that females of the genus *Photinus* use as a mating signal; male fireflies from several different genera are attracted to these 'femmes fatales', and are subsequently captured and eaten (see Chapters 1 and 7 for more on fireflies).

Whereas in this example the fireflies are the predators, in other cases the reverse is true and an insect may mimic its major predator and thereby reduce the risk of being eaten by it (Fig. 5.5).

A slightly different matter is *automimicry*, or mimicry that occurs within a single species when a population includes both mimics and models because of a palatability dimorphism. For example, monarch butterflies have been mentioned as a classic Batesian model, but not all monarchs are equally disagreeable. Their caterpillars eat various milkweed plants in different parts of the monarch's range and these vary in the amount of cardenolides they contain, some having little or none. The butterflies'
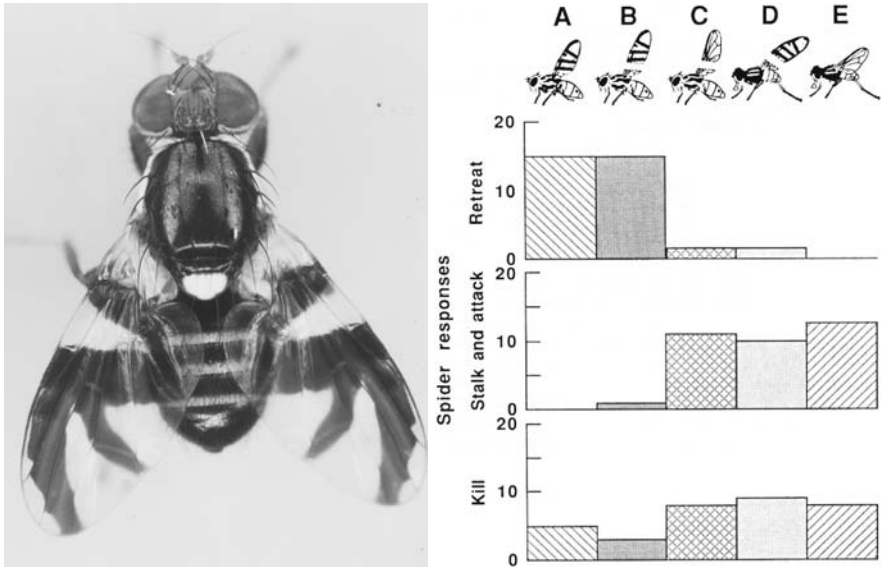
Fig. 5.5 Sending false signals. The tethritid fly *Zonosemata vittigera* has a leg-like pattern on its wings (*left*) and waves these patterns such that these 'legs' mimic the agonistic territorial displays of its primary predators, jumping spiders. In response, the spiders do not attack, but either return the display or retreat. Both the pattern and the behavior are necessary for effective mimicry. In transplant experiments (*right*), spiders attacked tephritids with house fly wings and house flies with tephritid wings. Each treatment used 20 flies, and responses were measured as the highest level of aggression attained during 5 minutes of interaction in a test arena

palatability depends on the amount of cardenolide eaten as larvae; this means that individuals in a population vary in their palatability to predators. Those lacking chemical protection are effectively mimics of their fellow species mates that are distasteful.

Many insects change shape, size, and behavior during growth and metamorphosis; when different instars imitate entirely different models it is called *transformational mimicry* (Fig. 5.6). Beetles and other guests of ants sometimes greatly resemble their hosts (Chapter 4); mimetic resemblance that facilitates cohabitation with a mimic's host, its model, has been termed *Wasmannian mimicry*.

The mimicry catalog could go on and on. However, as in other areas of insect behavior, studies of mimicry have steadily been stepping back from a natural history of individual examples to a broader synthetic view—one that includes modeling, predator behavior (including the psychological processes of learning and forgetting), and evolutionary dynamics. A major driving force has been the inadequacy of older theories to explain the phenomenon of imperfect mimicry. As more and more mimicry systems have been studied, it has become clear that most Batesian mimicry, in particular, is of rather poor quality, at least to human eyes looking at its visual aspects. This poses a theoretical puzzle. Conventional evolutionary theory
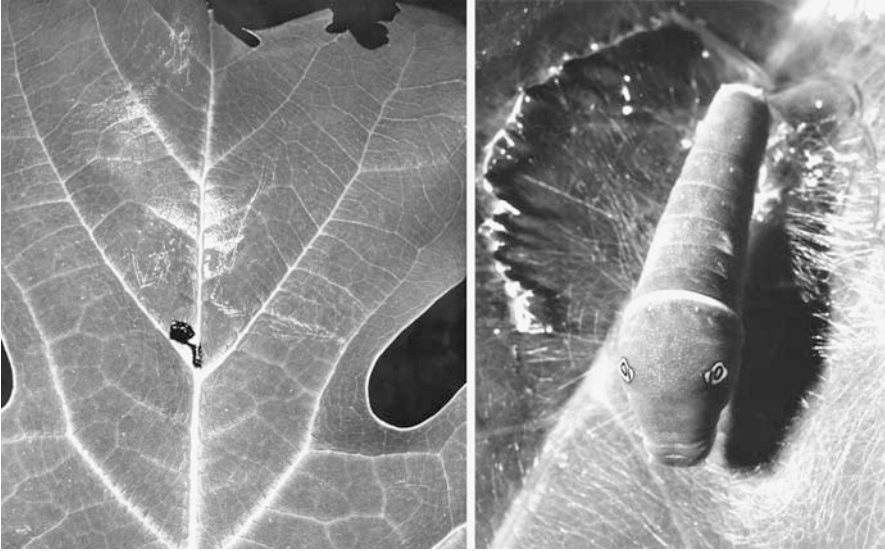
Fig. 5.6   Changing tactics. Transformational mimicry in larvae of the eastern tiger swallowtail butterfly, *Papilio glaucus*. (*left*) a first-instar larva resembles amorphous bird droppings, and rests in full view at the center of a leaf. Notice the nibbled spot at the leaf tip. These larvae feed only at night, when their diurnally active predators have stopped hunting. (*right*) Older larvae have grown too large to effectively resemble droppings. Colored bright green like the leaves they feed upon, they also possess eyespots and perform a striking snake-like display (see Fig. 5.12) when disturbed

would predict that because individuals with closer resemblance to the model gain more protection, Batesian mimics should be under constant selection to improve their mimetic resemblance; hence eventually only very good mimics should exist. A variety of (often not mutually exclusive) new explanations for this seeming puzzle have arisen; testing, proving, and disproving them should keep mimicry researchers busy for some time. One key to the puzzle may lie in the fact that many if not most vertebrates tend to avoid stimuli similar to, but not identical with, an original conditioning stimulus, a learning phenomenon called *stimulus generalization*. Experimental studies have revealed that under certain conditions, stimulus generalization provides advantage to a wide gamut of prey even in cases where they may appear only vaguely alike to our perception.

5.3.4 Aposematic Defenses: 'I'm Dangerous!'

The Carolina locust, *Dissoteira carolina*, combines vivid yellow and black coloring with a loud crackling sound. Brightly colored bees and wasps sound a warning buzz sufficiently effective to be mimicked by a wide variety of non-relatives. Caterpillars that possess stinging hairs often undulate conspicuously as they crawl about. Other

insects swing rhythmically, produce rattling or rustling noises, or adopt various bizarre display postures.

With bright, contrasting colors and shapes and conspicuous behaviors, a wide variety of insects literally advertise their presence to the world. They are described as *aposematic*, an adjective that is used most often in the context of visual cues but can be applied to any conspicuous cue or behavior that indicates special capacities for defense. Classifications always involve arbitrary choices, but with aposematic defenses, the division between passive 'primary' defenses and active 'secondary' defenses breaks down almost completely. The general maxim for an aposematic insect is almost always, 'If you've got it, flaunt it!'

Aposematic coloration in insects tends to follow definite patterns of rather limited variety—most frequently combinations of red, yellow, or orange on a contrasting background, often black. The color pattern of a bumblebee is an example. Such patterns contrast sharply against natural backgrounds that are generally green, brown, gray, or blue.

The advantages of the end product seem obvious. When one is poisonous, noxious, or otherwise disagreeable or dangerous, it pays to advertise. Standing out brightly differentiates oneself clearly from cryptic palatable prey. It also may jolt potential predators out of any non-discriminating 'state of mind.' Limiting the number of patterns enhances the efficiency of the warning by limiting the amount of information that a predator must learn for accurate feeding judgments. It is even possible that vertebrate predators have innate biases against yellow and red that aposematic insects have been able to exploit. All these ideas are supported by experimental data to some extent, though less than overwhelmingly. Because prey signaling and predators' cognition probably coevolved, it is generally difficult to establish independent experimental evidence for any of these ideas. Happily, they are not mutually exclusive.

Why and how did aposematic defense arise? Ever since Charles Darwin first wrestled with an explanation for brightly colored caterpillars and Alfred R. Wallace suggested that their bright colors might advertise unpalatability, the evolution of warning coloration has intrigued and puzzled people. How could warning colors have arisen? If most of a population is cryptic but a few colorful mutants arise, wouldn't predators immediately remove them from the gene pool? Maybe not. There is evidence that the mere fact of being bright and/or different can offer protection. It seems most likely that aposematic colors evolved in response to vertebrate predators, particularly birds, rather than insect predators. Insects perceive light at the red end of the spectrum poorly, if at all (see Chapter 7); red presumably appears gray or black to most and would therefore be of little significance as a signal to other insects. On the other hand, birds readily perceive bold patterns of red or orange. Faced with something unusual, vertebrate predators often hesitate. Many birds, in particular, will actually avoid novel food items.

At first, scientists had their hands full just cataloguing aposematic examples, which seemed to occur almost everywhere they looked, from brightly colored poisonous tropical butterflies to bitter-tasting ladybug (ladybird) beetles (see Plate 5). However, over the years, research on aposematism has become more sophisticated

and complex, shifting to a search for underlying cognitive, behavioral, frequency-dependent and coevolutionary mechanisms. For example, among saturniid moths, striking life history adaptations exist which correlate to their apparent defensive strategies. For example, unpalatable aposematic species tend to have a longer life span following reproduction than do cryptic, presumably palatable species. The apparent explanation is that even after reproduction distasteful moths can confer some protection on their siblings by serving as a predator's learning experience. In contrast, the greatest benefit a cryptic species could confer to its relatives would be to remove itself from the population soon after breeding so as not to chance that a predator might develop a 'search image' for its species.

5.4 Active Messages

When disturbed, swallowtail and parnassian butterfly caterpillars suddenly evert a snake-like 'forked tongue' (osmeterium) secreting intensely odorous butyric acid derivatives. Solitary wasps and their prey play games of cat and mouse, and the prey does not always lose. Blister beetles often ooze irritating hemolymph from leg joints when handled.

Of course, the simplest response to attempted predation is to simply run or fly away, if you can. Most insects do this if you attempt to grab them, and cockroaches are masters at it (see Chapter 2). For insects that inhabit burrows or make portable cases simply withdrawing or retracting their bodies is usually sufficient to avoid being eaten. Tiger beetle larvae that live in burrows, case-making caterpillars and case-bearing beetle and caddisfly larvae all exemplify this type of disappearing act. However, secondary defenses exist in astonishing variety; we will consider them under three broad groups of active insect defense messages—attack, startle, and group actions.

5.4.1 Attack: 'I'm Turning the Tables!'

When threatened, *Solenopsis* fire ants both sting and bite; clamping down with their mandibles secures the hold they need to jab their stinger into the enemy. Although they do not have operative mouthparts, certain insect pupae such as mealworms have evolved 'gin traps' that give them the ability to 'bite'; along their abdomen segments, clefts with sharp hardened borders can be clamped shut, trapping attackers.

The insect arsenal includes many morphological adaptations—powerful mouthparts, leg spines, raptorial forelegs, and a whole host of other such features—that can be used highly effectively for protection, and the behavioral line between defense and offense can be very thin and finely drawn. However, when it comes to actual attack, chemistry reigns supreme. The allomones involved in offense and defense tend to be blends of compounds. The secretions of some pentatomid bugs,

for example, include as many as 18 components. The functional significance of such mixtures appears to lie in their increased chance of repelling diverse sorts of predators, combined with the ability of one chemical to alter the physical and/or chemical properties of another.

Consider the use of venom, for example. The 'aculeate' Hymenoptera are so-named for their weaponry—glands associated with the egg-laying apparatus secrete venom and the ovipositor itself has been transformed into a sting. Solitary wasps (Pompilidae, Crabronidae, and Eumeninae) primarily use their venom to paralyze prey, but among the social bees, wasps, and ants the sting and venom have come to be retained solely for defense/offense. Occasionally such stings can cause violent and severe reactions in humans, an example of anaphylaxis, a generalized reaction to foreign proteins to which the body has become sensitized. Males hymenopterans are incapable of stinging, although some have a well-developed spine (pseudo-sting) at the end of the abdomen which is realistically thrust at molesters and may sometimes even draw blood.

Many non-stinging insects also use secretions and excretions in a manner that ranges from defense to active attack. Most of them discharge their chemical defenses only in response to direct contact stimulation, but both intermediates and exceptions occur. Hemiptera such as *Rhopalus* collect secretions in depressions on their body walls; when bothered, they dip their legs into the accumulated chemical and then wipe their legs on the enemy target.

Some insects' hemolymph contains noxious poisons as a passive defense. However, to minimize the chance of being eaten and maximize the chance of escape many species provide relatively non-harmful ways for predators to taste one's toxic hemolymph. One way is to have active control over the release of hemolymph when under attack (Fig. 5.7). Such *reflex bleeding*, often occurring from leg joints, is

Fig. 5.7 Bleeding reflexively. When gripped with forceps, an ithomiine day-flying moth from the Neotropics foams released hemolymph with air from its spiracles

highly developed in the Mexican bean beetle, which may even rotate its leg around to bring the oozing knee in closest contact to the point of stimulation.

When handled or disturbed, a wide variety of arthropods respond by regurgitating or defecating. Often very effective as predator repellents, such *enteric discharges* might almost be considered a form of short-range attack. The familiar frothy 'tobacco juice' regurgitate of some grasshoppers, for example, is quite toxic to mammals. It is a topical irritant to eyes, may induce vomiting when swallowed, and may cause severe symptoms and even death when injected. When tethered grasshoppers placed beside ant colonies are induced to regurgitate, the fluid causes their assailants instantaneously to disperse and begin intense cleaning movements. When pieces of cut-up grasshopper, some of which have been treated with regurgitate, are placed along ant trails, foragers carry away only the untreated pieces. Such protection can be extremely important, particularly in defense against massed predators such as ants. Various morphological and behavioral adaptations prolong the effectiveness of such residual secretions (Fig. 5.8).

Spraying is a common way to apply non-injected secretions, and it is often accomplished with a high degree of accuracy and sometimes over a considerable distance. In general, these sprayed chemicals are much stronger than most enteric discharges. The predaceous reduviid bug *Platymeris rhadamantus* sprays its saliva directionally several feet in response to predator attack; the toxic fluid, ordinarily used to kill prey, is said to be similar to cobra venom. The large two-striped walking stick *Anisomorpha buprestoides* of the southeastern United States is exceptional in that it will spray approaching birds from a distance, whereas most non-stinging

Fig. 5.8   Prolonging repellency. (*left*) The pupal stage of a *Chrysomela* leaf beetle hangs fully exposed to predators on the undersides of the host plant. Persistent odor of the larval defensive secretion impregnates the shed skin, which remains attached (*arrow*) and acts as a potent repellent to foraging ants. A second larva preparing to pupate is also present. (*right*) A larva of the chrysomelid beetle *Cassida rubiginosa* forms a shield of cast skins and feces that is held on a fork projecting from its hind end. When branched spines on its body detect a predator's probing, it interposes the shield between itself and the enemy, often in such a way that fecal material is smeared upon the offender. After even a brief contact with the pasty material, ants immediately flee and clean themselves

insects require direct contact stimulation before discharging their chemical defenses. Some of the commonest ant species use formic acid as a poison spray and thus have been used as a natural source of this acid from Roman times until quite recently. Formic acid is a potent irritant and effectively repels a variety of potential ant predators. It also serves as an alarm odor (see Chapter 6) that alerts nestmates to the source of the disturbance. The ants employ stereotyped postures to control spraying direction (Fig. 5.9a).

Probably the best known spraying insects are the 500+ species of carabid ground beetles known as bombardiers (Fig. 5.9b). They occur through much of the world, and vary in size but all have essentially the same defensive mechanism. The chemicals discharged are 1,4-benzoquinones, irritant chemicals that many other arthropods also have independently evolved the ability to produce. What is remarkable about the bombardiers is that they do not store their benzoquinones as such. Instead, they produce them by explosive synthesis at the moment of ejection, mixing the contents of two internal chambers and catalyzing the reaction with two kinds of enzymes. In the process, enough heat is generated to bring the resultant discharge to the temperature of boiling water. Excellent marksmen, bombardiers can spray in virtually any direction to accurately target any part of their body that is subjected to assault. The combination of a burning and stinging spray and the audible popping sound that accompanies the emissions is understandably effective against a wide range of potential predators, including humans.

The active principles of most defensive secretions are highly volatile substances of low molecular weight, usually strongly odorous and irritating and in some cases even painful to inhale. Often, they are present in very high concentrations. How do these arthropods withstand their own discharges? In many cases, external immunity appears to be gained through possession of an especially impervious integument. The cuticle of Hemiptera with defensive glands, for example, is generally impermeable to hemipteran secretion unless abrasion takes place. Internally, secretions do

Fig. 5.9 **Taking aim**. (*left*) A carpenter ant, *Formica integer*, responds to an alien in the nest by bending its abdomen under its body and directionally spraying formic acid that both repels the intruder and alerts nestmates. (*right*) A bombardier beetle aims its abdominal tip so accurately that it can spray its hot quinone secretion in any direction

not come into contact with living tissue because the storage glands are membranous saclike invaginations of the body wall, and thus are lined with cuticle as well.

But how can the glands *produce* the poisons without poisoning themselves? Some arthropod gland cells possess certain more or less elaborate cuticular chambers and ducts; toxicant synthesis occurs within the lumen of these cuticular organelles, not in the cytoplasm of the living gland cells associated with them. Such a situation has been shown in certain tenebrionid beetles. Other arthropods (like the bombardiers mentioned above) have 'reactor glands' constructed in such a way that chemical precursors of the secretion are mixed only at the moment of discharge.

Not all defensive/offensive secretions are purely chemical in effect. Many arthropods manufacture sticky or slimy materials that mechanically hinder predators. From their pointed cephalic nozzles *Nasutitermes* soldiers (Fig. 5.10) eject a sticky, resinous terpene-containing secretion that dries quickly in the air. Mechanically incapacitating or even killing insect predators, it also acts as an alarm substance inducing other termites to converge upon the site. The nymphs of some cockroach species have rear ends coated with a sticky secretion; when attacked by ants, they sling slimy droplets over some distance. Although analytical studies have failed to reveal any chemically active substances in this material, ants targeted by the fluid are instantly incapacitated. As a final example of secretion taken to the extreme, the workers of a tropical formicine ant protect their colony by literally blowing themselves apart. The large mandibular glands of these ants take up not only the head, but much of the abdomen. When an ant is under assault, it compresses its abdomen so rapidly that it bursts, casting the sticky contents of its mandibular glands in all directions, effectively trapping attackers in the glue.

Fig. 5.10   Squirting string. Soldiers of *Nasutitermes* orienting to a predator. These termites possess a hollow nozzle at the front of their heads, from which they shoot strands of a sticky secretion produced in their frontal glands. Attacking arthropods find the tacky filaments almost impossible to remove; the material is also a potent irritant

5.4.2 Startle: 'I'm Not What You Thought!'

When disturbed while at rest, the giant Io moth spreads its forewings, abruptly exposing a pair of huge, white-centered black spots on the upper surface of its hind wings. The sluggish Australian katydid *Acripeza reticulata* lives in leaf litter and probably escapes predation because of its grayish, bumpy exterior; when disturbed, females raise their wings to reveal a vivid abdominal color pattern of reds, blues, and black. Crane flies drop off their own legs when attacked.

Passive 'primary' defenses such as disguise, aposematic coloration, and mimicry are useful against enemies only to a point. Systemic chemical defenses can provide a ramped up but still essentially passive second line of defense. In this section and the next we consider some more active approaches based on the concept of unexpectedly confronting a potential predator with novel morphology or behavior so unexpectedly that it causes the animal to hesitate or retreat. For example, some fulgorid bugs (Fig. 5.11) have lizard-like false heads; if a predator is still undeterred, they suddenly expose large colored wings. Similarly, when pecked by a bird, the large distasteful lubber grasshopper typically flips up its front wings while unfolding and erecting its ruby-red hind wings.

To *startle* is to disconcert or frighten by a sudden shock or surprise. One common method of achieving a startle effect is through such *flash coloration*, the phenomenon in which the prey is cryptic when at rest, but upon being threatened, reveals previously hidden brilliant colors and/or patterns while escaping. Many startle displays include conspicuous structures that are combined with other behaviors that heighten the startle effect (Fig. 5.12). Flash markings are most common on the wings of Lepidoptera but are also found occasionally among many other insects. Early on, these circular marks were named *eye spots*, another example of the way in which the label that is placed on something can affect the research questions that are asked about it. Traditionally, eye spots have been thought to startle predators simply because they look like the eyes of a vertebrate, perhaps one of the predator's own enemies. In this sense, they could be considered a special case of mimicry. Research showed that the more motion-like the markings appear (by arrangement of colors in concentric rings and/or by rhythmic shaking of the wings), the greater the startle effect upon birds.

Some biologists have suggested that eye spots are mimicking owl eyes because insectivorous birds may have an innate fear of these stimuli, owls being *their* predators. Three species of *Caligo,* the so-called owl butterfly, in Trinidad have enormous eye spots (15–20 mm in diameter) on the under side of their hind wings; another butterfly *Eryphanis* in Trinidad has smaller (6–7 mm), more irregular markings. At rest, all four species hold their wings vertically so that only one side is visible to an observer at a time, but the eye spots are continuously displayed. It may be that *Caligo* are mimicking *Hyla* tree frogs (Fig. 5.13), while *Eryphanis* are mimicking *Anolis* lizards, two vertebrate predators common in the resting microhabitat of the butterflies. To birds viewing the butterflies from a distance, the eye spots do not interfere unduly with the overall cryptic pattern. However, the lizards, which have limited binocular vision, maintain territories based on body size; seeing *Eryphanis*
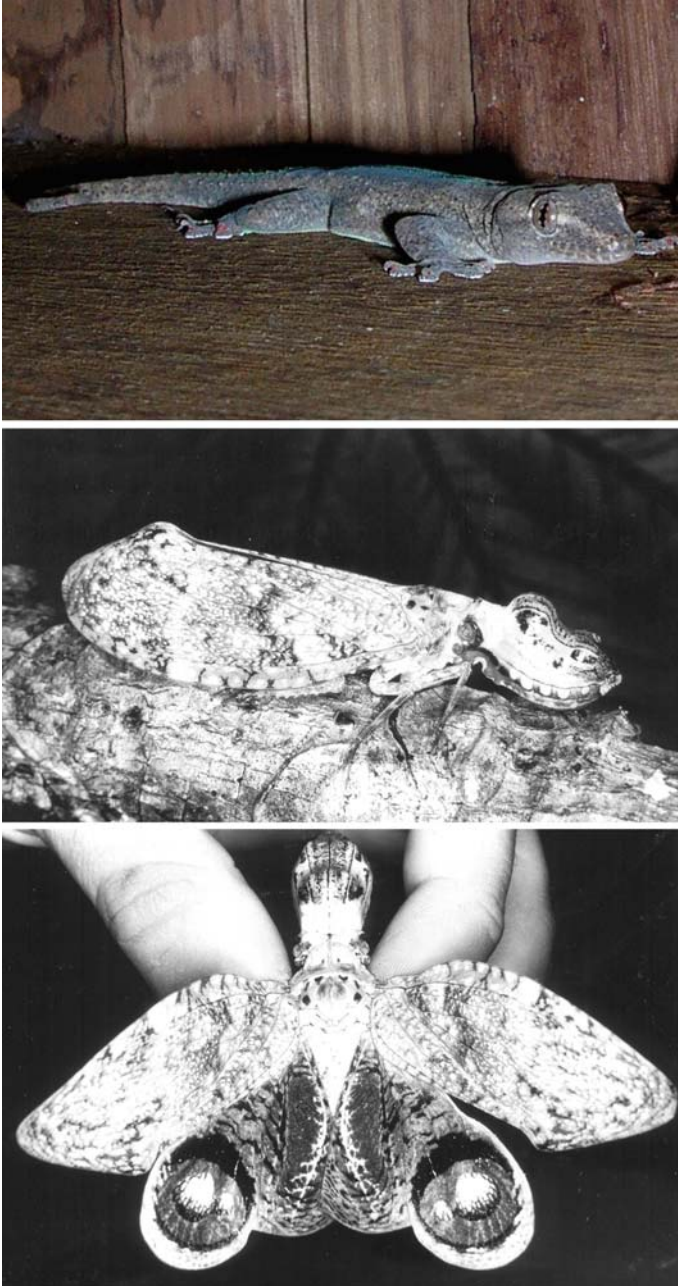
Fig. 5.11   Mimicking a predator? (*center*) *Lanternaria*, a large fulgorid bug from Panama, has a hollow sham 'head' and lizard-like markings that cause it to resemble a small carnivore such as a gecko (*top*). If this first line of defense fails, it flashes open its wings to reveal vivid eye spots (*bottom*)

Fig. 5.12   Startling display. The mature larva of the tiger swallowtail, *Papilio glaucus,* responds to danger by abruptly everting its forked defensive gland, the osmeterium, from beneath its neck integument. The side nearest the danger tends to be extruded furthest; in some cases the caterpillar may even arch its body and wipe the horns directly upon the offender. The osmeterium, which contains butyric acid, is commonly colored bright yellow or red. Thus, the defense is probably a combination of a visual threat and a repellent odor
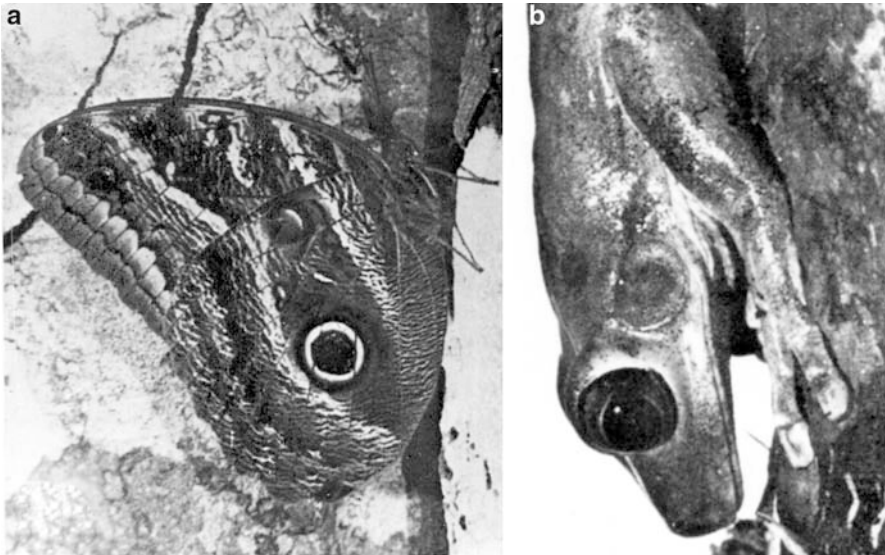
Fig. 5.13   Imagining a resemblance? Apparent mimicry of arboreal carnivores by a large butterfly, *Caligo*, that rests by day on tree trunks. (**a**) The mimetic pattern on the butterfly's wings is said to include not only the eyes but the head profile, pectoral region, and amphibian typanum. (**b**) The supposed model is the tree frog *Hyla crepitans*, a widespread predator that also spends the day resting on tree trunks

at close range as larger rivals of their own species, the lizards avoid them. At the same time, the larger *Caligo* resemble full-grown tree frogs that are quite capable of eating lizards, and thus the lizards avoid them as well.

Another hypothesis, not mutually exclusive, is that eye spots may distract or redirect a predator's attention from more vulnerable body parts. Many of the small lycaenid butterflies commonly known as 'blues' have eye spots on the underside of their hind wings and, close to them, long wing 'tails' that somewhat resemble antennae. It has been suggested that these 'tails', which are kept in motion by the resting butterfly, draw attack away from the true head where a wound would be fatal. Attacking the eye spot instead, a predator gains only a piece of wing for its efforts. It is certainly true that for most vertebrates, ourselves included, an eye spot has an inherent conspicuousness that is difficult to ignore (Fig. 5.14).

Many cryptic insects use flash coloration in reverse, making normal camouflage more effective through sudden contrasts. Thus, for example, many grasshoppers that are colored to match the stony or sandy soil when they settle have hind wings of brilliant red, blue, or yellow. The grasshoppers are highly conspicuous in flight, but they conceal their hind wings so abruptly upon landing that they appear to vanish. A wide variety of other startling display behaviors have also evolved in otherwise cryptic insects. Some orthopterans perform stereotyped defensive displays when discovered (Fig. 5.15), raising their long spiny legs in the air over their heads. Various moths react like whirling dervishes, dramatically flapping their wings about and rocking from side to side, thus warming up their flight muscles while temporarily startling their predator. In this way they can often escape before the predator is able to react.
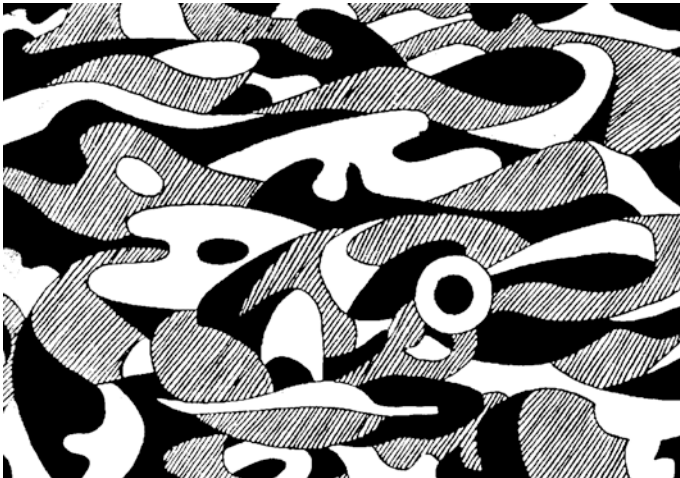
Fig. 5.14   No ignoring it! This diagram illustrates the inherent conspicuousness of an eye spot, which attracts attention to itself in preference to a variety of other, and even larger, objects in the visual field
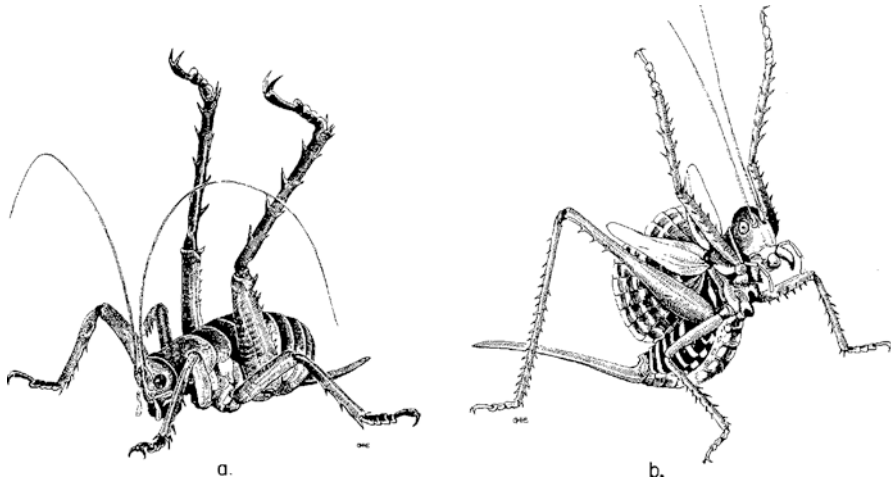
Fig. 5.15   Flailing in defense. Display in two normally cryptic orthopterans. (**a**) The weta *Deinacrida heteracantha* from New Zealand. (**b**) The katydid *Neobarettia spinosa* from Mexico

The strategy of startling a potential predator includes another very dramatic and widespread behavior. In the same way that a fleeing escapee might slip free from a jacket grasped by his assailant, many insects elude potential predators by leaving behind various dispensable body coverings, a phenomenon known as *autotomy*. Perhaps the most familiar of these are the easily shed scales which cover the wings of butterflies and moths; the loose hairs of adult caddisflies and the scales of silverfish and bristletails may be similar protections against entrapment. Legs of crane flies represent a more extreme example of dispensable body parts. The larvae of certain carpet beetles use interlocking hairs for defense; on their abdomens, they bear prominent tufts of barbed setae that easily detach and hopelessly entangle small predators such as ants.

Detachable coverings need not be strictly morphological. Gathering on their back a variety of debris from feces to old cuticle to the sucked-out remains of prey, larvae of groups as diverse as assassin bugs and lacewings construct shields for protection and camouflage. Other species are able to maneuver their shield with considerable agility against predators, in actions that sometimes cross over from defense to attack (see Fig. 5.8).

5.4.3 Group Actions: 'We're in This Together!'

Some *Nasutitermes* termites make daylight forays above ground in true military fashion; columns of workers are guarded against arthropod enemy trespass by flanking rows of soldiers oriented with their spraying snouts pointed outward (see Fig. 5.10). If its nest is tapped, the mound-building ant, *Formica rufa*, rushes out and hundreds of workers eject their formic acid spray toward the sound of the disturbance.

One of the most-often cited selective advantages of living in a group is protection against predators. There are several ways that an individual might benefit from not being alone. One is the *encounter effect*, which affects the probability that a predator will locate a group. As group size increases, the rate that groups encounter predators also increases, but not as quickly as expected, probably because the apparent group size rises more slowly than actual size. (That is, a group with 1,000 individuals does not look twice as big as one with 500 individuals, because some are hidden behind others.) An individual's predation risk is also lowered by a second factor, called the *dilution effect*. This is basically the idea of 'safety in numbers'; if a predator is going to eat only one prey, an individual is better in a large group than alone.

An individual's position within the group also affects its predation risk, of course. In 1971, a compelling explanation was offered by W. D. Hamilton, one of the pioneers in thinking about evolution as a game between competing phenotypes. Some early ethologists had felt that natural selection at the population level was necessary for aggregations and social groups to form; cooperative behavior had to evolve 'for the good of the group' rather than for the good of the individual. Hamilton argued that rather than cooperating with one another to form a group, under some conditions a population of prey animals was simply acting as a *selfish herd*, in which all the individuals were trying to use each other as shields against predators. Because individuals at the outside of the group were most likely to be picked off, individuals—looking out for their own self-interest—were competing with one another for the safer positions toward the middle. Thus, while the herd looked like a unit moving together, it actually emerged from the uncoordinated behavior of self-serving individuals. However, even though being in the center may reduce the risk of predation, there often is a trade-off in the form of a lowered food supply.

Defense through group action is particularly well developed in gregarious and social insects. The use of chemical communicating substances for warning purposes (such as inter- and intraspecific alarm odors) is widespread, but is especially well developed among ants. When such a substance is of sufficient quantity, it triggers rapid dispersal of nearby individuals. Highly volatile, it fades rapidly unless reinforced, thereby minimizing overreaction.

Young offspring are often especially vulnerable to predators, so it is probably no surprise to find that in many species, 'larvel herds' (see Plate 37) and group living appear to be an adaptation to protect them. (We'll be returning to this subject in Chapters 9 and 10.) For example, females of the bug *Elasmucha grisea* defend their eggs and nymphs by shielding them with their body and lunging aggressively at intruders. Often two or more females will guard clutches side by side with one another on a leaf. In experimental pairings, jointly guarding females lost significantly fewer eggs to predatory ants than single females did.

When disturbed, swarms of a wide variety of insects seem to 'explode' into a mass of erratically swirling individuals. For species that regularly aggregate for various purposes, such group 'panic' can be a good defense strategy. The unpredictable random flight of fleeing animals may stymie a predator more effectively than an orderly retreat would. Many predators must fixate upon one individual to successfully attack, and this is difficult to do amid erratic movements undertaken by

a number of closely spaced individuals. Such defensive behavior probably also has elements of a mass startle effect.

Mobbing, a type of group defense in which a predator is harassed by a number of maneuverable prey individuals, has long been known among colonially nesting birds. Many social and/or communal insects have also developed this effective behavior. *Bembix* sand wasps, for example, nest in aggregations; when a potential predator approaches, a score of male wasps may fly up at it, buzzing ominously and loudly but harmlessly. While mobbing, prey animals may approach, threaten, or occasionally physically attack a predator. Often, even though the predator is not actually injured, it moves off. This is probably not only due to the harassment but also to the fact that its probability of successfully capturing a prey is very low amidst all the commotion.

Chapter 6
Chemical Communication

6.1 Introduction

Over a century ago, the French naturalist Jean-Henri Fabré confined an unmated female giant peacock moth in a container hidden on his desk; the following evening, over 40 male moths arrived, in Fabré's words, 'eager to pay their respects to their marriageable bride born that morning.' The container was not airtight, and because even the empty container was of intense interest to the attracted males, Fabré suggested that the attraction must be chemical, but he was puzzled because he could not smell anything emanating from his female moth.

Communication through chemistry has been found to be a persistent theme in almost all animal taxa. Chemical communication is both the oldest and the dominant method of communication among organisms; early metazoans relied extensively on chemical communication for timing gamete release and to mediate the union of gametes.

Biologically significant chemicals have been found in both sexes and all life stages of many species, not just of insects but spanning the zoological universe. These are chemical hotlines, not polite conversational perfumes. They communicate matters vital to survival, such as the presence of danger, the identification of friends and foes, the call to arms or emigration, the availability of food, and the urge to reproduce.

Today the role of odors in animal communication is so well established that it is difficult to appreciate that it has been only relatively recently that advances in chemistry and technology have permitted humans to eavesdrop on the private lives of insects and other organisms where chemical communication is often the dominant mode. To date, the largest number of communication chemicals in the animal world has been found among the members of the largest class of animals, the insects. It is here that they have been studied longest and here that science knows most about their modes of action.

6.2 Mechanisms of Chemical Communication

It is a hazy summer morning just before dawn, and a man follows a footpath to a clearing in the middle of an apple orchard. Reaching up, he removes the tray that

hangs from a wooden post and smiles with satisfaction: the sticky tray top is covered with small rust-and-yellow moths. As he starts back toward his pickup truck, the man pauses to watch a flying moth. It zigzags, comes closer, then hovers over the tray, extending its genital claspers. As its wingtips brush the cardboard and are caught by the gummy surface, its abdomen curves upward, throbbing convulsively as the moth tries to mate with a polyethylene disc in the center of the tray.

What has happened here? The scene was a carefully chosen test site, the man a field entomologist; the moths were male red-banded leaf rollers (*Argyrotaenia velutinana*). The plastic disc was dipped in a compound that smelled like a secretion produced by a virgin female red-banded leaf roller. Male moths were lured by the smell to the trap where, instead of mating, these destructive apple orchard pests were captured.

The observation that odors secreted by some insects function as stimulants, inciting those of the opposite sex to mate seems, rather obvious today. In fact, the German medical doctor and botanist Philipp Franz von Siebold proposed such an idea about 170 years ago. But during the 1800s the phenomenon of chemical communication was largely ignored or disbelieved. Even Fabré, who easily accepted the idea that insects could detect the odors of other insects, could not believe that such odors could operate over such long distances; it simply strained credibility to think that a single female moth could inject into the vast atmosphere enough of a substance to be perceived by males kilometers away. This would be, he thought, like tinting an entire lake with a single drop of dye.

6.2.1 Odor Creation and Reception

Where do insect communication chemicals originate? How are they received? Do insects smell their chemical messages or taste them? In 1900 an American biologist, A. G. Mayer, undertook some simple experiments to establish the mechanism by which male promethea moths (*Hyalophora promethea*) are attracted to females. When he placed five female moths in a glass jar topped with mosquito netting, Mayer noted that male promethea moths over 100 ft away were immediately attracted. Next, he inverted the jar and packed sand around its mouth so that air could not escape; now males were no longer attracted. So perhaps smell was involved; was sight also involved? Mayer wrapped female moths loosely in cotton to make them invisible; males not only came, they grasped the cotton in their abdominal claspers in typical copulatory attempts. On another set of moths, Mayer replaced female wings with male wings; males still came and mated without hesitation. Having ruled out the role of sight in male attraction, he performed one more experiment to establish that only chemical cues were involved. He set up a small wooden box containing females, so that air blown into the box came out through a small chimney. True to prediction, the males were attracted not to the box but to the chimney top, even when the vicinity contained fumes of carbon disulfide and diethyl sulfide.

Where were the moth's odors being emitted? Mayer severed female moth bodies and placed the pieces in various locations. Males released five feet away flew

to the abdomens and ignored the remainder. How were the odors being received? Males with their abdomens cut off still responded; so did males whose spiracles were covered with glue. However, males whose antennae were gummed up did not seek females. In fact, they showed no excitement even when held within 2.5 cm of virgin females.

Insects produce their odors in many ways; this variety and complexity is particularly striking among the social species (Fig. 6.1). Chemicals come not just from the abdomen but often from the head or thorax, produced by exocrine glands (clusters of secretory cells whose products are discharged to the outside of the body). Sometimes, single chemicals are produced, but more commonly they are complex blends.

Once produced, the chemicals are sent forth as liquid streams, droplets, thin films, aerosols, or gases. Emission rates and concentrations may be controlled through adjustable nozzles, retracting applicators, evaporation pads, or other equally elaborate devices. Among the more spectacular are the male arctiid moths that possess feather-like coremata that can be pumped in and out to waft their chemicals into the evening air (see Plate 16).

Producing chemicals is only part of the picture, of course; receiving and reacting to them is the other part. Just as with vertebrate animals, one can say that insects both taste and smell. Also like in most vertebrates, the chemosensory system of insects seems to rely far more heavily upon smell than on taste. This is probably no surprise. Taste involves the reception of waterborne compounds with a limited range of qualities, often in fairly high concentrations, at close range. Odor, on the other hand, involves reception of chemicals over a greater range and often at much lower concentrations; though these chemicals are usually in gaseous form, they may also be either airborne or waterborne. Because the two senses are so closely allied, rather than considering them separately, many biologists simply speak of insect chemoproduction and chemoreception.

How are tastes and smells received? The external surface of insects is covered in cuticle, so it is the place to begin. On various structures, particularly the antennae, mouthparts, legs and ovipositor, chemoreceptor cells provide 'windows' to the outside world. These are surrounded by the characteristic cuticular sensilla that comprise the most obvious external parts of every chemosensory organ. They occur in at least four morphological forms: bristles or hairs, pegs, plates, and pits (Fig. 6.2).

All chemosensory sensilla have one or more pores through which chemicals can pass. Gustatory and olfactory sensilla are quite similar structurally, but the former have only a single pore and the latter have many. Once an odor molecule passes through the pore(s) it binds with specific proteins, triggering a cascade of reactions that ferry it through the fluid media of the sensillum lumen to the dendrite of a nerve where it activates receptors and is changed into electrical action potentials that travel along axons to the brain. Axons from gustatory sensilla on the head lead to the subesophageal ganglion; those from olfactory sensilla terminate in the deutocerebrum. Sensory filtering occurs at multiple levels in the nervous system, but initial specificity and sensitivity is achieved by the odorant binding proteins.

**Fig. 6.1 Producing
communication odors**. The
highly developed exocrine
gland system of wasps, bees,
ants, and termites showing
locations of glands most
commonly used in behavioral
interactions. All the glands
shown secrete chemicals to
the outside. Some, such as the
mandibular gland, have
storage reservoirs and release
their chemicals in bursts as
needed; others secrete
chemicals more or less
continuously
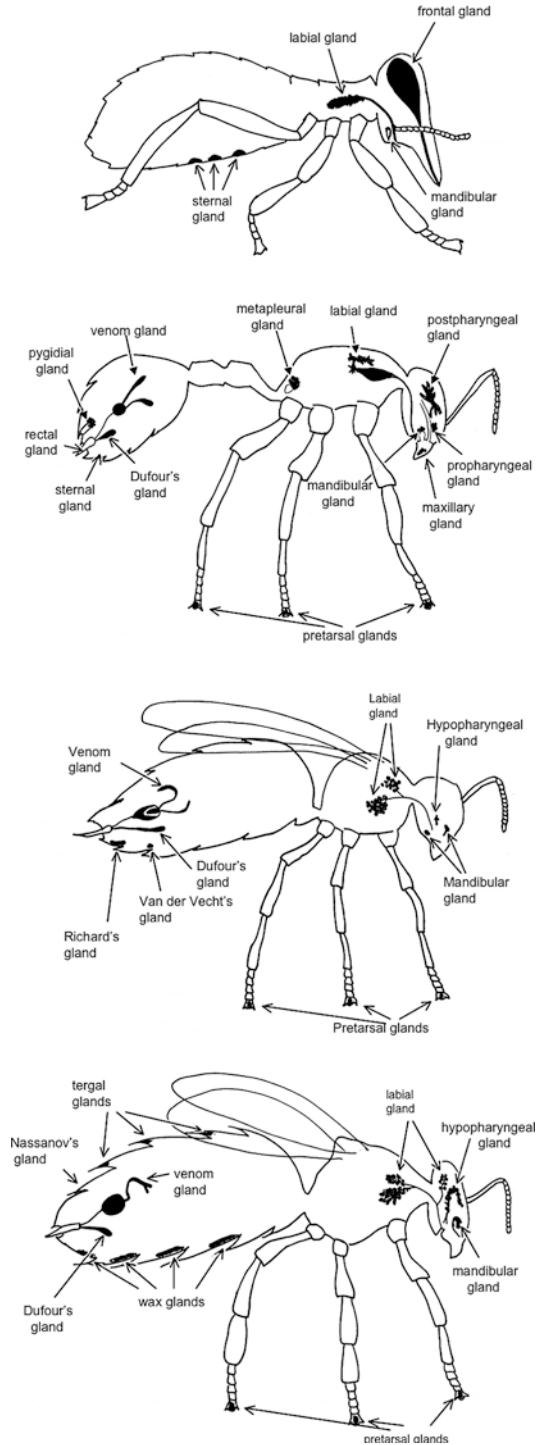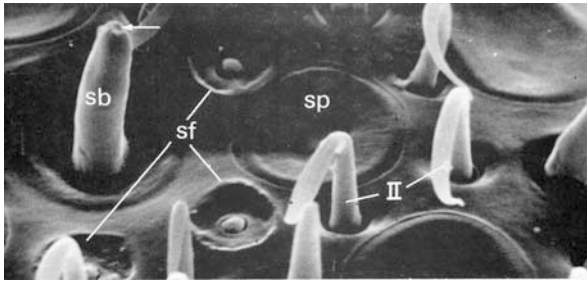
Fig. 6.2   Perceiving odors. Scanning electron micrograph (3,900×), showing part of the surface of segment 10 of a worker honey bee's antennal flagellum. Four types of sensilla are evident: sf = sensilla companiformia, sp = sensilla placodea, sb = sensilla basiconica, II = sensilla trichodea. The *arrow* points to the pore at the tip of one sensillum. A single antenna may have more than 8,000 sensilla trichodea alone. The sensillae companiformia are likely contact chemoreceptors

To function, the system also requires a rapid enzymatic breakdown of the odorant and other chemical flotsam that may impact it over time. The process by which the receptor's active site(s) are cleared, renewing its sensitivity to incoming molecules, must happen very quickly (on the order of milliseconds) to permit neural integration of the rapid directional changes that are observed during an insect's movements along an odor gradient. This striking behavior depends on antennae, the best-studied chemosensory receptors of insects. Use of two identical sets of receptors probably serves to maximize the sensitivity and efficiency of the system. Moths flying upwind in an odor plume and ants following an odor trail characteristically trace a zigzag route in which each antenna appears to be moved alternately in and out of the odor field. The 'out' antenna suddenly stops sending signals to the brain; as though seeking to restore a balance of input from the two sides, the brain causes a steering change which soon results in overcompensation toward the opposite side, and so on. If both antennae remained continuously in the odor field, habituation might quickly occur. By passing in and out of the threshold concentration level, maximal sensitivity to the stimulus would be likely to persist. In addition, such a system imparts a clear orientation axis to the signal path. Orientation experiments using ants or bees with amputated or crossed antennae lend support to these ideas (Fig. 6.3).

The sensitivity of many insects to odor molecules is further enhanced by antenna design, as is evident from a brief glance at one well-studied pair of antennae, those of the male silkworm moth (Fig. 6.4). It appears that the spacing and arrangement of the antennal hairs allows them to act like molecular sieves; the width of the mesh they form is so small that chemical molecules, because of their fast thermal movements, cannot pass through without contacting the hairs and being preferentially absorbed. The physics of airflow over structures this small obviously also must factor into their design. The sensitivity of male gypsy moths is likewise so great that scientists estimate that the 30 g of disparlure, a synthetic gypsy moth sex attractant, already on hand will be enough to bait some 60,000 traps per year for the next 50,000 years.
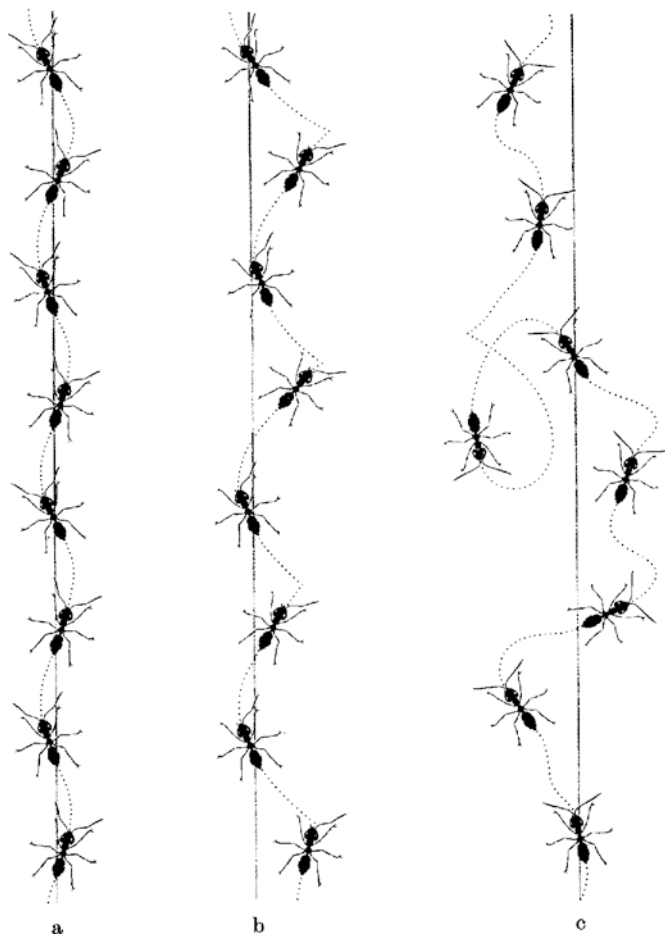
Fig. 6.3 Following a chemical trail. Trail following by *Lasius* worker ants with normal and altered antennae after trail odor was applied along the straight line. (a) Normal trail following, a tropotaxis in which the ant zigzags evenly first to one side then to the other as its paired antennal receptors alternately move in and out of the trail's vapor space and perceive a diffusion gradient. Each time an antenna leaves the odor tunnel, the ant swings back to the opposite side. (b) With its left antenna amputated, the ant repeatedly overcorrects to the right side. (c) With its antennae crossed and glued, the ant is disoriented and relocates the trail with difficulty; its overall progress in the proper direction is probably mediated by visual cues

Responses of a single olfactory sensillum can be measured electrophysiologically using microelectrode probes. Studies of whole antenna responses employ an electroantennogram (EAG) that measures the summed receptor potentials in the whole antenna when an odor puff is passed over it. Signals from the antenna are amplified and displayed on a screen. Like most sensory neurons, antennal chemoreceptors are spontaneously active and display a constant low level of firing or background

Fig. 6.4 Finding females. In response to the odor of a female, the male silkworm moth *Bombyx mori* begins fluttering its wings at 40-50Hz. Males of the commercial strain, having lost the ability to fly, walk toward the odor source while continually vibrating their wings, an action that increases the flow of air over the antennae about 15 times more than just walking. The male's plumose antennae each contain 60–70 branches. Each branch is in turn covered with about 17,000 olfactory hairs that average 100 μ in length. About half of these receptors are tuned to detect the female's sex pheromone, whereas the antennae of the female do not react to this scent at all. Electrophysiological recordings indicate that when a single biologically relevant molecule strikes a single receptor, it elicits a detectable response. However, about 200 molecules must arrive simultaneously before the male begins an upwind searching movement

noise. For reliable efficiency, some of the better man-made electronic detection systems currently require input about twice the background noise (a signal-to-noise ratio of about 2:1). In contrast, the male silkworm moth shows a positive behavioral response at the incredibly low signal-to-noise ratio of 0.125:1.

While these techniques are useful for screening potential attractant and deterrent chemicals, full behavior-based laboratory and field trials are needed before a chemical can be conclusively said to be communicatory (Fig. 6.5), because physiological state, ecological context, and nervous integration are all intimately involved in behavioral activation.

6.2.2 Communication Through Chemistry

The story of Fabré and his peacock moths is generally accepted as the first definitive evidence of communication by chemistry, but almost a century passed before microanalytical techniques reached the point in development that would permit identification of the minute quantities of chemical that were involved. Beginning in the period after World War II, however, the field of insect chemical communication grew quickly. As knowledge about chemical communication systems has grown, the subject has rapidly become more complex, and so has the terminology to deal with it.
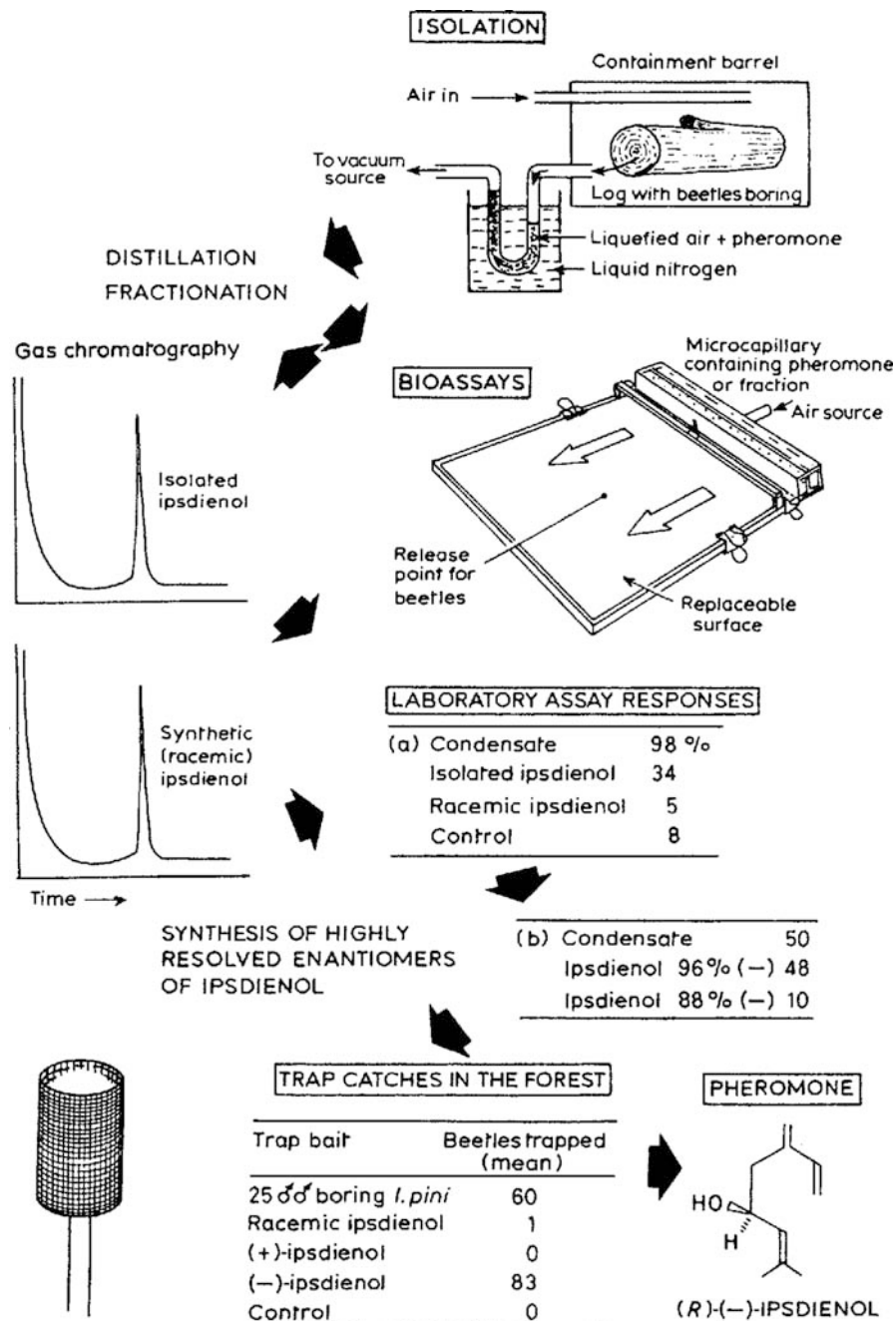
Fig. 6.5 Proving chemical communication. Example of the procedure leading to identification of the aggregation attractant of the bark beetle *Ips pini*. The stages involve the collection, purification, identification, synthesis, and field testing. At nearly every stage appropriately designed behavioral bioassays are essential

In 1959, the German chemists Peter Karlson and Adolf Butenandt and the Swiss zoologist Martin Lüscher proposed a new name for some of these messenger chemicals to replace the contradictory term 'ectohormone' then in use. From the Greek *pherein*, to carry, and *horman*, to excite, they derived the word *pheromone*—a substance secreted by an animal that affects the behavior of other animals of the same species. Initially it was thought that a pheromone would be a single chemical, but as detection and bioassay methods became more sophisticated, most pheromones proved to be blends of two or more components (see below) that are typically active in very low concentrations. That same year, the first pheromone was chemically isolated and identified—the sex attractant of the commercial silkworm, *Bombyx mori* (Case Study 6.1).

Case Study 6.1: Identification of the Mate Attractant of the Silkworm Moth, *Bombyx mori*

Today powerful new devices are routine in the chemist's toolbox, revolutionizing the study of animal and plant odors, and a single insect may be sufficient to identify and characterize an emitted odorant molecule. However, the first time took 30 years and over 500,00 moths.

   Bombyx mori is the most famous caterpillar in the world—the silkworm whose cocoon, spun from a single strand 500 to 1,300 yards long, furnishes the material for a thread and cloth not yet duplicated by any synthetic fiber. The only truly domesticated insect, the silkworm moth can no longer maintain itself in a natural environment but survives only under cultivation, where most individuals live only until the pupal stage, then are plunged into boiling water and their cocoons unraveled. However, in each generation a few moths are allowed to survive to furry, greenish-white adulthood to furnish eggs for new progeny. Neither sex can fly, and therefore the male cannot easily scout the terrain to find a mate. Yet it had long been known that female *Bombyx* in some manner attract males from extraordinary distances (see Fig. 6.4).

   In 1939, the German chemist Adolf Butenandt, who had previously gained fame for his discovery of the identity of human sex hormones, reasoned that a biochemical lure in the bodies of virgin females was probably responsible. Although his available tools would now be regarded as primitive—he lacked such now-standard equipment as the gas chromatograph—he began to work on the isolation and identification of the substance. By 1959, Butenandt and his associates had processed half a million female silkworm moths and had extracted from the abdomen tips just twelve-thousandths of a gram of a derivative of the active compound.

   Next, the researchers used a combination of chromatography, infrared and ultraviolet spectroscopy, and chemical structural analysis coupled with biological assays to see which fractions of this derivative elicited male wing fanning. They obtained a substance which, in minute quantities, was as attractive to male silkworm moths as the most seductive virgin female. It was a

primary alcohol with the formula *E*-10,Z12-hexadecadien-1-ol, which they named 'bombykol'. It was the first sex attractant identified in the Lepidoptera and the first to be chemically characterized.

Within a few years after Butenandt's remarkable feat, Edward O. Wilson and William H. Bossert proposed dividing pheromones into two functional groups according to their mode of influence: releasers and primers. *Releaser pheromones* stimulate an immediate and reversible behavioral response mediated wholly by the nervous system; these pheromones are thus by definition chemical 'releasers' in the terminology of the ethologist (see Chapter 2). They are widespread in insects and serve a great many functions, sex attraction and alarm being especially important ones.

Primer pheromones, on the other hand, act to physiologically alter the endocrine and reproductive systems of the receptor animal, re-programming it for an altered response pattern. In a sense, the receptor's body is 'primed' for new biological activity, although such activity may not appear until some future time and may require triggering by another releaser pheromone. Primers are best known in social insects where they mediate a range of social interactions; in a highly populous colony where it would be impossible for the queen to physically control the workers, they have obvious adaptive significance. Primer pheromones are also important in desert locusts, mediating maturation and phase change that facilitates swarm synchrony.

Other attention turned to substances that transmit external chemical messages that affect individuals or populations of a species different from their source. These were termed *allelochemicals* (Greek: *allelon*, of one another). Allelochemicals may affect the growth, health, behavior, or population biology of other species. Two categories of allelochemicals have been recognized: allomones and kairomones. *Allomones* are chemical agents of adaptive advantage to the organism sending them; *kairomones* (Greek: *kairos*, opportunistic), on the other hand, are of adaptive value to the organism receiving them.

All pheromones fall under the broader umbrella classification of *semiochemicals* or *infochemicals*. In short, an infochemical is any chemical produced by one organism that incites a response in another organism. Figure 6.6 puts some semiochemicals into their behavioral context.

Even with so much terminology, some chemicals that affect behavior do not fit neatly; for example, compounds that are released by fermenting and decaying fruit attract parasitoid wasps that attack the larvae of certain fruit flies. A number of other categories have since been proposed, but classifying the diverse responses of organisms to chemicals does not necessarily enhance understanding. Furthermore, the same compound may sometimes have multiple roles depending upon context, and, as we have noted before, the very labeling of behavioral phenomena tends to color subsequent interpretations of it.

Semiochemicals

```
                    Semiochemicals
                   /              \
        Intraspecific action    Interspecific action
                |                    /         \
            Pheromone          Kairomone      Allomone
           /        \         (benefits       (benefits
      Releaser    Primer       receiver)       sender)
          |         |              |              |
```

Alarm	Sexual maturation	Pheromones	Defense secretions
Sexual	Caste determination	Allomones	Repellents
Aggregation	Development	Toxins	Floral scents
Marking	Physiological state	Metabolites,etc.	Lures
Recruitment		used in host/prey	
Identification		finding	
		Floral scents	

Fig. 6.6   Classifying semiochemicals. Pheromone releaser effects are classical stimulus-response reactions mediated wholly by the central nervous system. With primer effects, behavior is usually induced not by the pheromone but by later external stimuli for which the pheromone has 'primed' the animal's physiology

    Nevertheless, these basic categories are broadly useful. Allomones tend to include compounds having roles in aggressive relationships, such as defensive secretions and repellents (see Chapter 5) and odors mediating mutualistic relationships such as flower scents that attract pollinators (see Chapters 4 and 9). Kairomones include host location cues such as natural plant products that attract herbivorous insects (see Chapter 4) and prey scents that attract predators and/or parasites. Note that from the standpoint of selection, kairomones must be viewed as evolutionary 'backfires' for the emitting organism; they were originally selected to serve either pheromonal or allomonal functions of benefit to the emitter, but secondarily they have come to be used by other organisms (herbivores, predators, parasitoids) to its detriment.

6.3 The Functions of Chemical Communication

A pair of bright orange patterned butterflies cavort in the air above a patch of goldenrod flowers, performing loops and tight rolls, one occasionally hovering briefly above the other, rising and falling on invisible air currents. Below them on the ground several ants scurry along an invisible line weaving among the plants. Close examination of the goldenrod reveals a group of yellow aphids along some of the stems, some of whom have glistening droplets of liquid on the tips of their cornicles; near them a black spotted lady bug is contently munching on one less fortunate group member. What do these different observations have in common? All are

examples of chemical communication that serve different purposes. In the following sections, we'll be examining some of these purposes in more detail.

Any time an organism produces a signal, there is at least potentially an intended receiver. However, keep in mind that signals also can be intercepted for use by a variety of illegitimate receivers, for example, predators, parasites, and competitors. Furthermore, even for the intended receiver, the message that the communicator encodes may differ somewhat from the meaning that the event might have for the recipient. Finally, in interpreting communicative emissions one must be careful to distinguish functions from incidental effects. Functions must increase the fitness of the sender in order to evolve; the same does not necessarily hold true for incidental effects. For example, pregnant female rabbits release hormones into the circulatory system that, when picked up by feeding fleas, stimulate flea reproduction. The function of the hormone—rabbit reproduction—is positive for the rabbit; the effect—an increased flea population—surely is not.

6.3.1 Finding and Choosing Mates

Dance flies begin a tap-dancing courtship that includes a chemical exchange. The phantom midge *Chaeborus* grooms elaborate plumed antennae as he searches for cues that a female is nearby. Using pressure from its internal body fluids, a moth everts its abdominal scent brushes (see Plate 16).

Charles Darwin was well aware of the importance of chemical sexual signals, and in proposing his theory of sexual selection, he suggested that sexually selected signals would have many features in common, including the elaboration or expression of the signals in only one sex, development only in adults, often only in the breeding seasons, and use primarily or exclusively in mating. Chemical signals, and the scent glands that create them, commonly show all these characteristics.

Sexual selection can take many forms. The most fully studied are mate choice, in which members of one sex display to be chosen by the other sex, and 'contests' in which members of the same sex compete with one another to be the 'dominant' individual that will have exclusive or preferential mating choices. Both of these aspects are recurring themes in the area of chemical communication, as throughout all of biology.

Species recognition, mate recognition, and mate assessment are all non-exclusive functions of sex pheromones. Most often, however, the scenario begins with a female insect producing pheromones to which males respond, often over extraordinary distances (see Case Study 6.1). Such pheromones exist in a concentration gradient, and sometimes the same compound calls in the opposite sex from a distance at low concentrations and elicits courtship behavior at the higher concentrations encountered at close range. Alternatively different components of a pheromone blend come into play at different points in the attraction process. During pheromone release, certain stereotyped postures called 'calling behaviors' are common among a wide variety of unrelated insects (Fig. 6.7).
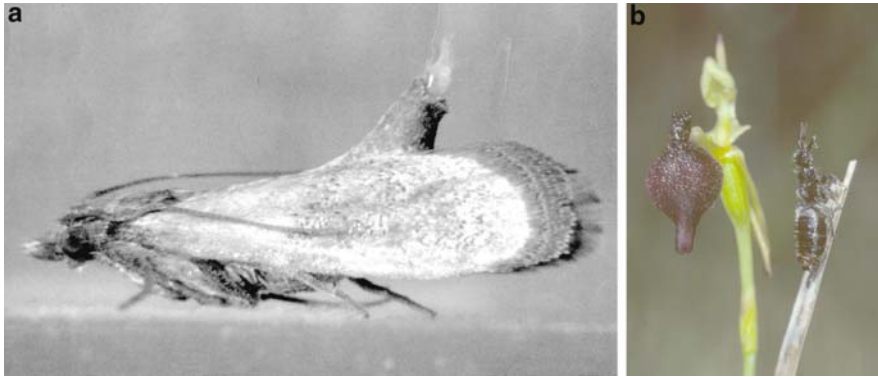
Fig. 6.7 Calling males from a distance. (**a**) Position adopted by a female Indian meal moth, *Plodia interpunctella*, during sex pheromone release. During calling the abdominal tip is elevated and glands in the intersegmental membrane between the eighth and ninth abdominal segments are extruded. A similar stance is taken by most calling moths as well as by a number of other unrelated insects. (**b**) A wingless thynnid wasp female releases her sex attractant in a characteristic 'calling' position atop a grass blade. However, competing for the winged male's attention is the flower of an orchid, *Drakea* (*at left*) that deceptively signals with the same odor and 'feel' as the female wasp. Male wasps are poor discriminators visiting several orchid flowers that they pollinate

A well-known prediction from sexual selection theory is that the limiting sex (almost always, the female) should put less effort or risk into display and attraction, not more, than the less-limited sex. In other chapters, we have noted that males are the producers of most visual or acoustic calling signals, as this theory would predict. So why should it be the female insect that produces these pheromone signals? There are some reasonable non-exclusive 'arm-chair theories' but few experimental studies to address this question. Signals in the chemical sphere may be energetically less expensive than producing sounds or active visual displays, and they may involve less risk of predators homing in on their source. It is also quite likely that males are actually carrying the larger burden of risk because their flight is energetically costly and exposes them to a higher risk of predation than the generally hidden, calling female.

It would be overly simplistic, however, to think of insect sexual attraction as simply 'females signal, males respond.' In many cases, odors also come into play once the sexes have been drawn within range of each other by other cues. They may be produced by either sex, but are usually emitted by the male and often as only part of a complex pattern of courtship behavior.

These male-emitted chemicals are delivered in several ways. The male monarch butterfly and its relatives display one type of system (Fig. 6.8); hairpencils are extrusible organs that function as tiny scent-filled brushes, wafting pheromone-rich clouds at close range over the female's antennae. Similar structures in male moths are called coremata. In some butterflies, special glandular scales called androconia occur on the male's wings. A courting male of the grayling butterfly (*Hipparchia*
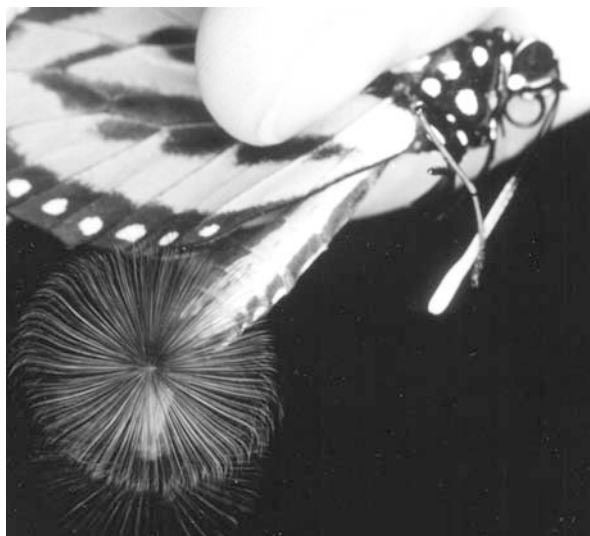
Fig. 6.8 Delivering perfumes to nearby females. Paired extrusible scent organs (hairpencils) at the tip of the abdomen of a hand-held male *Lycorea ceres* (Nymphalidae, Danainae), fully splayed open

semele) will actually clasp the female's antennae between his wings, bringing them into contact with these scent scales.

From tergal glands on their abdomens, several species of male cockroaches produce secretions on which the females feed prior to copulation (Fig. 6.9); the substance has been given the whimsical name 'seducin'. Other male-produced

Fig. 6.9 Maneuvering with lures. A courting male cockroach, *Nauphoeta cinerea*, raises his wings to offer secretions from his tergal gland secretion to a potential mate. When a female crawls upon his back to feed she is in the proper position for the male to connect his genitalia with hers, and if successful they will copulate in an end-to-end position

chemically diverse substances even include secretions passed to the female with sperm, which have the potential to affect many aspects of female behavior and physiology.

Only a few insects reverse roles from the very beginning, with the males producing long distance attractants. Most (but by no means all) of these are beetles. Male callers tend to occur in one of two situations. The first is with insects that gather in courting associations called leks (see Chapter 9); these males often use pheromones to attract females, especially among tephritid fruit flies, anthophorid bees, and various ants and social and solitary wasps.

The other situation is when males locate patchy resources needed by females and call, as occurs with male papaya fruit flies that call from fruits that will be oviposition sites. Sometimes, especially among beetles, both sexes may be attracted by the same scent; at an appropriate location such as a suitable host plant or other resource, they congregate and mate. Even in cases in which the original function of the pheromones involved is thought to have been sexual attraction, when both sexes are attracted these chemicals are generally called aggregation pheromones.

One or both sexes of some insect species use cuticular hydrocarbons as sex pheromones. Cuticular hydrocarbons are relatively involatile molecules that function at very close range or require contact for detection. They often play fundamental roles in species identification. In *Drosophila* fruit flies they are important in maintaining reproductive isolation between sibling species. When a courting *D. melanogaster* male taps a prospective mate with his front legs he receives contact pheromone signals via chemoreceptors on his tarsi; if it is the correct cuticular hydrocarbon for females of his species, he vibrates his wings and courtship proceeds to the next stage.

Unsurprisingly, the majority of the research on insect sex pheromones has been economically motivated and practically oriented. The specificity of such compounds makes it possible in theory to single out one particular pest species for detection, monitoring, and/or control. Manipulation of insect behavior by means of sex pheromones is a promising alternative to the use of conventional chemical insecticides, although in actual practice it often has been fraught with technical problems.

6.3.2 Assembly, Aggregation, and Recruitment

Quietly and quickly lift a pile of logs and you may see a large cluster of crickets beneath it. Look at garden plants and notice growing tips completely obscured by massed aphids or plant lice. Peer into the attic of a drafty home in late fall and observe clusters of lady bugs in the corners. Encounter a swarm of mosquitoes, a disconcerting experience; likewise for a honeybee swarm.

A wide variety of arthropods assemble for various purposes. In the previous section we considered sex pheromones, which attract only the opposite sex. Now, let us consider pheromones that attract both sexes and/or possibly even larvae.

In its purest sense, *assembly* refers to the process by which both sexes of a species come together prior to some activity, such as feeding, mating, or hibernation; almost

always, the signals that call them together are unrelated in any direct manner to the subsequent activity. *Aggregation*, the crowding together of individuals, is assembly's result. Usually, except in the social insects, aggregations are temporary groupings and pheromones are only one of several ways in which they are promoted and/or maintained. Among those insects possessing aposematic coloration (see Chapter 5), aggregations induced by pheromones are particularly prevalent. For example, a male-produced pheromone attracts brightly colored lycid beetles of both sexes to form prominent clusters, sending potential predators very conspicuous advertisements of their distasteful nature, as do the large hibernation aggregations of distasteful ladybird beetles (see Plate 5). Aggregations and other nonsexual associations are classified in Table 10.1, and the costs and benefits of such behavior are discussed in Chapter 10.

In conservation biology, aggregation size assumes particular importance in the context of threatened and endangered species because under-population has a number of serious consequences. Collectively these consequences are broadly referred to as *Allee effects*, after the pioneering animal behaviorist, Warner Clyde Allee, who first elucidated them in detail. Allee effects are (broadly) defined as a decline in individual fitness at low population size or density. If group size falls too low, the reduction or loss of behavioral interactions between individuals can constitute a severe threat to a species' survival or even doom its very existence. (The extinction of the passenger pigeon is a noteworthy example.)

One recurrent benefit of aggregations is to permit more effective exploitation of the environment than would be possible for single individuals. For example, the caterpillar-like larvae of the sawfly, *Neodiprion pratti banksianae*, feed in tight groups upon jack-pine trees. When young larvae were experimentally isolated from their companions they suffered 80% mortality, whereas among those allowed to remain in groups, only 53% died. Why? Newly hatched larvae have considerable difficulty chewing holes into the tough cuticle of the jack-pine needles. Each larva, even in groups, individually attempts to establish its own feeding site. When finally one cuts through into the inner tissues successfully, other larvae are quickly attracted to the cut, where their feeding widens the breach still further until soon all the larvae are able to feed. Another benefit, also illustrated well by *Neodiprion*, is enhanced defense (see Plate 17).

In still other cases, gregarious behavior clearly functions to bring the sexes together for mating, sometimes in combination with attraction to suitable host resources and oviposition sites. Bark beetles are a good example (see Case Study 6.2).

Case Study 6.2: Aggregation in a Bark Beetle, *Dendroctonus*

Small cylindrical scolytid bark beetles destroy millions of board feet of standing timber each year. Exactly how do they manage recruitment for their mass attacks?

Some of the most destructive of pests to coniferous forest in North America are the scolytids (now considered a subfamily of the Curculionidae), Their attack pattern is quite predictable. First, a small pioneer group selects a tree, usually one damaged in some way. They initiate an invasion and construct nuptial chambers beneath the bark. Shortly thereafter, an army of attackers of both sexes rapidly converges upon the site to continue the attack. By the time mating has taken place, the number of arriving beetles rapidly declines. But as a result of the mass attack, the tree usually dies.

Because of their economic importance, many studies have been conducted on a great many aspects of bark beetle behavior. In 1969, Julius Rudinsky puzzled over one component of the typical attack pattern of some scolytid species—after several hours of mass invasion of the host tree, the beetles' attraction stops very abruptly. It seemed unlikely that this behavioral change was due only to a cessation of pheromone production. It was too sudden, and Rudinsky knew that female frass may remain attractive to male beetles for days. He also knew that test logs containing only male-female pairs in the bark were not attractive to flying beetles.

Looking for an explanation, Rudinsky was struck by the well-known ability of many scolytids to make squeaky sounds (stridulation, see Chapter 8). In general, this sound-producing ability is more characteristic of one sex, the one that is not the original invader. Might this yield an answer?

Through a series of intriguing field experiments, Rudinsky set out to examine the exact role of stridulation in the Douglas fir beetle, *Dendroctonus pseudotsugae.* First, he artificially infested a log section with 30 virgin female beetles. Carefully, he covered their entrance holes with screen so that males could not enter and yet the females could still expel their boring dust. Then he set the test log inside a screen cage. As the females began to bore and produce pheromone-laden frass, beetles flew in to land on the cage, two males being attracted for every female that came. However, he saw no males stridulating. Then Rudinsky took 30 male beetles from an ice chest and placed a single male on each screened entry to a virgin female. As they warmed up, the males began to stridulate, and suddenly the arrival of flying beetles halted. He removed the stridulating males; flying males again began landing on the cage. Back and forth, on and off, at about 10-minute intervals, he could mask the attraction or renew it at will simply by alternately removing and returning the stridulating males to the screened entries of the attractive females.

Was the tiny chirping sound of the male really the signal responsible for the population-regulating phenomenon Rudinsky was observing? Not satisfied with this simple explanation, he attempted to establish more firmly that the stimulus was solely auditory. Again, he placed a freshly killed male on each screened female entry hole and found that, consistent with his theory, flying

males continued to arrive. However, this time he ran a parallel experiment—he cut the wing covers of 30 live beetles so they could not stridulate, and placed them in the same position. When these silent males rested on the screened holes, they had no effect upon the stream of flying males that continued to arrive. But as soon as the screen was removed so the silent males could enter and join the female, again the flight aggregation stopped. Because the stream of beetles could be halted without stridulation, the auditory signals could not be the only ones involved!

Were the females involved in the attraction? By whacking a hammer on the log bark just above each entry hole, Rudinsky killed the females inside their galleries. Beetles kept arriving, apparently due to residual attraction. Then he added males. Again they stridulated—but flying beetles kept on arriving! Rudinsky removed the females entirely from some logs before adding extra males, but again the males' stridulation was incapable of halting the immigration.

The puzzle was solved. The arrival of large numbers of beetles quickly leads to the discovery of the infesting females by males that stridulate as they dig their way into the gallery to join the female. Responding to the chirps, the female begins releasing a chemical that acts as a 'mask' or anti-aggregative pheromone that camouflages the normally attractive odors she has produced in her frass. This in turn serves to inhibit flight response; therefore the number of arriving beetles drops off sharply and suddenly.

Later, Rudinsky demonstrated that electronic playback of recorded male sounds has the same effect, thus definitely confirming the novel interaction of sound and chemistry that mediates the beetle' aggregation. A major fraction of the anti-aggregative pheromone has been identified as the ketone 3-methylcyclohex-2-en-1-one (MCH), a multi-functional pheromone that plays many concentration-dependent roles in insect behavior. It was later discovered that both this and another isomer of MCH are also released by the entering male.

Typically, beetles of only one sex initially select the individual host tree. (In monogamous *Dendroctonus* beetles the female excavates the entrance tunnel, whereas in polygamous *Ips* the male performs this function.) Then as the pioneer beetles begin to attack, they discharge a long-range pheromone derived from ingested host monoterpenes. This simultaneously serves two purposes: attracting additional individuals of both sexes and inducing the opposite sex to enter the nuptial chambers and mate (Fig. 6.10). In low concentrations, in synergistic combination with other host- and beetle-produced chemicals, the pheromone attracts both sexes and causes males to stop and stridulate. At higher concentrations, it prevents flight aggregation of both sexes.

The communication system of bark beetles would seem to have high adaptive value, promoting an even distribution of available mates, preventing overcrowding with subsequent brood mortality, and allowing the cooperative mass attack
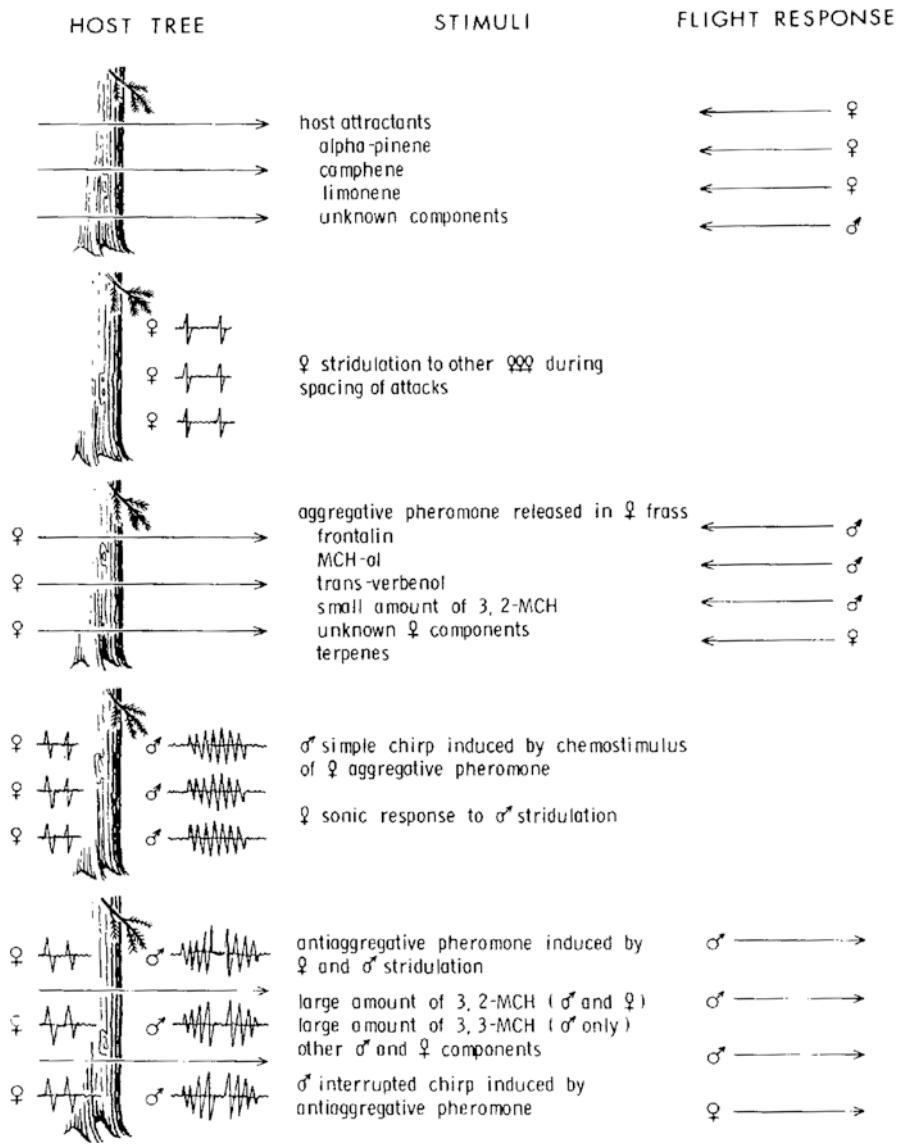
Fig. 6.10 Starting and stopping an aggregation. Summary of the interaction of olfactory and auditory stimuli in the aggregation response of the Douglas fir beetle and its subsequent inhibition

necessary to overcome the host tree's resistance. However, such an explanation is somewhat difficult to reconcile with natural selection theory that reasons that to be selectively advantageous benefits must accrue to individuals. In addition, aggregation poses a problem in that the bark is a finite resource and each individual uses it at a cost, so additional responders can be viewed as competitors whose effect upon the beetles already present would be to lower their individual fitness. Are there alternative explanations?

While both sexes are attracted, it does not necessarily follow that their interactions denote cooperation (although there may be Allee effect benefits to the signaler). Responders may be exploiting the senders' message as a shortcut to host location without assuming the risks of attacking resisting trees—in essence, cheating. Responding males may be eavesdropping, hoping to gain mating opportunities by intercepting some of the females that are attracted. Context is also important. Low densities of beetles would be unlikely to be able to subdue a living tree and thus would achieve little or no per capita reproduction, but an already-dead host would present little challenge.

If initial colonizers of live hosts experience high mortality, might their behavior be regarded as altruism (see Chapter 10)? Or are they perhaps manipulating responders to help them defeat the host? Depending on context, there are likely to be some evolutionary trade-offs; the trick is to maximize the odds of successful host colonization while minimizing the impact of competitors. Also, it should be noted that conspecifics are not the only players. The same pheromones that serve as aggregation attractants also are exploited as kairomones by a suite of generalist and specialist predators and parasites of the beetles and these predators and parasites may disproportionately affect late-arriving beetles, increasing their costs relative to their benefits. Finally, recall from Chapter 4 that plants are not passive in their interactions with insects. They might be expected to counter by evolving ways to interfere with the beetle's communication system, possibly masking or inhibiting signals.

Many other examples of insect aggregations occur, many of which are pheromone mediated. Cockroaches often congregate inside of kitchen cabinets. When experimentally offered simple roosts made of filter paper, groups of *Blatella germanica* cockroach nymphs invariably preferred to aggregate on those kept in the stock cockroach culture for several days rather than roosts of fresh filter paper of the same size (Fig. 6.11). When their antennae were removed, however, the cockroaches aggregated about equally on both roost types, thus implicating a role for olfactory cues in their preferred choices. In order to determine the source of the putative pheromone, various cockroach body parts were isolated and washed in ether, and fresh filter paper impregnated with the extracts. Abdominal extracts caused the strongest aggregation, and eventually the pheromone source was determined to be in the feces, presumably originating from rectal pad cells.

The adaptive significance of cockroach aggregations is still not entirely clear. However, it has been shown experimentally that German cockroaches reared in isolation grow at a slower rate and suffer greater mortality compared to those raised in groups. Amelioration of the physical environment may also be involved, since individuals in groups would be less prone to desiccation. In nature such aggregation could also benefit individual survival in the face of predation, a selfish herd effect. Interestingly, cockroach aggregation pheromones do not appear to be species specific; nymphs of several unrelated species in three different cockroach families aggregate in response to each others' pheromones. However, nymphs appeared more responsive to their own species' pheromones, and a few species appeared to be repelled by fouling produced by other species. In addition, at least two species produce their aggregation pheromone in their mandibular glands, so one cannot simply
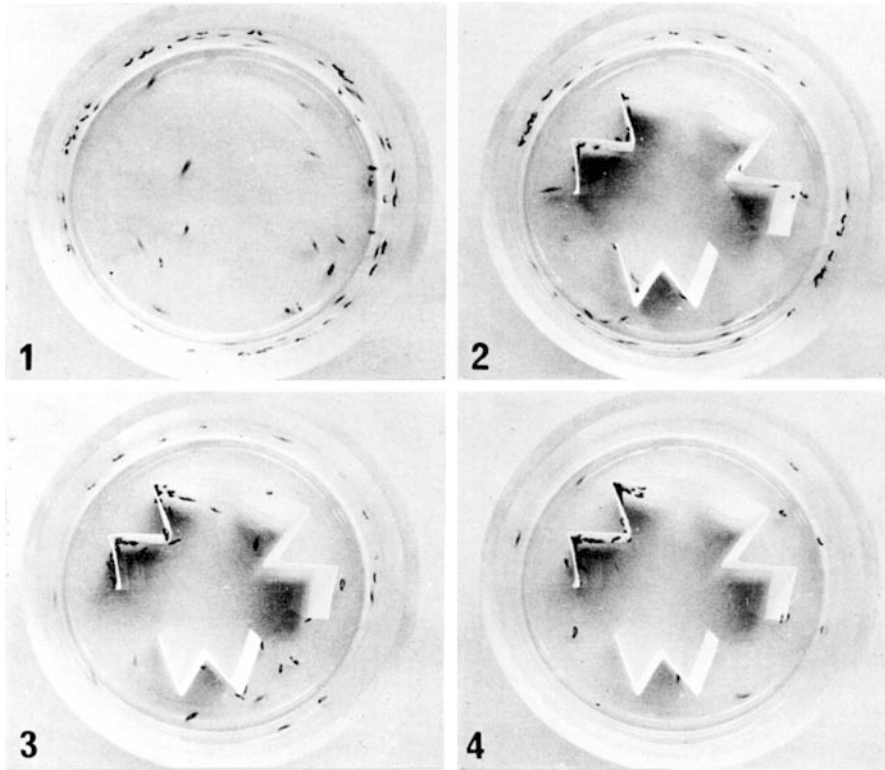
Fig. 6.11 Investigating roach aggregation. Sixty first instar nymphs of the German cockroach, *Blattella germanica*, were introduced into a glass arena with three folded filter paper roosts: two made of fresh paper, the other (*at upper left*) of paper left in a stock roach culture for 24 hours prior to the experiment. Progressively greater preference for the conditioned roost occurred through time: (1) start of experiment; (2) after 1 minute; (3) after 25 minutes; (4) after 45 minutes

assume that all species of cockroach produce a fecal aggregation pheromone simply because other species collect on paper contaminated by them.

Although most aggregations are temporary, as we have mentioned, some are persistent, most notably those forming social insect colonies. Those colonies whose social lives are most highly developed exhibit extensive direct food sharing (trophallaxis, see Chapter 4). Also nearly universal among the social insects is clustering behavior. Workers removed from a nest and placed in bare surroundings will quickly gather in one or several little groups. If the mother queen and/or some larvae are with them, this occurs even more rapidly and the grouping is even tighter.

Of all the types of pheromonally induced insect assembly, perhaps the most dramatic is exhibited by a fertilized social insect queen, continuously surrounded by a retine of crowding, licking, food-offering attendants (Fig. 6.12). The effect is least marked in small colonies or where there are multiple laying queens. However, tightly massed workers may number into the hundreds upon the distended bodies of the 'physogastric' queens of army ants, fire ants, and termites. Several investigators

Fig. 6.12 Regulating the workforce. (*left*) A honey bee queen is surrounded by a retinue of workers attracted to her by queen mandibular pheromone. (*right*) As the schematics show, the pheromone component called homovanillyl alcohol (HV) bears a striking structural resemblance to dopamine, a biogenic amine that plays a central role in insect behavioral regulation and motor control

have shown that pheromones are involved; with army ants, in fact, merely allowing the queen to sit on untreated balsawood strips will transfer enough scent to make the strips highly attractive to workers.

Whenever joint efforts are needed—whether for exploiting a food source, repairing a breach in a nest, or moving to a desirable new nest site—individuals of a great many insects, particularly among social species, are able to chemically summon others of their kind. Although the category is admittedly a loose one, this special case of assembly has been termed *recruitment*, that is, communication that brings conspecific individuals, often nest-mates, to some point in space where work is required.

The simplest cases of recruitment appear to border on the unintentional. Honey bee workers, for example, can recognize food odors both from smells adhering to the bodies of successful foragers and by the scent of nectar regurgitated by them. Even in the absence of communicative dancing, workers that have previously encountered a similar odor will search the site for it again. In a slightly more advanced form of recruitment, some social insects leave chemical 'footprints' to attract others, such as the odor trails laid by both walking honey bees and some wasps in the vicinity of their nests. While honey bee recruitment to pollen and nectar resources is mediated by the famous dance language (see Chapter 8), there is also a unique scent to the dance. Waggle-dancing bees also release small amounts of four hydrocarbons into the air space surrounding them, and these odors stimulate the dance followers to exit the hive, thereby increasing foraging activity for the colony.

Recruitment undoubtedly has reached its highest development among the ants, bees, wasps, and termites, though it certainly is not restricted to them. Although trail following has long fascinated biologists, the mechanism behind this behavior was unclear until 1959 when it was first elucidated in fire ants, *Solenopsis invicta*.

In essence, workers travel through a 'vapor tunnel' created by the diffusion of the evaporating pheromone blend (primarily *Z,E*-β-farnesene) that flows from the Dufour's gland as the trail-laying ant draws the tip of its extruded sting lightly over the ground surface. Recruitment in fire ants also provides a good example of insect *mass communication*—the sharing of information that can be transmitted only by a *group* of individuals. Far from being random, the number of *S. invicta* workers leaving the nest to move along a particular foraging trail is in direct response to the summed amount of trail substance laid down by those workers already returning from the food source. Both quantity and quality are mass communicated. At first, increasing numbers of ants arrive; then, as the food becomes crowded, the arriving ants become increasingly unable to contact the food and begin to turn back without laying trails. Thus, numbers equilibrate at a level that is a linear function of the area of the food source. As this area declines, so does the number of trail layers and hence the number of newly approaching workers. Quality of the food source can also be mass communicated through an 'electorate' response in which individuals 'choose' whether to lay trail or not after inspecting the food find. Through such aspects of mass communication, trail pheromones can provide a control that is more complex than one might predict from individual responses alone.

The tent caterpillar *Malacosoma americana* is a familiar early spring sight in eastern North America, with its glistening silken webs in crotches of apple and cherry trees. These gregarious caterpillars forage in groups, laying down silk threads impregnated with trail odors as they travel. Foraging episodes are cyclical, occurring about every six hours, when hungry groups leave the tent in search of fresh foliage. During the outbound initial search the chemical marks are intermittent, termed exploratory trails. After locating a productive patch of new leaves and feeding to repletion the group heads back to the web; this time individuals drag the tip of their abdomens along the silk lining the branches, laying down recruitment trails (Fig. 6.13). Unsuccessful foragers return to the nest periodically and if they encounter a recruitment trail they will immediately follow it out to the food resource.
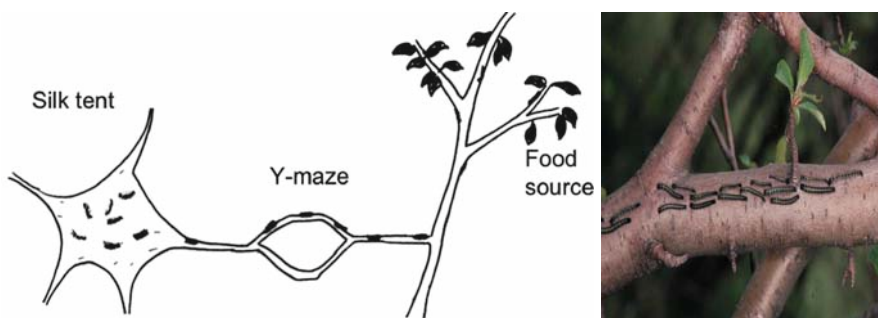
Fig. 6.13 Studying recruitment. (*left*) Apparatus for experimental analysis of recruitment to food in the eastern tent caterpillar, *Malacosoma americanum*. Caterpillars roost in a silken tent to which they continually add silk secreted by their labial glands. (*right*) At intervals, groups travel out along a branch in search of food, laying silk along the route; if productive food patches are found, the caterpillars feed and then return to the tent, this time heavily impregnating the silk trail with a pheromone (principally 5β-cholestan-3-one) from a sternal gland at the tips of their abdomens. Other hungry caterpillars selectively follow the trails back to the food source

The tent caterpillar system has feedback loops similar to those in the mass communication system of the fire ant, in that recruitment is elective. Individual caterpillars mark in response to the quality of the food site (which in addition to nutrition, may also reflect density of caterpillars), and other individuals use this information to evaluate food patch quality and preferentially move out only to highest quality patches. The overall effect promotes a high degree of coordinated synchrony among the entire group, increasing the efficiency not only of foraging, but also of thermoregulation (important for food processing), and defense. Group members are initially all siblings, but groups often merge when more than one egg case was laid on the same tree. Apparently bigger is better—experimental sibling groups of 100 caterpillars grew to 150% the body mass of their siblings that were in groups of only 30 caterpillars.

6.3.3 Alarm and Alert

In 1609, in what may be the earliest explicit description of an insect pheromone, Charles Butler commented about an aspect of honey bee behavior already common knowledge among beekeepers:

> When you are stung, or any in the company, yea, though a Bee have strike but your clothes, specially in hot weather, you were best be packing as fast as you can: for the other Bees smelling the ranke favour of the poison cast out with the sting will come about you as thicke as haile: so that fitly and lively did he express the multitude and fierceness of his enimies that said *They came about me like Bees*.

Alarm and defensive behavior often go hand in hand, and in some cases a single substance simultaneously releases both behaviors. For example, disturbed nymphs of the pyrrhocorid bug *Dysdercus intermedius* secrete a fluid from the third dorsal scent gland; the compound is used simultaneously for defense and for releasing alarm behavior. In other cases, different components of a pheromone blend release different aspects of the response. For example, one of the multiple components of the sting-released honey bee pheromone has been identified as isopentyl acetate, which smells like bananas; alone on a cotton ball it continues to attract and anger other worker bees but does not release attack behavior.

Alarm and alert pheromones are alike in that both are produced under conditions of immediate or potential threat, but the responses they elicit grade into several functional categories; defense, dispersal, agitation, aggregation, and recruitment are among the more common. For example, subterranean ants of the genus *Acanthomyops* have populous colonies crowded into relatively small caverns. When stimulated by alarm pheromone, they rapidly converge toward the source of disturbance and meet the danger head-on. Related ants in the genus *Lasius* normally nest in smaller colonial groups in more exposed situations under rocks or logs; their response to disturbance is to scatter as if in a panic and run hurriedly about. Both species employ undecane as the principal component of their alarm pheromones, but *Lasius* is much more sensitive at lower concentrations, in effect, possessing an 'early warning system' for rapid evacuation when danger threatens.

A similar concentration effect involves citral, a mandibular product of certain Neotropical stingless bees. In low concentrations droplets of citral are highly attractive to workers of *Trigona subterranea* and serve as a trail pheromone used in recruitment. High citral concentrations in the nest vicinity, on the other hand, release alarm and attack behavior. Some unrelated stingless bees that have lost the ability to collect their own pollen also use citral to disorient other bees whose nests they raid for pollen. *Lestrimelitta limao* scouts that manage to penetrate nests of susceptible *Trigona* species release citral inside, causing a complete breakdown in the social organization of *Trigona* as well as being a strong attractant to other *L. limao* workers.

Since insect aggregations, whether temporary or permanent, constitute a jackpot for effective predators, selection for efficient protective behaviors has undoubtedly been especially strong among aggregating species. The existence of alarm-alert pheromones has been demonstrated for many. Gregariously feeding green peach aphids discharge a volatile sesquiterpene from their abdominal cornicles when disturbed (Fig. 6.14); this acts as a powerful dispersal agent for nearby aphids that are likely to be clone-mates, possibly a behavior favored by kin selection (see Chapter 10). Both nymphs and adults of the bed bug, *Cimex lectularius*, discharge a
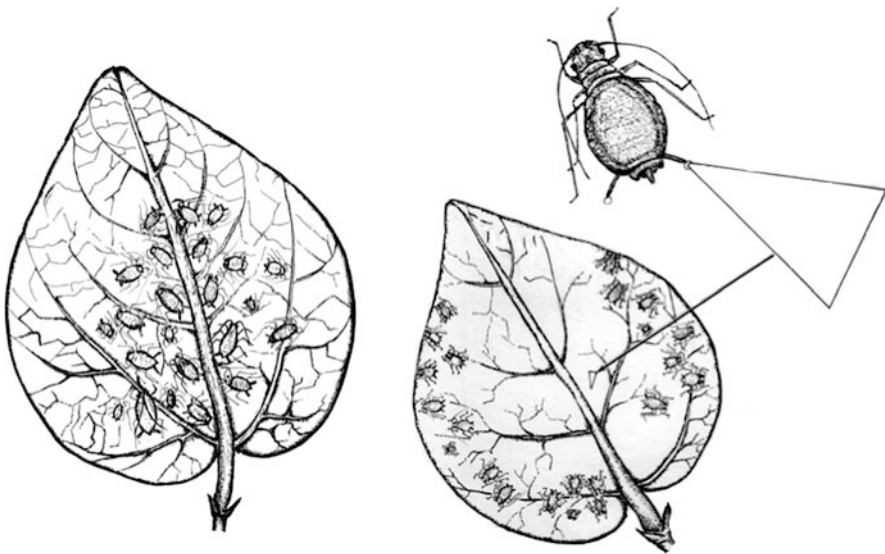
Fig. 6.14 Spreading the alarm. As shown in this pheromone bioassay for the green peach aphid, *Myzus persicae*, when a filter-paper triangle daubed with *E*-β-farnesene pheromone secreted from the aphid's abdominal cornicles is introduced next to a cluster of feeding aphids, it takes less than five minutes before most aphids have left the area and some have dropped off. This alarm dispersal behavior is characteristic of a variety of aphids, but depends on context. Ant-attended aphids tend to remain feeding, relying on their ant guards for protection. Ants are attracted to *E*-β-farnesene, as are some predators, such as the multicolored Asian ladybug. In their glandular leaf hair, some solanaceous plants produce *E*-β-farnesene that may help to protect them from aphid attack

multi-component pheromone from thoracic glands in response to irritation; alerted individuals exhibit a response similar to that of aphids.

However, the most widespread occurrence of chemical alert systems is among the social insects, particularly in those species forming large colonies. Evidence of alarm-alert pheromones exists for all of the more highly social Hymenoptera and termites, where it is key to mustering the collective force of the colony for defense of the fort. A concentrated resource bonanza such as the stored honey and helpless brood in the honey bee hive establishes the need for effective recruitment against a wide range of threats, including vertebrates and even conspecific robbers from other nests. Japanese honey bees (*Apis cerana japonica*) are subject to raids by giant hornets (*Vespa mandarina japonica*) that attempt to recruit additional raiders by marking the victim's nest with pheromones from sternal glands. In response, guard bees release alarm pheromone that recruits a counterattack force massed just inside the nest entrance. If a hornet tries to enter the nest, it is quickly engulfed by a buzzing ball (see Plate 18). Hundreds of bees add more alarm pheromone and also mark the hornet with additional secretions that transform it into a chemical beacon for still more recruits. Surprisingly, instead of stinging the hornet to death, Japanese honey bees kill by roasting it. Generating swarm heat, they raise the core temperature in the ball to about 47°C, just below the bees' own upper thermal tolerance.

6.3.4 Host-Marking

After laying an egg inside or upon a host, bean weevils, various parasitoid wasps, and a host of other insects leave a pheromone mark (Fig. 6.15); other female

Fig. 6.15 Marking a host. A female *Trissolcus basalis* (Hymenoptera: Scelionidae) draws her ovipositor tip across the cap of the host egg, marking the spot where she has just laid her own egg. Such chemical marking repels other conspecific females and minimizes the likelihood of multiple oviposition on a single host

conspecifics usually avoid laying their own eggs in or on these marked hosts. Ovipositing female Mediterranean fruit flies, *Ceratitis capitata*, readily discriminate between infested and uninfested host fruits; in a graded response, they adjust their propensity to oviposit accordingly, marking hosts after egg deposition and avoiding or reducing egg clutches in already marked fruits. Apple maggot flies (*Rhagoletis pomenella*) behave similarly.

The advantages of such a system seem obvious. Few hosts or host plants can support an unlimited number of parasites or predators. Too many attacks, and a host usually will die, often taking its attackers with it. Thus, there would be strong selective pressure for attackers to develop some way to assess host suitability and in particular, to detect the presence of preexisting eggs or larvae, whether they be one's own, those of a conspecific female, or another species entirely. Marking pheromones confer advantages both to the signaler and to the receiver. For both, they reduce competition; an ability to distinguish between occupied and available hosts and selectively choose the latter enhances the survival of one's offspring. In a limited resource the earliest offspring would have a head start over any latecomers, and likely would triumph in any competition.

Visual inspections can and undoubtedly do sometimes provide cues, but for insects chemistry appears to be overwhelmingly favored. Host-marking pheromones have independently evolved many times, and are now known to occur in more than 200 species of parasitoid wasps and more than 30 species of herbivorous insects across eight families of Diptera, Coleoptera, and Lepidoptera. All lay their eggs in or on hosts of restricted size that can support the successful development of only a limited number of offspring. Where marking pheromones have been investigated in detail, they generally have been shown to be non-volatile chemicals detected by contact chemoreceptors. A study of this behavior appears in Case Study 6.3.

Case Study 6.3: Host-Searching by an Ichneumonid Wasp, *Pleolophus*

Why is this solitary ichneumonid wasp, noted for low, slow egg production, still consistently one of the most common parasitoids on its sawfly hosts?

Many sawflies in the hymenopteran families Diprionidae and Tenthredinidae feed in the trees as larvae, but drop to the forest floor below to pupate. Here they may be attacked by any of a number of predators and parasitoids. In the case of the sawfly *Neodiprion swainei*, a serious defoliator of jack pine trees in North America, one of these parasitoids is the ichneumonid wasp *Pleolophus basizonus*. Compared to other parasitoids, this ichneumonid is known to have a rather slow rate of egg production and oviposition; a typical female lays only two to four eggs per female per day. Surprisingly, when Peter Price collected sawfly cocoons from different areas in Quebec, Canada, he found that *P. basizonus* was consistently the most abundant parasitoid species to be reared from them. How were these 'poor layers' able to compete so successfully against 18 other species of parasitoids

also competing for the same host? The question was of more than purely academic interest, since this wasp had been purposely introduced several years previously for biological control.

Maybe *Pleolophus* was simply more efficient than her competitors in some other aspect than oviposition rate, Price thought. For example, the wasp might search more efficiently or regulate her oviposition more carefully. He placed three mated female *Pleolophus* with varying numbers of sawfly cocoons into each of several caged 'arenas' that simulated the sandy, lichen-covered forest floor in careful detail. Six days later, he split open the cocoons to count the number of eggs laid within. At all cocoon densities he tested, the frequency with which he found only one *Pleolophus* egg per *Neodiprion* cocoon was much higher than expected from a random attack. In fact, at the highest cocoon densities, the oviposition pattern was extremely regular, with almost no wastage of eggs through multiple ovipositions in the same host. Apparently, searching females could discriminate between parasitized and unparasitized hosts. There were no visual signs of parasitism, so the discrimination presumably had some chemical basis.

A number of other investigations with other parasitoid species had uncovered cases in which conspecific females would interfere with each other during oviposition, particularly if they were confined in a small area at high parasitoid:host ratios. Price reversed his experiment and varied the numbers of wasps but kept the number of cocoons constant in each cage. Then, for two days he watched the cages at hourly intervals and recorded the wasps' positions. As crowding was increased, he observed more females climbing on the cage sides in what looked like an escape reaction. It appeared as though rather than interfering with one another, *Pleolophus* were doing their best to avoid one another.

Was this behavior also chemically mediated? Placing a barrier across the middle of an arena, he released a single female in one side and allowed her to search for 6 hours while watching continuously and recording her searching pattern. She was then recaptured and released again in the center of the arena with the barricade removed, and the amount of time subsequently spent in each half was recorded. As a control, Price similarly observed the behavior of a female released in a fresh arena. Analyzing the results of several such trials, Price found that 7 of 19 females tested exhibited a clear recognition and avoidance of areas they had previously searched (Fig. 6.16). Several variables remained uncontrolled, but avoidance was frequent enough to suggest that females were depositing some 'trail odor' on the substrate as they searched and that it served later to repel them, promoting dispersal. In fact, later studies showed that even different species of parasitoids attacking the cocoons are able to recognize and avoid areas previously searched by *Pleolophus*. Price's studies thus were some of the first to report long-distance repellency of possible competitors by a solitary endoparasitoid.
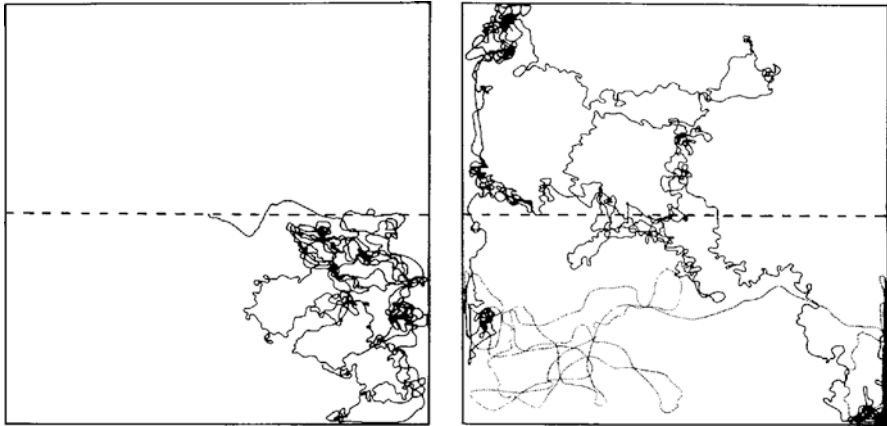
Fig. 6.16 **Host-searching**. Movements of a female ichneumonid wasp, *Pleolophus basizonus*, following her release in the center of a glass-covered experimental arena. The *dotted line* marks the position of a removable barrier. (*left*) The upper half of the arena had been searched previously for 15 minutes by the same female; her avoidance of it during the subsequent 15 minutes is clearly shown. (*right*) The female's movements for 30 minutes in a fresh (control) arena. The dashed line depicts instances when the female crawled on the underside of the arena cover

It is important to remember that insects also can detect chemical and/or physical changes that eggs or larvae induce and use these as signals; simple feeding damage would be an example. Thus, three types of studies are used as evidence that a marking pheromone is actually involved: description of a putative host-marking behavior; biological assays of behavioral responses to extracts of putative marking pheromones; and identification of sources of marking pheromones and mechanisms for their detection.

Modeling studies suggest that a major selection factor for the evolution of pheromonal marking has been to avoid self-superparasitism, that is, a female laying eggs again on a host where she already has offspring, and potentially reducing the survival chances for both clutches as a result. The models suggest that when hosts are sufficient, other conspecific females might gain from taking notice of her marks and using them; when few unparasitized hosts are available, they might do better to ignore the marks. There is, in fact, abundant experimental evidence that some female parasitoids can adjust their rate of superparasitism according to the proportion of parasitized hosts that they encounter, as well as avoiding host areas that they have themselves previously searched.

Moving from host-marking behaviors to true territoriality requires only a short conceptual jump. *Territoriality* can be defined broadly as any space-associated intolerance of others of one's own species, or more narrowly as defensive behaviors based on real estate holdings. To be a true territory marking pheromone, the mark by itself must induce aversive behavior in conspecific intruders.

In both vertebrates and invertebrates, territories (defended areas) occur in a variety of contexts that most commonly involve feeding, breeding, or raising young.

(We'll be returning to territoriality in Chapter 9, in the context of courtship and conflict where it plays a major role.) Both major animal groups rely heavily on chemistry for territorial marking, but they generally employ it in different ways. Among vertebrates, a common behavior is to mark the perimeter of the defended area. This has not often been shown for invertebrates, probably simply because their territories are small enough in scale not to require it. The exceptions that have been noted generally have involved social insects with correspondingly larger territories.

No behavior has all benefits and no risks. Among the risks of employing marking pheromones is potential for attracting the attention of eavesdroppers (see Section 6.4.3). Several examples are known where marking pheromones are used as kairomones by parasitoids to more efficiently exploit a host-marking female's progeny. Other insects of one's own species may also eavesdrop. Weaver ants (*Oecophylla*; see Plate 19) are territorial ants that form extremely large colonies; in Kenya, a single *O. longinoda* colony was reported with 500, 000 workers that controlled the canopies of 17 trees. Their complex pheromonal communication (Table 6.1) includes marking their territories with fecal pheromones in a manner analogous to many vertebrates. In response to freshly exposed habitat, weaver ant workers increase their rate of deposition of anal spots, which persist for many days. When workers of an alien colony are given access to the marked surface in the complete absence of the original ants, the first individuals to arrive display intense aggressive posturing, opening their jaws and raising their abdomens while also showing intense interest in inspecting and antennating the spots. Soon afterward, the intruders begin to deposit recruitment odor trails as they return to their nest.

6.3.5 Recognition

Male and female *Nicrophorus* carrion beetles cooperating to rear a brood of young on a small vertebrate carcass can accurately distinguish partners from conspecific intruders after touching their antennae; the pair's individual chemical profiles become strikingly similar after several days together, but partner recognition appears to be based upon the reproductive status that develops after prolonged contact with the carcass, rather than upon a specific personal identification odor.

'Body chemistry' is more than simply a catchy phrase. Chemical profiles can be as distinctive as fingerprints, and in the insect world they facilitate the recognition and identification of familiar and unfamiliar, friend and foe. These chemicals, known as surface pheromones or *contact pheromones*, are based on cuticular hydrocarbons, but in many cases, they may be composed of a combination of species-specific or sex-specific odors and environmentally derived ones (as, for example, from food sources).

An insect's body is covered by a cuticle with an outermost layer composed of a complex mixture of lipids. Some of these lipids are waxy substances that function as moisture barriers; many insects can change the amount of wax on their cuticle in response to seasonal changes, and species in hot, dry environments typically

Table 6.1 Recruitment in *Oecophylla longinoda,* one of the most sophisticated communication systems known for any ant

Chemical signal(s)	Tactile signal(s)	Movement pattern(s)	Apparent function
Odor trail from rectal gland; regurgitation of liquid crop contents	Antennation; head waving, mandible opening with food offering	Signpost marking; looping trails laid around food source; main trail directly to nest	Recruitment of major workers to immobile food source, especially sugary materials
Odor trail from rectal gland	Antennation; occasional body jerking	Signposts and looping trails only after physical contact with terrain; main trail directly to nest; increase in frequency of anal spotting	Recruitment of major workers to new terrain
Odor trail from rectal gland	Antennation; tactile invitation for transport; physical transport of nestmates	Main trail directly to nest; no signposts; predictable carrying sequence of nestmate categories	Emigration of colony to new nest site
Short looping odor trails from sternal gland; gland surface exposed as abdomen is lifted	None	Trails short, looping, and limited to vicinity of contact with enemy	Short-range recruitment to enemies
Odor trail from rectal gland	Antennation; at higher intensities, body jerking	Main trail directly to nest; no signposts	Long-range recruitment to enemies; used with short-range recruitment, especially intense during territorial wars with conspecifics

have greater amounts of wax than closely related species that live in more moderate surroundings. However, for some time it has been suspected that the hydrocarbons in this cuticular lipid mixture play another important role—that of recognition cues when insects encounter each other. Over the last few decades, technological advances allowed the studies necessary to confirm this suspicion for many insect examples (Table 6.2), and appreciation for insects' use of cuticular hydrocarbons for chemical communication has grown tremendously.

For the vast majority of insects, recognition of one's own species is necessary only for copulation. Contact pheromones are certainly important even in these cases. Certain cerambycid beetles attempt to mate with conspecific females only after touching them with their antennae. When a male cricket contacts another male with his antenna, he becomes aggressive, but when the same individual antennates a female, he initiates mating attempts; if filter paper impregnated with female

Table 6.2 Major recognition functions of insect cuticular hydrocarbons (CH)

Implied question	Selected examples and mode of action
Are you a member of my species?	Beetles: *Conophthorus*, 8 species recognize each other through CH profiles.
Are you the same gender as I am?	Flies: *Drosophila*, sexes recognize each other by relative abundance in same CH set; *Glossina*, distinctive CH set in each sex.
Are you a member of my colony?	Ants: *Leptothorax*, queen-produced CH;
To which caste do you belong?	Termites: *Reticulitermes* castes differ in relative abundance of CH components.
What is your dominance status?	Ants: *Dinoponera*, dominance recognized by relative quantity of one CH out of 80+; *Harpegnathos*, dominance recognized by variations in CH correlated with oogenesis in both queens and workers.
Do you want me to do some task?	Ants: *Pogonomyrmex*, tasks determined by CH proportions, with appropriate environmental input.
Are you closely related kin?	Bees: *Apis*, CH profile plus exposure to hydrocarbons in comb wax.
Can you recognize that I am alien?	Beetles: *Zyras, Diaritiger,* CH mimics that of host ant *Lasius*. Parasitoid wasp: *Lysiphlebus*, CH mimics that of host aphids. Social wasps: *Polistes sulcifer*, a social parasite, changes its CH to that of closely related host after nest takeover.

body-wash extracts is touched to a male's antenna, it also elicites mating behavior. However, it is among insects that have adopted a gregarious or societal existence that unfailing recognition of conspecific individuals over a wide range of circumstances assumes utmost importance. Inasmuch as mutual antennal contact seems to be the most universal greeting, olfactory and tactile cues appear to be primarily responsible for this recognition.

At first glance, nest-mate recognition among social insects such as ants appears to be a casual affair, usually no more than a pause and perhaps an exchange of antennal strokes. However, should an alien insect be encountered within the nest, some of the scope of this communication is swiftly and unmistakably revealed. Even if it is the same species and only from a different colony, the intruder normally evokes hostility; if it is of a different species as well, the resident insect's inspection is swift, the attack violent. Usually the alien is instantly killed or driven from the nest. Such nest-mate recognition in most cases is based principally if not exclusively on 'colony odor'. Colony odor is an example of a class of pheromones characteristic of social insects, the so-called *colony pheromones*. These signals, which have both genetic and environmental components, affect all colony members, causing these members to respond in context-dependent ways.

A common feature of nearly all social insect recognition odors is that individuals learn them at a particular life stage, usually within a short time of their emergence to the adult stage. Such an imprinting-like system has two advantages. First, it allows colonies to have a unique *colony odor* that incorporates both

genetic and environmental components. Second, it serves to mask any underlying genetic heterogeneity that can arise from a queen mating multiple times. The learned odor bestows on each individual a reference template against which it can compare the odor of others it interacts with in the future. Either they match or they don't, enabling fairly straightforward discrimination between nest-mate and intruder.

By definition, the insects in social insect societies live as members of castes, subsets of the colony or group that are morphologically distinct and behaviorally specialized. Thus, for a complex insect society to function, the recognition capacity of individuals must extend beyond colony odor to include distinguishing, and acting appropriately toward, the caste, life stage, and dominance level of nest-mates. For example, certain paper wasp individuals must be given preference in trophallactic food exchanges, and worker ants must segregate eggs, larvae, and pupae into separate piles. How a reliance on pheromones can mediate such complex discriminations brings us to the subject of the next section.

6.4 The Information Content of Pheromones

Consider a single insect sitting on a leaf, releasing a pheromone into perfectly still air. Obeying the law of gas diffusion, the pheromone expands at a calculable rate in all directions surrounding the insect until it forms a sphere at whose outer limits its concentration is zero. Nested within this sphere is a second, more behaviorally interesting one, the *active space*—the zone in which the concentration is at or above the threshold level needed to evoke a biological response from other insects. The active space constitutes the pheromone signal itself.

Of course, perfectly still air is an oversimplification. If a breeze is blowing, the pheromone expands to form a cone downwind of the insect. Within the cone, the active space becomes not a sphere but a downwind semiellipsoid, rather like the upper half of a giant blimp lying on the ground with the emitting insect sitting at the tip of the airship's nose (Fig. 6.17). The stronger the breeze, the shorter the blimp (or 'odor plume') becomes. This simple model does not account for surface drag nor for the fact that most attractant vapors, being heavier than air, will tend to fall before being fully dispersed, thus effectively flattening the top of the active space. In fact, most real odor plumes are turbulent and unpredictably meandering; a swirling smoke cloud from a chimney provides an apt visual analogy. However, the active space concept can be used in combination with linear measurements and gas diffusion laws to generate some predictions and generalizations about the use of pheromones in functionally different communication systems.

6.4.1 Physiological Adjustments: The Q/K Ratio

Suppose that one knows both the amount of pheromone released and the behavioral threshold for perception for some insect. To quantify the amount of pheromone
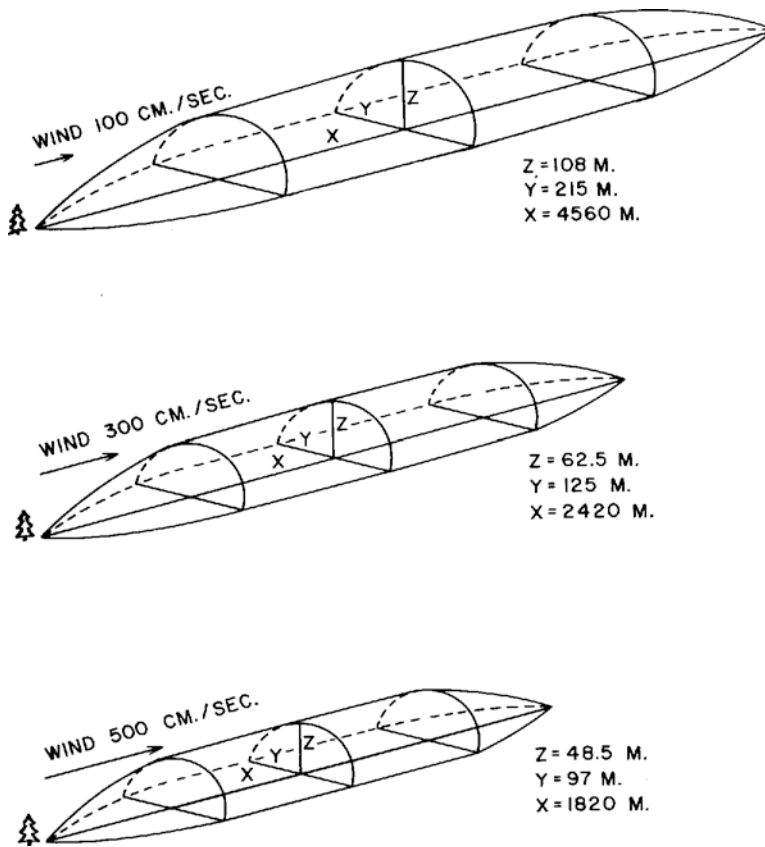
Fig. 6.17 Modeling pheromone movement. A simplified depiction of the active space of the gypsy moth sex attractant, as deduced from linear measurements and general gas diffusion models. Height and width are exaggerated in the drawing. As wind speed increases, there is a contraction of the space within which the pheromone from a single, continuously emitting female is sufficiently dense to attract males

released, let us consider it to be the number of molecules the insect emits per unit of time (or as a single puff), and call it Q. For purposes of brevity, let us call the potentially responding insect's behavioral sensitivity threshold K and measure it in molecules per unit of volume. The interval between release of the pheromone and disappearance of the active space is called the signal duration or fade-out time; using the blimp-like model of Fig. 6.17, it is the time required for the longitudinal axis of the active space to diminish to below the receiver's perceptual threshold. Behaviorally, variations in the active space of a signal would be expected when pheromones serve different purposes. How might this be achieved?

Both intuitively and by studying the model, one can recognize two ways: vary the rate at which the pheromone is sent or vary the receiver's threshold of perception. Basically, the characteristics of any pheromone system can be expressed as a Q/K

ratio. The highest Q/K ratio corresponds to a pheromone system with a great signal distance and slow signal fade-out time. Conversely, low Q/K ratios characterize systems having rapid fade-out time and a relatively small active space. A theoretically infinite variety of systems exist as intermediates along the continuum; they result from changing the values of Q and K independently of each other.

Consider the respective information transfer strategies of mate-seeking moths and alarm-sending ants. A virgin female moth may need to broadcast her desirability over a span of miles for several hours before she attracts a male. Obviously, a slow fade time for her pheromone would be advantageous; it would be desirable also to increase the area in which a potential mate could encounter and respond to the scent, i.e. to have a large active space. This necessitates a high Q/K ratio, accomplished by increasing Q, decreasing K or both. Because there will be metabolic limits on Q (the amount of pheromone the female moth could manufacture and continuously pump into the environment) it is more efficient to change the threshold for perception. To achieve a large Q/K, the value for K will have to be extremely low; in behavioral terms, the male receiver must have a very low threshold of perception, an example of which is the silkworm moth (see Fig. 6.4).

When an ant worker generates an alarm, it is advantageous that other workers be able to locate it sharply in time and space. For this to happen, a signal must have a relatively short fade-out time; correspondingly, it requires a much lower Q/K value, which can be accomplished either by lowering the emission rate or raising the threshold of concentration, or both. The citronella ant, *Acanthomyops claviger*, uses an alarm pheromone with a Q/K between 10^3 and 10^5 cc/second; signals take about two minutes to reach an effective radius of about 10 cm and eight minutes to fade out. If the citronellal alarm pheromone had as high a Q/K as some moth sex lures, a one-ant alarm might theoretically keep the colony in a perpetual unproductive state of chaos and panic. On the other hand, were the citronella alarm pheromone to have an even lower Q/K value, the signals would be relatively useless because they would not travel beyond the distance within which other ants could perceive the danger directly themselves.

6.4.2 Pheromones as Language: Syntax and Lexicon

Because they have tended to be more thoroughly studied and thus simpler to understand, most examples so far have involved single chemicals as pheromones. Often even such 'simple' systems are quite complex, communicating different information at different concentrations or in varying contexts. For example, we have mentioned (see Case Study 6.2) that males of the Douglas fir beetle stridulate when they detect low levels of the pheromone MCH. However, under a high concentration of MCH the chirps of the male beetles change from those of the female attracting calls to a longer, interrupted chirp with quite different acoustic properties; this latter call is characteristic of both courtship with females and rivalry contests with conspecific males.

Intuitively, one would expect to find many insects using such multifunctional single pheromones; being small animals, it would be particularly advantageous, allowing economy in their receptor systems without sacrificing behavioral diversity. This phenomenon, termed *pheromonal parsimony*, is particularly characteristic of the class of pheromones releasing alarm in social insects. Among ants, some alarm substances are produced by the pygidial gland, others by mandibular glands. For example, both harvester ants (*Pogonomyrmex badius*) and leaf-cutter ants (*Atta texana*) use the same alarm pheromone (4-methyl-3-heptanone) secreted from the mandibular glands, and in both species, differing concentrations of this odor elicit very different behavioral responses. Upon perceiving relatively low concentrations ants are attracted toward the source; as they move they cross into a much higher concentration of the pheromone. The respective active spaces can be visualized as nested concentric hemispheres in what is actually an intensity gradient to which the receiver can orient; within the inner of these, ant behavior changes from simple attraction to frenzied aggression.

An alternative to the multifunctional single pheromone is to evolve different pheromones that serve the different functions but produce them in different exocrine glands. Recruitment pheromones in termites are apparently all produced in the termite's sternal gland, but despite considerable convergence in the trail-laying behaviors of ants and termites, among the ants trail pheromones are produced from at least eight different glands, and in some cases more than one gland is involved in recruitment communication.

The insect pheromone language is clearly not composed of an infinite number of chemicals different within each species and unique to each message. In order to achieve and maintain chemical uniqueness and promote privacy during communication with such single chemical systems, insects would need to synthesize increasingly more complex molecules; this strategy obviously would have its upper limits, dependent upon such factors as the biosynthetic capabilities (energy cost) of the organism, physical characteristics (such as volatility) of the molecules used, and the neurological complexity of the receiver. Thus, among distantly related species, there has been considerable evolutionary convergence in pheromone chemistry, even while the uses to which the pheromones are put remain quite distinct. For example, both stingless bees (*Trigona* spp.) and *Acanthomyops* ants use citral as a pheromone, for recruitment trails in *Trigona,* and for alarm in *Acanthomyops*. Asian elephants even share the same sex pheromone with 140 species of certain small moths!

Despite the intuitive logic that it would seem adaptively advantageous for insect chemical communication to be species-specific, in tests of single chemical compounds under laboratory conditions, many pheromones have appeared to lack specificity even at the generic level. How can this apparent discrepancy be reconciled?

First, what appears to be a lack of specificity may not be so after all. The odor environment of an insect is enormously complex; an ordinary terrestrial community may contain hundreds of thousands of animal species and scores to hundreds of plant species each producing its own characteristic odors. Superimposed on this are seasonal and diurnal cycles of production and multiple other factors operating under
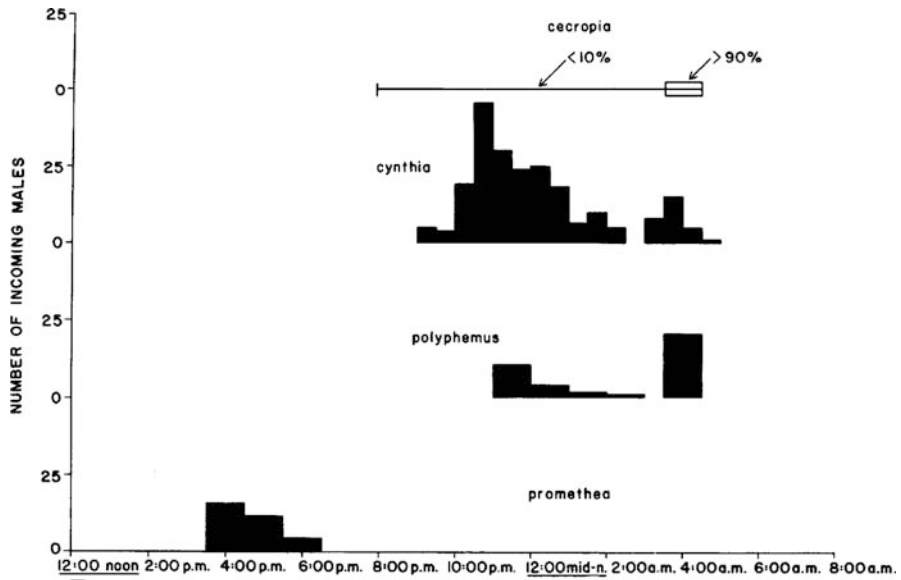
Fig. 6.18 Interacting systems. Males of four North American species of giant silk moths (Saturniidae) each have a differing time of peak flight activity. Seasonal separation also exists; most cecropia males emerge in May; polyphemus moths, in late May to early June; cynthia and promethea moths, mostly in June. While the respective female sex attractant pheromones are known to be very similar, caged females of one species almost never attract males of another species because of these temporal and seasonal differences

field conditions. For example, males of different species of giant silk moths differ in the periodicity of their flight activity, and thus vary in their responsiveness to female sex pheromones according to the time of day or night (Fig. 6.18).

Female silk moths also call only during certain time periods of the daily cycle, and the periodicity of both male flight and female release of sex pheromones can be influenced by ambient temperature during development. When pupae of one giant silk moth species, *Antheraea pernyi*, were kept at 25°C, the adult females initiated calling behavior about 6 hours after lights-off. However, when pupae were kept at 12°C, the resultant females advanced the onset of their calling to 2 hours after lights-off. Corresponding shifts in flight activity also occur in males under these temperature regimes. Hormones (especially juvenile hormone, see Chapter 2) mediate both male responses and female calling times by acting on the different parts of the nervous system involved in processing olfactory information. Circadian rhythms cued by photoperiod and perhaps by temperature or other environmental factors set the hormone secretion cycles.

Second, tests of a single chemical seldom represent the natural situation. Insect exocrine systems are extraordinarily diverse (see Fig. 6.1), with a multitude of glands and wide variations in the ultimate uses of a given gland and its products. Furthermore, the products themselves are often complex. For example, at least 50

volatile compounds are present in the Dufour's gland of a carpenter ant, *Camponotus ligniperda*.

In human language development, the use of a different word for every message in every language has been superseded by the greater efficiency of coding systems based upon combinations of words. While a single word can send a message, adding others produces an almost infinite variety of meanings; consider the different behaviors elicited by 'Help!' 'Help me,' 'Help me love,' and 'Help me kill.' An analogous strategy has been evolved by insects and allows them to send messages more efficiently: pheromone blends or multi-component pheromones. Multi-component pheromone blends are probably the rule in arthropods rather than the exception. Such systems have arisen in two ways: by the use of specific blends of chemical produced within a given gland and, perhaps less commonly, by the use of various combinations of glands releasing pheromones simultaneously or in succession.

Honey bees have one of the most complex pheromonal communication systems so far identified; they possess 15 known glands that produce an array of compounds. A classic example of a pheromone blend is the so-called 'queen substance' or *queen mandibular pheromone* (QMP) secreted in the mandibular glands of the queen honey bee. It affects social behaviour, maintenance of the hive, swarming (see Plate 20), mating behaviour, and inhibition of ovary development in worker bees.

A principal QMP component is the fatty acid *E*-9-oxo-2-decenoic acid. On its own, it is both a sex attractant and an aphrodisiac. Combined with *E*-9-hydroxy-2-decenoic acid it acts as a primer pheromone and inhibits worker's ovary development, queen rearing, and rate of juvenile hormone biosynthesis; the latter thereby regulates the onset of age-related tasks such as foraging.

In addition to these, QMP includes three more chemical components that act synergistically to elicit retinue attraction. The queen's *retinue pheromone* is now known to have nine chemical components (not all synergistic components originate from the same gland) and is the most complex pheromone system known in any organism. The complete blend is translocated to all her body surfaces by self-grooming and elicits the distinctive retinue response among worker bees, causing them to lick, antennate, and groom their queen (see Fig. 6.12). Virgin queens produce significantly less (or none) of many of the nine components and are thus much less attractive to workers than mated, actively egg-laying queens.

It is not unusual to find a chemical blend produced within a single exocrine gland. For example, in ten *Myrmica* ant species, a variety of natural products are used for the same communicative purpose—alarm. Among eight of the species, the same two chemicals (3-octanone and 3-octanol) are present in the mandibular glands, but in highly varying ratios. In one, the two chemicals are combined with a third major constituent. Two other species have none of the previously mentioned compounds but shared a single compound characteristic of them alone. As an interesting aside, it has been shown that many of these same ant alarm chemicals have significant allomone effects, inhibiting the germination of grass seeds collected as dietary staples by various myrmicine ants.

In general, the pheromone blends of closely related species have diverged and diversified mainly by varying the ratios of chemical mixtures produced in the same exocrine gland. In moths, for example, the multi-component pheromones typically consist of one abundant component and several minor ones; different related species tend to use the same components, probably because of shared biosynthetic pathways, but in unique combinations or ratios. Synergistic effects, in which a blend elicits stronger responses than any component alone, are common.

One of the most complex chemical signaling systems occurs among weaver or green tree ants, *Oecophylla* (see Plate 19); five different recruitment systems have been identified, using pheromones from two different glands combined with various tactile signals to mediate a range of tasks from foraging to emigration to new nest sites to responses to enemy threats (see Table 6.2). This is a striking example of signal economy, with specificity arising from the different combinations of tactile and chemical elements. Recruitment to food and to new terrain are both initially guided by pheromones from the rectal gland; subsequently, characteristic head waving and jaw opening specify food whereas body jerking denotes new terrain.

Allomones—the other major class of chemical releasers of behavior—often also consist of chemical 'cocktails' and many of the above considerations apply equally to them. In addition, as defensive secretions, multi-component allomones sometimes may simply overload predator receptor systems, thereby effectively hiding the insect chemically from its enemies.

6.4.3 Exploitation and Code-Breaking

The aptly named 'shampoo ant' *Formicoxenus* obtains the colony-specific odors of its host *Myrmica* via active mutual grooming soon after eclosion. The larvae of certain syrphid flies emit chemicals that cause their ant hosts to treat them as another 'ant larva.' Many parasites and predators use the aggregation pheromones of bark beetles as kairomones to find their prey. In a similar manner, parasitic tachnid flies find their spined soldier bug (*Podisus maculoventris*) hosts by zeroing in on sex pheromones released by males.

Because chemicals are involved in so many aspects of insect behavior, it should not be surprising to find that some species turn the tables and exploit chemical communication systems for their own benefit (Table 6.3). We have already noted some examples, such as the beetle guests of ants discussed in Chapter 4.

Illicit receivers that intercept the signals of their hosts are widespread, and exploitation can take many forms. One is code-breaking (a behavior sometimes called eavesdropping, although that term has auditory implications). An illicit receiver of a different species (or sometimes, another insect of the same species) may decipher a chemical message meant for another receiver, and modify its own behavior as a result. At a more assertive level, the receiver may actually

Table 6.3   Classification of semiochemicals by benefit (+) and cost (−) to signaler and receiver

Semiochemical	Effect on signaler	Effect on receiver	Communication
Pheromone	+	+	Mutualistic
Allomone	+	−	Deceit, propaganda
Kairomone	−	+	Eavesdropping

steal the message. For example, the cuticular hydrocarbon 'uniforms' of host ants are acquired by some of their obligate social parasites. Such camouflage exploits the manner in which the ants themselves acquire their colony-specific odors, via grooming and trophallaxis.

A second form of exploitation of the chemical system occurs when an insect actively produces chemicals that mimic the chemical messages of others. Illicit chemical signalers of this type abound in the insect world. The 'adoption' and 'appeasement' gland secretions of some species of rove beetles (see Fig. 4.11) elicit host behaviors allowing the beetles to integrate themselves into ant societies. Among social species, a common method of gaining chemical congruency with the host is to actively biosynthesize the host recognition odor. Still another type of exploitation involves disrupting normal communication. Some slave-making ants spread panic throughout a colony by mimicking the alarm pheromones of their hosts; in the confusion, they take over the victims' pupae (see Chapter 10).

At least three factors appear to facilitate evolution of chemical code-breaking among insects. One is the design of olfactory systems, with their broad sensitivity to odors of all sorts. Another is the ability to evolve extreme tuning to any odor that provides a selective advantage. A third is the relative ease with which many insects can learn olfactory cues, an ability that has been widely reported for insects ranging from crickets to parasitic wasps. Thus, it appears that the risk of exploitation is one cost of reliance on chemical communication systems. Why does natural selection not eliminate it? Perhaps if the deceiver is rare relative to the genuine signal sender or receiver, then the cost of the deception can be tolerated, because the legitimate use of the signal will be more selectively advantageous.

6.4.4 The Chemical Channel and Other Signal Modes

One of the most striking characteristics of chemical communication systems is certainly their ubiquity, not just in insects, but in most groups of organisms including plants and bacteria. Some scientists have suggested that chemical communication be considered one of the fundamental attributes of life itself. How does it compare with other modes of communication?

From the simplest to the most complex, any communication system must fulfill two major criteria—it must be ecologically appropriate and it must fall within the sensory and motor ranges of the species concerned. An efficient system will likely

possess several of the following features as well: (1) qualitative and/or quantitative specificity, (2) rapid rate of information dissemination, (3) efficiency over considerable distance, (4) directionality of transmission, (5) wide range of information content, and (6) persistence *or* ability to start and stop quickly.

As we have seen, chemical communication systems possess most of these attributes and are certainly as fully versatile and sensitive as acoustic and visual communication to be considered in the following two chapters. In addition, they possess certain unique advantages. For one, they are the only major communicatory mode to have signals capable of lingering in the environment. Second, for chemical signaling, time and space take on a special meaning, for the sender and receiver do not have to be simultaneously coordinated as demanded by visual or acoustic communication. As a third point, like sound, chemical signals are able to go around environmental barriers although, unlike acoustic signals, chemical messages may be difficult to modify on short notice.

In concluding this section it is appropriate to consider the odorant chemicals themselves. Edward O. Wilson and William H. Bossert have convincingly argued (Table 6.4) that airborne odorants should have a carbon number between 5 and 20 and a molecular weight between 80 and 300 due to volatility constraints. In addition, they predicted that chemicals used for purposes requiring a high degree of specificity (such as sex attractants) should have greater molecular size than those odor signals used to elicit behaviors (such as alarm) for which species uniqueness is less essential. In the main, these predictive generalizations have been upheld by accumulating empirical data although size restriction does not apply to waterborne and contact odorants.

Table 6.4   Chemical criteria proposed for airborne pheromones

Molecular diversity	Olfactory efficiency	Energy expense to produce	Volatility	Other considerations
Carbon number<5, molecular weight <80				
Very limited	Low	Low	Very high	Possible difficulty in glandular storage
Carbon number 5-20, molecular weight 80-300				
Increasing exponentially; great number of unique compounds possible	Increasing steeply	Intermediate	Intermediate	Differences in diffusion coefficient in this range do not cause much change in properties of active space
Carbon number >20, molecular weight >300				
Astronomical	Further increases probably confer little or no further advantage	Great expense required to synthesize and transport large molecules	Low	May lead to difficulty in maintaining adequate active space

6.5 Chemical Communication and Insect Control

Since 1959 when the term pheromone was coined, pheromone study has flourished, the beneficiary of two major technological advances. The first was the introduction of gas chromatography, later coupled with mass spectrometry to permit the identification of miniscule amounts of secretory products. The second was the development of more sophisticated neurophysiological (especially electroantennogram) techniques that have led to better understanding of insect chemoreceptor systems. Concurrently, the development of predictive physical models about pheromone behavior has allowed analysis and understanding of odor transmission in nature. In the past 50 years, research on insect pheromones has grown steadily, driven by hopes that pheromones might be put to work to control insect pests. The idea of species-specific manipulation of insect communication systems without adverse effects on other organisms has considerable appeal. The use of pheromones for pest control offers several obvious advantages over conventional insecticides. Pheromones are nontoxic and non-persistent; being species specific, they elicit behavioral responses at extremely low doses.

Practical applications using insect pheromones are based on two main approaches: (1) air permeation leading to communication and mating disruption, and (2) attraction to point-source lures for population monitoring and for control by mass trapping. Mating disruption has found widespread application primarily against moth pests. Mass trapping has proved useful against various moths, beetles, and flies; obviously, this method is most efficient when the pheromone lures attract females. If attractants and repellents can be combined, it can result in an effective 'push-pull' pest management system (Fig. 6.19).
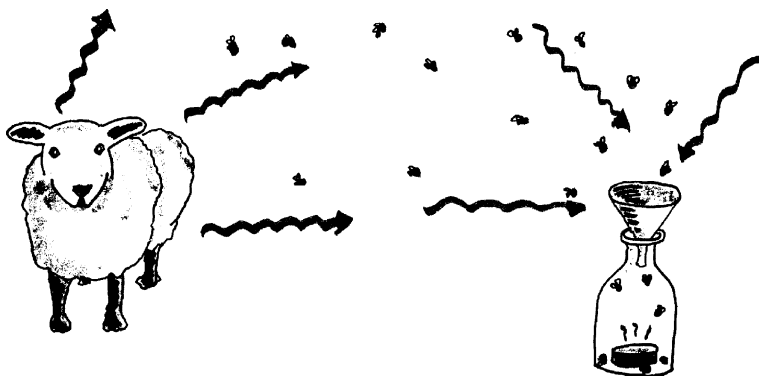
Fig. 6.19 Behavioral manipulation. Insect pest control approaches often incorporate semio-chemicals that affect behavioral responses. Integrating chemical stimuli that act to make a potential resource unattractive to the pests (e.g., repellants, alarm pheromones) while at the same time luring them to an attractant source (e.g., sex or aggregation pheromones) constitutes an appealing 'push-pull' pest management system

The main behavioral mechanisms underlying mating disruption are sensory fatigue or habituation, competition between natural and synthetic sources of pheromone, and camouflage of a calling female's odor plume. A host of practical issues need to be addressed for each pest situation. Cost-competitiveness is always an issue, and variable pest population densities complicate making blanket recommendations. Pheromone dispenser technology is an important related critical area of research; economical and efficient materials must be developed that can release sufficient pheromone amounts over an extended period and that can be easily deployed over large area. Climatic variables such as temperature, humidity, and wind must also be factored into the overall equation for implementing and achieving pest management, and every situation is different. Collaboration between the various stakeholders (researchers, growers, chemical industries, and the public) is essential.

Nevertheless, there has been exciting progress in many cases, and notable success in some. For example, sustainable control of the codling moth (*Cydia pomenella*), a major pest of apples that has become resistant to many insecticides, has been achieved through pheromone-mediated mating disruption over large areas worldwide. This commercially viable technique is now commonly used in control of several dozen pest moth species.

Relatively inexpensive pheromone-baited traps are now also widely used to monitor the occurrence and spread of pest insects, especially invasive species. The spread of the gypsy moth (*Lymantria dispar*) is monitored with sticky traps that snare attracted males. Boll weevils (*Anthonomus grandis grandis*), once the scourge of the cotton crop in the southern United States, have been eliminated almost entirely in that region by an intensive cooperative effort of growers and government agencies. A key factor in the success of this program has been the area-wide use of pheromone-baited traps used to detect local spot re-infestations that can be treated immediately to prevent population establishment.

By predicting the outbreak of a large infestation, pheromone lures have been useful in timing, calibrating, and eventually reducing the application of insecticides, thereby facilitating integrated controls that include the use of natural enemies. For example, consider a program in use against three of the world's most destructive fruit pests—the Mediterranean fruit fly, the melon fly, and the oriental fruit fly. All three are present in Hawaii but not currently on the mainland of the United States; accidental imports have, however, repeatedly occurred. Deployed about ports of entry, triple-baited traps containing synthetic attractants combined with insecticide have proven very effective in detecting new infestations. It is estimated that this early warning system has saved millions of dollars in potential eradication costs.

Thus, today chemical communication ranks as a vigorous, growing area of study within insect behavior, driven by both intellectual curiosity and practical concerns such as the desire to better control pest species while simultaneously reducing the use of pesticides.

Chapter 7
Visual Communication

7.1 Introduction

Small black paper balls pulled through the air on a string with sufficient speed will attract male flies, which fly after and grab them. When dragonfly nymphs are presented with various still objects against a background of moving stripes, they will snap at them. Backswimmers, *Notonecta*, placed in a tank with white sides are unable to avoid being swept downstream in a current. What is going on?

In all of these cases, the insects involved are using visual orientation (see Chapter 3) in the context of behavior. However, the above are not examples of insect visual communication, because to communicate there must be at least one intended receiver. In the context of orientation, vision is extremely important to most insects, as it is to most animals in general. However, for communication, insects tend to rely more heavily upon their other sensory systems.

Working primarily with vertebrates, the early ethologists found visual communication to be an unusually appealing subject for behavioral study for at least two major reasons—the tremendous amount of information that visual signals can carry, and the fact that visual systems play a dominant role in the behavior of humans. Therefore, it is not surprising that in the development of ethology over the last century, processes of visual communication have played a starring role. Konrad Lorenz, for example, derived many of his theories from the study of fish and bird *displays*—structures and behavior patterns that function as visual signals between conspecific animals. Niko Tinbergen's landmark 1948 paper on social releasers also took most of its examples from visual signals. Ethologists have found that at least two important signaling phenomena are more readily studied in visual signals than in auditory or chemical signals. One is the origin of signaling structures; the other is the evolutionary transformation of signals from their original purpose to assume new roles, a process known as *ritualization*.

In addition to their central role in the development of ethological theories, visual communication systems have formed a fertile ground for development of two of the behaviorist's most powerful tools: the use of models and the use of disguise. While neurophysiologists might manipulate relatively few stimulus variables with good result, the types of behavior of interest to ethologists often could be elicited only

by more complex stimulus patterns. The development of ways in which to approach the study of these was one of the outstanding achievements of pioneer ethologists.

The first method, using biologically meaningful simple models, gained its early impetus in Germany from the use of artificial color patterns to study visual attraction in honey bees. However, while this worked well in some cases, at other times it was just too difficult for an experimenter to effectively imitate all the necessary stimulus configurations, particularly when they might involve more than one sensory mode. This limitation could be overcome, however, by the use of disguise, altering live animals in such a manner as to develop a model that looks and acts like the live animal (which it is!) minus certain key characters. For example, the butterfly *Nymphalis io* responds to predation attempts by rapidly lowering its wings, exposing four eye spots (see Chapter 5) that mimic the vertebrate eye rather closely. Wondering whether these eye spots help the Io butterfly escape predation, A. D. Blest obscured the spots on some individuals. When he compared predation by yellow buntings upon these models with predation on equal numbers of unaltered individuals, the unaltered, eye-spotted individuals escaped 76% more often than the disguised butterflies did.

7.2 Bioluminescence

Larvae and larviform adult females of *Phrixothrix* beetles are sometimes called 'railroad worms' because, like twin lanterns, luminescent organs of their body glow green while those on their head glow red. The predatory larvae of some small dipterans called fungus gnats are unique among flies in producing their own light. Groups of fireflies sometimes blink in unison.

For centuries scientific investigators and curious lay observers alike have been fascinated by the production of light by living organisms, or *bioluminescence.* The phenomenon is more widespread than most people realize, and apparently has evolved independently many times (some say up to 30 times or more). Bioluminescence occurs widely in vertebrates, invertebrates, bacteria and fungi. Ninety percent of deep-sea marine life is estimated to produce bioluminescence in one form or another. Even symbiotic organisms carried within larger organisms are also known to bioluminesce. Among the Insecta, self-luminescent species occur at least nine families in five orders: Collembola, Hemiptera, Diptera, Dictyoptera, and Coleoptera. The intensity of luminescence varies greatly from one insect species to another. In some species, it is so low as to be visible to human beings only by the completely dark-adapted eye. (If humans had more sensitive eyes, they would probably consider more insects luminous.)

Bioluminescence has been described in more beetles than any other group. Fireflies, lightning bugs, or blinkies—adult lampyrid and elaterid beetles—are the most well known probably because there are over 2,000 species and many are widely distributed. Some fireflies are exceedingly bright for their size. The common eastern United States firefly, *Photinus pyralis*, has a flash that varies from 1/400th to 1/50th

of a candle. As in other bioluminescent organisms, the light contains no ultraviolet or infrared rays; yellow, green, or pale red in color, its wavelength ranges from 510 to 670 nm (usually 550–580 nm).

7.2.1 The Physiology of Insect Light Production

All fireflies glow as larvae. In Europe and Asia, the latter are often called glow-worms. In the Americas, 'glow worm' also refers to larvae in the related beetle family, Phengodidae, and in the fly genus, *Arachnocampa* (see Plate 21). Among the adults, some (mainly diurnal species) are not luminous, but in most fireflies, either both sexes or females only emit light from the underside of the lower abdomen; the well-innervated luminescent organs are specialized regions of fat body beneath localized areas of transparent epidermis. The yellow-green glow comes from a layer of light-producing cells (photocytes) with a massive tracheal supply; these rest upon a layer of cells packed with urate crystals that reflect the emitted light. The luminescent reaction is very efficient, with a yield of over 90% and almost no energy lost as heat; in *Pyrophorus* beetles, it has been judged to be less than 1/80,000th of the heat produced by a candle flame of equivalent brightness.

How is the light actually produced? In 1885 the French physiologist Raphael Dubois experimented until he found the answer. In a dramatic demonstration, he removed the light organ from *Pyrophorus*, a luminescent click beetle, ground it up in water, and left it until the light went out. Then Dubois removed a second light organ from another beetle and ground it into boiling water; after a short time, its light was also extinguished. When he combined the two extracts the light reappeared! In this manner, Dubois showed that two substances were required for the light, and that one of these was inactivated by heat. These were named luciferin and luciferase, both after Lucifer, the bearer of light.

We know today that luciferin and luciferase are not specific molecules. They are generic terms for a pigmented substrate and its associated enzyme, respectively. In the presence of oxygen, the luciferase, and the cellular energy source ATP (adenosine triphosphate), luciferin oxidizes to oxyluciferin, an unstable compound that is in such an excited state it yields a photon of visible light. Interestingly, because ATP occurs among virtually all organisms, this bioluminescent reaction has been used in distant space probes searching for extraterrestrial life. A probe scoops up planetary soil into in a chamber that contains luciferin and luciferase; if even simple life were present, its ATP would cause a glow that could be picked up by sensors and transmitted back to earth.

Luciferin is more or less identical in all insect species that produce light, but luciferases occur in such a diverse array that they have proven useful in molecular phylogeny studies. The most thoroughly studied, however, is that of *Photinus pyralis*, the initial source for the genetically engineered luciferase now being produced in the laboratory for a number of purposes. In recent years, genes coding for luceriferase production have been inserted into many different organisms, from

potatoes to fish to silkworms. Luciferase is also used in forensics and in human and animal medicine.

When insect larvae glow, the light is on more or less continuously, but most adult fireflies produce brief flashes of light that are vital for their courtship. How does a firefly control its flash pattern? Pliny the Elder's famous *Natural History* offered the opinion that fireflies turn their lights off and on by opening and closing their wings. Because this encyclopedic work covered almost the entire field of ancient knowledge and was based on the best authorities of that time, this statement was repeated again and again all the way into and through the Middle Ages.

Insect physiologists have now studied the system in some detail (Fig. 7.1), and have shown that firefly flashes are controlled by gating the supply of oxygen to the light-emitting cells. A nerve impulse that does not travel all the way to the insect's 'lantern' as one might expect, but instead via tracheal end cells to tracheolar cells that are usually filled with fluid. The impulse results in changes in the cells' osmotic potential, so that fluid levels drop and oxygen can reach the photocytes for the oxygen-requiring light reaction. During the dark part of the flashing cycle, the tracheoles refill with fluid, oxygen can no longer reach the photocytes, and the flash turns off. Interestingly, flashing can be turned on and off experimentally. If spontaneously flashing fireflies are placed in a chamber where the atmosphere can be rapidly changed from oxygen to air, they being to glow continuously instead; changing the gas stream back to air turns the continuous glow back to spontaneous flashing.

7.2.2 Bioluminescence as a Communication Method

Why do railroad worms have red and green lanterns? Do fungus gnats in the family Keroplatidae use their light to lure potential prey? When fireflies sometimes blink in unison, what do they accomplish?

Bioluminescence serves many purposes in the animal world in general, and among insect species in particular, and its functions are often different for various life stages. For immature fireflies, for example, bioluminescence appears to be a warning signal to predators, because many firefly larvae contain chemicals that are distasteful or toxic.

For most adult fireflies, the production of light is used to locate other individuals of the same species for reproduction. Courtship typically takes the following sequence: Males initiate flashing during flight at species characteristic times (often around sunset) in a well-defined habitat area; their flight paths are also species characteristic, especially during moments of light emission. Females remain stationary and, upon perceiving a male flash, answer with their own flashes, which follow that of the male after a brief, again species-characteristic delay. Repeated flash–answer sequences soon bring the sexes together, with copulation following.

In eastern North America, the commonly seen fireflies belong mainly to two beetle genera; the larger ones are *Photuris,* and the slightly smaller ones are *Photinus.*
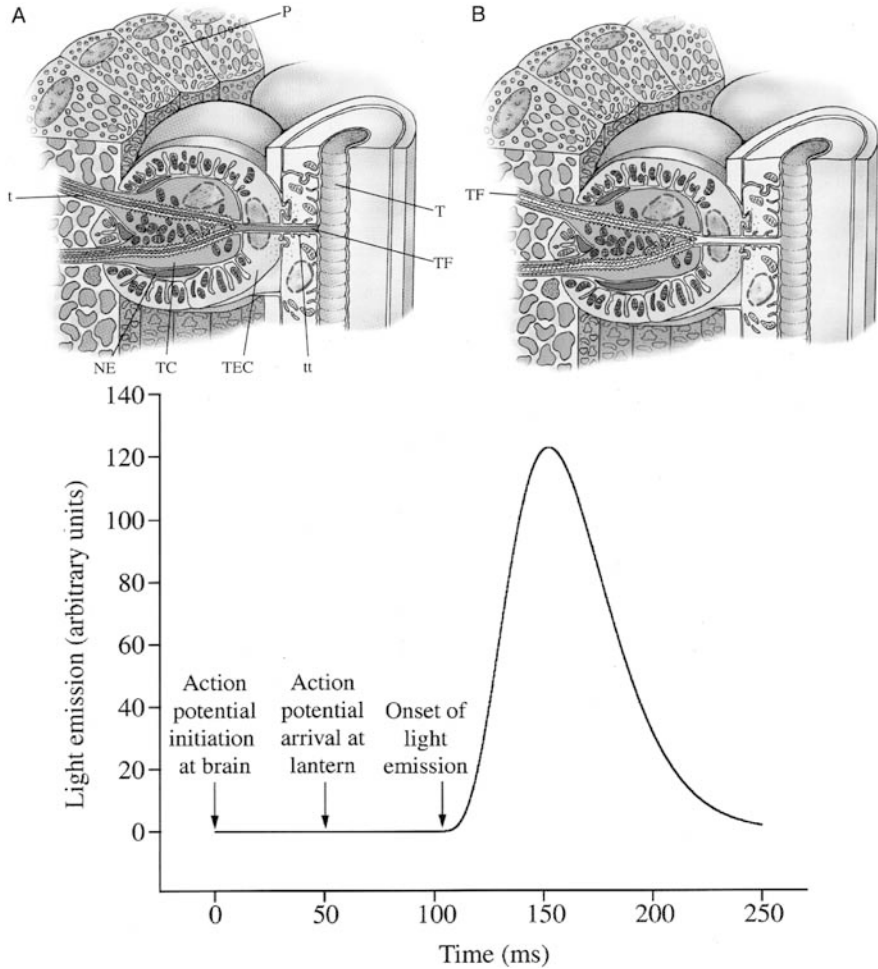
Fig. 7.1 Controlling the flash. (*above*) Adult fireflies produce discrete rapid bursts of light by changing the length of a column of tracheolar fluids and thus controlling oxygen access to the light-emitting cells (photocytes). These changes are actively brought about by nervous stimulation of the tracheal end cells, which share similarities to other cells that function as sodium pumps. P, photocytes; NE, nerve end; t, tracheole; TF, tracheolar fluid; T, trachea; TC, tracheolar cell; TEC, tracheal end cell. (A) Increased fluid length blocks oxygen to the photocytes, producing the dark phase of the flash cycle. (B) When fluid length decreases, the photocytes have the oxygen necessary to produce light. (*below*) Only about 40–60 ms pass between the arrival of the nervous action potential at the insect's 'lantern' and the start of light emission, with maximal light occurring within 100–150 ms after action potential arrival

Both genera include several cryptic species that are morphologically distinguishable only in minor details of body color. In the 1950s, Herbert Barber showed that flash patterns clearly distinguished otherwise-confusing species of *Photuris*

fireflies. A decade later, building on this work, Jim Lloyd researched the flash pat-
terns of *Photinus,* using electronic devices to produce artificial flashes of known
duration and to accurately measure the female's response delay (see Fig. 1.16).
By varying different signal parameters, Lloyd learned that female *Photinus* were
discriminating male light pulse length, the interval between pulses, and/or pulse
number. Furthermore, males were able to discriminate between differing female
answer delay times. In addition, Lloyd confirmed that the flash signals of sympatric
species differed significantly, but that those of species that normally did not occur
together were often very similar. In other words, refined isolating mechanisms had
evolved only where there was a possibility of reproductive mistakes being made.

Do *Photuris* speak a different flash language from *Photinus*? Female *Photuris*
had long been known to be carnivorous, but imagine his surprise when Lloyd
observed *Photuris* females attracting and devouring *Photinus* males by mimick-
ing the flash responses of *Photinus* females. This has become a classic example
of aggressive mimicry (see Chapter 4); conspecific males are not eaten.

As aggressive mimics, female *Photuris* are quite versatile and effective; they
can adjust their flashes to attract males of at least four species with distinctively
different flash patterns, and they generally succeed in capturing at least one male
for every ten attempts (see Plate 22). Later studies by others showed that a *Photuris*
female becomes a *femme fatale* only after having mated. Mating induces a suite of
behavioral changes, including locomotor activity, answering postures, predaceous
behavior, and response to flashes of males of different species.

The complex flash exchange systems found in *Photinus* and *Photuris* are not
typical of all fireflies, but instead probably represent a quite advanced level of evo-
lutionary development for the group. Some more primitive species known to use
pheromones have continuously glowing females, and in other species females turn
on their glow only in response to glowing males.

Many behavioral and ecological adaptations serve to enhance bioluminescent
communication efficiency. Females of most species climb up on perches during
hours of mating activity. Flashing males assume flight altitudes so that their light is
directed toward the ground ahead of them, and many species execute aerial maneu-
vers which enhance their chances of seeing or being seen by females (Fig. 7.2). In
addition, most fireflies exhibit habitat specificity and/or orientation to a mating site;
these further restrict the areas that males patrol, reducing 'background noise' and
the chances of interspecific interaction. Restricted periods of activity, seasonally or
diurnally, have similar advantages.

Perhaps the most extreme example of such ecological and behavioral restric-
tion is that of the 'firefly trees' found in parts of tropical Asia. At times the firefly
population in a grove of trees will flash on and off synchronously, hour after hour,
night after night, for weeks or even months. More than 30 similar reports have been
published describing these oriental firefly displays, occurring principally from man-
grove trees along brackish rivers. Such behavior is best known in tropical Southeast
Asia, but not restricted only to there. In the United States, one of the most famous
sightings of this phenomenon occurred near Elkmont, Tennessee in the Great Smoky
Mountains during the second week of June 2005.

Fig. 7.2 Flashing for mates. Patterns of light flashes of five species of *Photinus* fireflies, illustrating differences in habitat and flash parameters that help to maintain reproductive isolation between the species
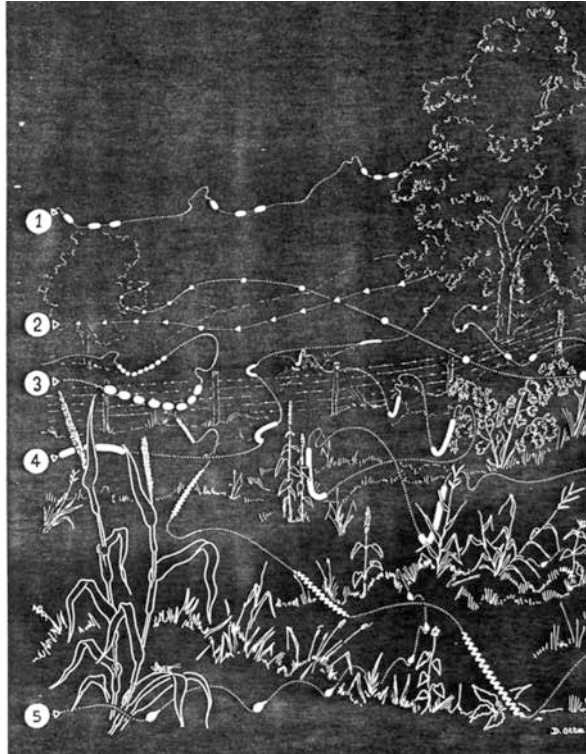
Many reasons have been proposed for these massive synchronized displays, including 'a sense of rhythm,' 'an organic law of rhythmic appreciation,' 'sympathetic telepathy,' and a whole host of other similar non-explanations with anthropological overtones. One writer even went so far as to attribute it to the twitching of the observer's eyelids, remarking that 'the insects had nothing whatever to do with it!'

Through extensive fieldwork with oriental fireflies in Thailand and Borneo and use of photographic and photometric analyses, John and Elizabeth Bucks showed that synchrony of great numbers of individuals is indeed nearly perfect. They hypothesized that flash synchrony is controlled by an internal resettable pacemaker. Contrary to earlier reports, both males and females occur in these trees, although the females do not participate in synchronous flashing. In some instances, aggregations in a given tree may include more than one species, resulting in a complex combination of flashes that is still presumably effective for each species involved. The Bucks considered synchronous flashing to be part of a complex of behavior patterns (congregation, selection of certain trees, flashing, etc.) for enhancing mating under otherwise difficult conditions. The firefly trees appear to serve as quasi-permanent rendezvous, and synchrony appears to increase their efficiency as beacons. Adult fireflies in these tropical areas live for only a few days and therefore

must find mates quickly if they are to reproduce before they die. A single prospective mate is nearly invisible among the thick, tangled plants of these swampy areas, but many males flashing synchronously are easily seen by other fireflies, both male and female.

7.3 Light Reception

A preying mantis waits, motionless as a statue, until a small fly ventures within strike distance. As observers, we watch with fascination as the insect's eyes silently track the fly, and we cannot help but wonder: Does it see the world as we do?

Until late in the seventeenth century, people assumed that insect vision was essentially similar to ours. Then the invention of the microscope gave curious humans a close-up look at the eyes of a common fly and set off a scientific debate that took about 300 years to resolve. When Antoni van Leeuwenhoek first saw at an insect's eye through his microscope, he was so surprised that he subsequently wrote a letter to the Royal Society of London, saying:

> Last summer I looked at an insect's cornea through my microscope. The cornea was mounted at some larger distance from the objective as it was usually done when observing small objects. Then I moved the burning flame of a candle up and down at such a distance from the cornea that the candle shed its light through it. What I observed by looking into the microscope were the inverted images of the burning flame: not one image, but some hundred images. As small as they were, I could see them all moving.

Do some or all insects really see the world as a mosaic of tiny images? Popular works depict insect vision like that, and one can buy novelty viewers that allow children to imagine that they 'see as insects do', but are they correct? What does an insect actually see? And how? Taking into account both insect neurology and the significant variation that occurs in this very large segment of the animal world, the answers seem to condense down to one short statement—It depends on the insect—but working out the details has taken over two centuries, and still continues today.

7.3.1 Receptors and Form Perception

Sometimes, arboreal *Cephalotes* ants fall or jump from trees; when they do, they orient their trajectories toward light-colored objects, which in their environment are usually tree trunks or lianas. Many caterpillars rest with the darker surface of their body directed toward the brightest source of light, producing a counter-shading effect (see Fig. 5.2), even though they appear not to have eyes. Moths will fly to illuminated glass that allows ultraviolet light to pass through, even when it appears opaque to us.

How an organism behaves depends greatly upon the way its world appears. When an insect regards a complex scene, it obviously cannot and does not notice every

detail. (Nor do we.) What it sees, or rather, what it responds to, depends on what its evolutionary history has preprogrammed it to 'look' for. An insect's response is also determined by properties intrinsic to the photoreceptors themselves and the manner in which they relate to higher centers in the brain.

Insect eyes vary a great deal in form and location, but are of two basic types: compound and simple. Simple eyes include the larval eyes, or *stemmata*, of holometabolous insects and the dorsal *ocelli* present in most winged adult insects; interestingly, the two are apparently not embryologically related. Larval stemmata vary in size, number, and complexity. Fly maggots have only small pockets of photosensitive cells in the cuticle. A lepidopteran caterpillar typically has six stemmata on each side of its head, which look like simple white circles; with these, some caterpillars can differentiate shapes and orient toward boundaries between black and white. Other larvae, such as those of predaceous *Cicindela* tiger beetles, have stemmata that apparently work as well as many compound eyes, making one wonder why the insects did not retain eyes like this into adult life.

The winged adults of most orders and the nymphs of hemimetabolous species usually have three true dorsal ocelli on the top of their heads. They appear to be 'good' eyes with a wide view and a lens; some also have a reflective layer and some have a mobile iris. However, the retina is very close to the lens, so they are apparently profoundly out of focus. Then what is their purpose? Currently the best hypothesis is that they are horizon detectors that contribute to equilibrium when the insect needs to make a fast correction during flight. Being unfocused allows the receptors to respond to overall light distribution rather than every small leaf shadow. The ocelli also are very sensitive to low light intensities. In certain bees and wasps there appears to be a correlation between large ocelli and activity peaks at dawn or dusk. (It is also known that insects can perceive light directly via the brain cells as well as through their compound eyes and ocelli; some have other photosensitive tissues as well.)

The best-studied and presumably most important visual organs in the majority of insects are the *compound eyes*. With the exception of certain specially adapted parasitic and cave-dwelling species, most adult insects have a pair of these prominent organs, bulging to varying degrees from either side of their head so as to give a wide field of vision in all directions. Composing each compound eye, and extending inward like narrow columns, is a group of densely packed hexagonal units called *ommatidia*. Most people think they know this from looking at insects, but in reality this is modern knowledge gained from microscopic and photographic close-ups. All we can view directly is a vague bumpiness, because the facets of an insect's compound eye are too small to be resolved with the naked eye. The number of ommatidia in an insect eye varies greatly; while the common house fly has about 4,000, dragonflies may have as many as 28,000.

There is considerable diversity in the structural detail of ommatidia in different insect groups. However, basically each ommatidium consists essentially of two parts. One is an optical, light-gathering part (the lens or facet, and the crystalline cone). The other is the sensory part (retinal cells and their differentiated margins called rhabdomeres or *rhabdoms*) that perceives the light radiation and

transforms it into electrical energy for nerve transmission. Each crystalline cone also contains pigmented shield cells that help protect its actual light-sensitive chemicals.

Yet, while all compound eyes look superficially quite similar, their insides vary in some fundamental ways that relate to an insect's behavior. Like all other organisms, insects depend on light energy for their vision, but too much can be damaging. Sunlight is particularly hard on pigment cells, so insect eyes basically come in two different optical types (Fig. 7.3) that let different amounts of light strike the rhabdoms.

Adult insects that are active during the day generally have *apposition* eyes that limit the amount of light reaching the retinal rods. Each retinal rod receives light only through its own lens. Light from other facets is intercepted by pigments that act like a screen. The field of view of each rhabdom occurs next to (*apposes*) the field of its neighbor, thus giving the eye its name. This is the kind of insect vision mimicked by children's toys and popular literature. It produces an overall erect image that is made up of a mosaic of adjacent fields of view. How coarse or fine a particular part of the image appears will depend on the number of facets per unit area. Many nocturnal and crepuscular insects have a different system that gives a much brighter image at night. A *superposition* eye converges (or *superimposes*) light rays from many lenses onto each retinal rod. Because the effective aperture now is no longer the width of a single facet but may be ten to thirty facets or more, the image is brighter but more diffuse. By design, a superposition eye is much more sensitive at low light levels than an apposition eye would be, but in addition, many superposition eyes also have a tapetum, a mirror-like cell layer in the back that reflects light outwards so that it passes twice along the retinal rod, doubling its effect on the light-sensitive retinal pigments. Instead of a mosaic, all superposition eyes produce a single deep-lying erect image in the vicinity of the retina. (This distinguishes them not only from apposition eyes, but also from camera-type eyes in which the image is inverted.)

When light is reduced, a day-flying insect usually just becomes inactive. But if too much sunlight is damaging, what happens when a night-flying insect is in daylight? Remarkably, whereas the shielding pigments in apposition eyes are stationary, those in superposition eyes can migrate. At low light intensity, the pigments move into the distal part of the cells, allowing light from adjacent ommatidia to pass through and strike the rhabdom below. Upon exposure to bright light, the pigments disperse to form a protective curtain that prevents the spread of light from adjacent facets, and the eye functions like an apposition eye.

This migration also explains why the eyes of many moths seem to glow at night but not during the day. At night, the tapetum near the base of the moth's eye reflects light but during the day, the shielding pigments that have moved into place absorb most of the light before it is reflected back.

Although we know that sight differs among animals, we do not know what animals actually perceive. There is an important distinction between having light illuminate the retina, and understanding what is being seen. Perception across the

Fig. 7.3 Seeing the light. (*above*) Robber flies (such as the one shown here feeding on a solitary bee) typically have such acute vision that they are able to catch their prey on the wing. Like most other diurnal insects, the Asilidae have apposition eyes that screen light from adjacent rhabdoms, so that each lens forms its own relatively sharp image. (*below*) Nocturnal insects such as this firefly typically have superposition eyes that gather light from many lenses to form a brighter but more diffuse image. In addition, adjustments in both the colored screening pigments and the middle-wavelength pigments in photoreceptors optimize the firefly's reception of intraspecific signals

animal kingdom is the subject of much ongoing research. Consider the simple question of whether an insect can distinguish between one shape and another, the ability called form perception.

Much of our present knowledge of insect form vision comes from honey bee behavior during training studies where choice of some shapes has been rewarded with food. However, there are several limitations and difficulties implicit in these studies. Perhaps the most striking has been that all such training studies have been complicated by the bee's spontaneous responsiveness to flicker (see Section 7.3.2, below). Moving shapes of all sorts are more attractive than stationary ones, and while bees could be trained to distinguish solid figures from broken ones, they could not distinguish solid from solid or broken from broken. The adaptiveness of such behavior is apparent if we consider a bee in its natural environment. Not only does wind cause flower movement, but when bees fly low over the ground in search of flowers they experience the passing of a radial cluster of flower petals as a burst of flickering. The regularity and high frequency of such flicker patterns identify the stimulus as readily as the total shape does to our eyes.

A second less immediately apparent limitation is that even these results are quite possibly open to question because they may be confounded by stimulus filtering appropriate to flower searching but not to other situations. Still a third limitation is that honey bees may not be the appropriate 'representative' insects to generalize from, any more than white rats are necessarily 'representative' mammals for all purposes. Certainly some other Hymenoptera, such as the predatory wasps *Philanthus* and *Ammophila,* use landmarks for topographic orientation (see Chapter 2) to an extent which implies a better ability to discriminate forms than would be expected from theories built upon honey bee observations.

7.3.2 Visual Acuity and Flicker Vision

Dance flies cruise just above the water surface, searching for drowning insect prey. How do they keep their bearings? Males of the hoverfly *Syritta* discern and begin to pursue a female while remaining beyond her visual detection range. What cues are they discerning that trigger this pursuit?

The term *visual acuity* is used in various ways. It can describe how well two close objects can be determined, or the smallest single object that an eye can detect, or (as often used experimentally) the finest grating of equal light and dark stripes it can resolve. A related term, resolution, is used in a loose way to mean the ability to resolve fine detail or determine the parts that make up an image.

The better the acuity, the greater the distance at which prey can be seen, mates can be located, or environmental structures can be used to navigate. The conditions under which acuity is measured must be specified, of course, because the amount of light available to the receptors affects the performance of any eye. As light becomes increasingly dim, one eventually reaches a point where there simply are no longer enough photons available to trigger the receptors to respond. In addition, contrast becomes less and less.

Assuming the light is adequate, how acute is an insect's vision in general? With so many lenses, at first glance one might think that insects should have excellent

vision—yet it has long been clear that for stationary objects at a distance, the compound eye is universally poor. Details of an object often fail to evoke responses at all. With some insects such as the honey bee, the eye receives fuzzy images even when the object is large and nearby. In 1894, a scientist named A. Mallock described the compound eye vision like this: 'The best of the eyes . . . would give a picture about as good as if executed in rather coarse wool-work and viewed at a distance of a foot.'

If insect eyes do not come even close to having the acuity and resolution of human eyes, then why not? For one thing, form and motion perception are very closely intertwined; just as in photography, image motion across the eye causes blur. This is more than a theoretical consideration. Insects have been measured routinely turning at speeds well into the hundreds of degrees per second, and in high-speed maneuvers, rotating at speeds up to several thousand degrees per second.

Furthermore, just as we have noted for so many other phenomena, an insect faces problems that arise from its relative size. Because each ommatidium has its own lens, and an insect is small, the lenses are very small. Small lenses are diffraction limited; to increase resolution by a factor of two requires doubling the diameter of each ommatidium as well as doubling the number of ommatidia in a row. Another way to state this would be to say that the eye would need to grow as the square of the required acuity. For an insect compound eye to provide the same resolution as ours, Mallock calculated, it would have to be huge—on the order of 38 ft (12 m) in diameter.

As one might expect in a large group such as Insecta, many subtle changes in eye structure have been found that increase visual acuity in specific ways that adapt their owners to different environmental conditions. Nonetheless, the acuity challenges inherent in the compound eye are great enough to have led one researcher, D.-E. Nillson, to comment, 'It is only a small exaggeration to say that evolution seems to be fighting a desperate battle to improve a basically disastrous design.'

If the design is so poor, why has it persisted when single-lens alternatives were and are apparently at hand? Researchers studying insect vision find this to be one of the intriguing unsolved problems. Currently, the best guess seems to be that visual acuity is less important than other advantages. One is that a compound eye excels in processing speed. Because the images are processed in parallel, the design allows for fast motion detection and image recognition.

For another, the compound eye excels in providing a panoramic view of the world with a large field of vision. Even ants, which have a relatively small number of facets on either side of their heads, can perceive almost the entire visual field above and below the horizon. Their 'blind spot,' an area hidden below the thorax and abdomen, has been estimated to be only about 10% of their total visual field.

A third major advantage is that some parts of the ommatidial mosaic can be fine-tuned to be more visually acute than others. It has long been known that the number of facets per unit area often varies in different directions in a given eye and in different regions of the eye. Since the middle of the last century, major technological refinements have allowed biologists to study insect visual acuity by noninvasive methods rather than the older histological techniques. A major outcome has been the

realization that insect eyes vary in ways that reflect their life habits and ecology. For example, one might reason that for many swiftly flying insects acuteness of vision in the vertical axis would be more important than in the horizontal; in fact, the curvature of their eyes lends very different dimensions to the ommatidial angles in these directions. Three broad patterns have been identified in apposition eyes. One is an overall pattern associated with forward flight (perhaps particularly through vegetation). The second is the presence of acute zones concerned with the capture of prey or mates. The third is horizontal acute strips associated with flat environments such as water surfaces.

Compound eyes also provide a unique way to determine distance. The eyes of an insect are fixed; it cannot move them independently of each other. However, as an insect directly approaches the object that it is viewing (or vice versa) the retinal image gradually appears closer toward the inner part of the two compound eyes, thus affording a method of judging distance. As the visual angle of the ommatidia becomes progressively less over the inner part of the eye, the object comes into sharper vision. Experimental work with predatory insects such as preying mantises and dragonfly nymphs (Fig. 7.4) demonstrates this well.

Compound eyes are better adapted to perceive motion than static form. In fact, reliance on an object's real or apparent motion (*flicker vision*) is so widespread that it may be regarded as one of the normal concomitants of vision with the compound eye. Because ommatidia recover very rapidly from light impulse stimulation, the insect eye has a remarkable capacity for seeing successively different images at very short intervals and thus for scanning a moving object. As a result, an insect may be able to resolve a finer pattern when it is flying than when it is at rest. Many predatory species, for example, respond only to moving prey; and given choices of stimuli, most insects show a preference for the shapes that cause the most flicker.
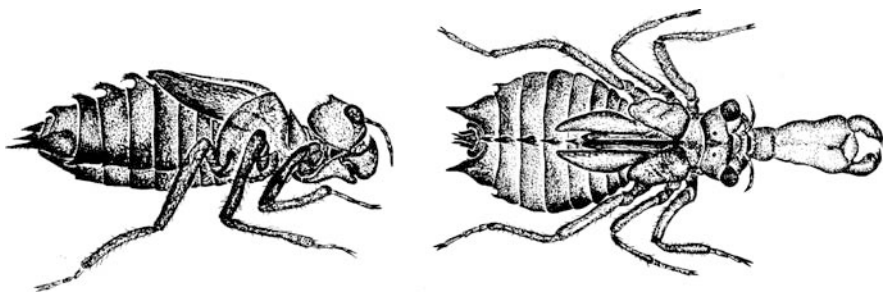
Fig. 7.4 Assessing prey distance. At the front of its head, a dragonfly larva (*Epicordulia*) has a two-jawed labium which is jointed in such a way that it cannot be moved sideways nor used except in the fully extended position (*right*); thus there is only one point in space where a prey can be caught. With its labium in the retracted position (*left*), the larva faces the prey directly and moves toward it, viewing the prey with increasing definition. When the prey's image falls on certain inner ommatidial elements, it is seen the most clearly. Here it is exactly within proper striking distance, which corresponds to the intersection of the optical axes of these ommatidia

Our own human attention is immediately attracted when sudden movement, flicker, or novelty interrupts an otherwise static scene. The same is true for insects. However, flicker is hardly noticeable to us when it exceeds a rate of about 20–30 changes per second. How do insects compare with us in this regard?

When a flickering light is presented to an animal, it is possible to determine the rate at which its eye crosses a threshold from being able to distinguish the flashes of light as discrete entities to see them as a single continuous light. This threshold value is called the *flicker fusion frequency*. For the purposes of presenting moving images, the human flicker fusion threshold is usually taken as 16 Hz. Flicker fusion is important in all technologies for presenting moving images; if the frame rate falls below the flicker fusion threshold for the given viewing conditions, flicker will be apparent to the observer, and movements of objects will appear jerky. To overcome this annoyance, frame rates are usually several times this threshold. (Current computer CRT displays usually operate at a vertical scan rate around 100 Hz.) Research with human subjects shows that the flicker fusion frequency can vary widely with such factors as the relative brightness of the flicker and its surrounding environment, the location on the retina where the image falls, and the fatigue level of the observer. Common experience also shows that under some conditions, humans can discern much higher flickers, such as the 100–120 Hz flicker produced by fluorescent lights with magnetic ballasts.

Though much less well studied than that of humans, insects' flicker fusion frequency also varies widely. However, within limits that are undoubtedly set by retinal mechanisms, there is a strong correlation between insect behavior and rate of flicker fusion. 'Slow eyes' with a flicker fusion frequency of as low as 5–10 flashes per second are characteristic of relatively slow-moving or nocturnal insects. Rapidly flying diurnal insects such as bees and flies, by contrast, may resolve flicker frequencies as high as to be 10 times as discriminating as the human eye. Male house flies, for example, respond to flickering stimuli during courtship and will court models with increasing responsiveness at flickers of up to 270 stimulus changes per second before beginning to decline; their flicker fusion frequency has been estimated separately through electrophysiological studies at 265 per second.

7.3.3 Polarized Light Perception

Hungarian mayflies were discovered laying egg masses on asphalt road surfaces near the stream from which they emerged. What perceptual misunderstanding led to such a completely unsuitable choice? Foraging in the evening, *Scarabeus zambesianaus* dung beetles that find fresh dung quickly make it into a ball and roll it away in a straight line; 40–50 minutes after the sun sets, they abruptly stop. Why?

For some insects, an additional advantage of compound eyes is their ability (perhaps aided by specialized ommatidia at the margins) to perceive light *polarization* (see Fig. 3.12). As sunlight passes through the earth's atmosphere, some of its waves

begin to vibrate in a specific direction. As perceived by an instrument or animal on the earth, both the degree of this polarization and the plane of vibration vary with the position of the sun above the horizon, and with the observer's elevation above the horizon. It is a complicated system, but insects as varied as house flies, European red wood ants, and desert locusts have been shown to orient by it. Some of the clearest examples of polarized light perception occur in many social Hymenoptera that must orient to find food and return to their nests. Because the plane of polarization changes as the sun moves across the sky, such *homing* requires these bees, wasps, and ants to have not only a polarized light compass but also a way to measure time lapse.

The first indication and then the first proof that animals might have the ability to detect this polarization was obtained through Karl von Frisch's studies of honey bee communication. The accuracy of the 'dance' (see Chapter 8) of a returning forager, which shares information on direction and distance of the food source with other workers, depends in part upon the polarized light pattern perceived from blue sky. Because its dances are goal directed, the honey bee affords a unique experimental opportunity to test orientation to polarized light. When the sky is completely cloud covered, bee dances are disoriented. If, however, a small patch of blue sky remains (even when the sun is not visible), bees dancing on a horizontal surface will orient correctly. If the plane of light vibration is altered artificially, as can be done by interposing polaroid sheets, the orientation of the dances changes correspondingly. For example, when the polaroid sheet is rotated clockwise by 30°, the bees will immediately shift the direction of their dances by about the same amount.

Polarized light orientation and/or time compensation undoubtedly occur in a number of contexts. When light bouncing off the asphalt that fooled mayflies in the introductory example above was assessed with instruments designed to measure polarized light, the road was found to reflect plane-polarized light the same way the sunlit water surface in a stream did. The dung beetles in the other example forage at the time of day when the light of the entire sky is polarized in one direction, and researchers with polarization filters could switch the direction of the dung beetle's trips. Although other factors might also be involved in the beetles' activity cessation, at the time at which they stop, the degree of polarization at the zenith of the sky abruptly decreases from 45 to 5%.

In many cases, however, showing that an insect can detect polarized light or mark time is not the same as showing it uses this information. *Schistocerca gregaria,* the desert locust, clearly responds to polarized light, and this response has been well characterized, but its use during migration has not been established. Monarch butterflies use a time-compensated sun compass during long migratory flights to Mexico (see Fig. 3.11). However, in both field and laboratory studies, the plane of polarization did not appear to make any difference in their orientation. Many Neotropical nymphalid butterflies reflect polarized light from their wings, but still missing are behavioral studies to prove that these reflections are used to identify conspecifics in the low light intensity of the forest foliage.

7.3.4 Color Vision

Mosquitoes and some flies have been shown to be attracted or repelled by specific surface colors, and by specific colored sources of light; interestingly, the surface colors they prefer do not necessarily correlate with the light source colors that attract them.

Color vision and color perception across the animal kingdom are subjects of much ongoing research; beyond a mere handful of species, science has a very limited understanding of the many ways that animals see. At its simplest, color vision is the ability to discriminate between two wavelengths of light. In a bit fuller detail, it is the capacity of an organism or machine to distinguish objects based on the wavelengths (or frequencies) of the light they reflect or emit. The nervous system derives color by comparing the responses to light from photoreceptors in the eye that are sensitive to different portions of the visible spectrum.

Three things are needed to see color: a light source, a detector (the eye) and a sample to view. Color is a rather strange phenomenon because it is not a property of the object—for example, a blue berry does not emit blue light. Instead, color is a quality constructed by the brain; the blueberry is blue to us only because human eyes can distinguish those frequencies of visible light that the berry reflects rather than absorbs. The theoretical significance of developing color vision is thought to be that it allows better discrimination of surfaces.

It appears that most insects have only two types of visual pigments—one absorbs green and yellow light and the other absorbs blue and ultraviolet light. The color vision of these species is limited, and somewhat resembles that of colorblind humans. Dichromatic insects are generally considered to have difficulty distinguishing between color blends. Other insects, notably honey bees, bumblebees, and many diurnal butterflies, have true color vision. They have three visual pigments, with absorption maxima in the vicinity of 360 nm (ultraviolet), 440 nm (blue–violet), and 588 nm (yellow). Within the range of their spectral sensitivity, these trichromatic insects can perceive a complete spectrum of colors and can also discriminate between single colors and mixtures of colors.

Humans also have trichromatic vision, so in this sense the color vision of these insects resembles our own. However, at least in the species that have been studied, their visible spectrum is shifted toward shorter wavelengths compared with ours (see Plate 23). For humans, only the wavelengths between about 400 mμ (ultraviolet) and 750 mμ (red) are visible; we cannot perceive the near-ultraviolet portion of the sun's rays that reaches the earth. In general, most insects respond to a range of wavelengths extending from the near-ultraviolet (300–400 mμ) up to a maximum around 600–650 mμ (orange).

Spectral sensitivity alone does not imply discrimination, but behavioral evidence supports the interpretation that many insects can and do distinguish between different wavelengths and hence possess true color vision. Near-ultraviolet light is the most effective region of the spectrum in directing phototaxes; the widespread use of ultraviolet lamps in insect traps is a practical application of this. The adaptive

significance of ultraviolet phototaxis may be that such light signals 'open space.' Much of nature, especially green foliage, absorbs ultraviolet wavelengths; the open sky, left as the only extensive source of ultraviolet rays, may signify room for free flight and maneuvering.

In his pioneering work on insect color vision in 1914, Karl von Frisch showed that honey bees were able to differentiate accurately between several major categories of color (see Plate 24): yellow, blue-green, blue (including violet), ultraviolet, and 'bee purple,' a mixture of the spectral extremes, orange and ultraviolet. Von Frisch's techniques employed simple Pavlovian conditioning: marked bees were allowed to feed at a sugar source while simultaneously being exposed to a particular color stimulus, then tested to see whether they would be attracted to the color in the absence of the food. Finally, if this proved successful, they were permitted to choose between the original color and a different, closely similar one to see whether the bees could discriminate between the two. In recent years these studies have been supplemented with electrophysiological techniques.
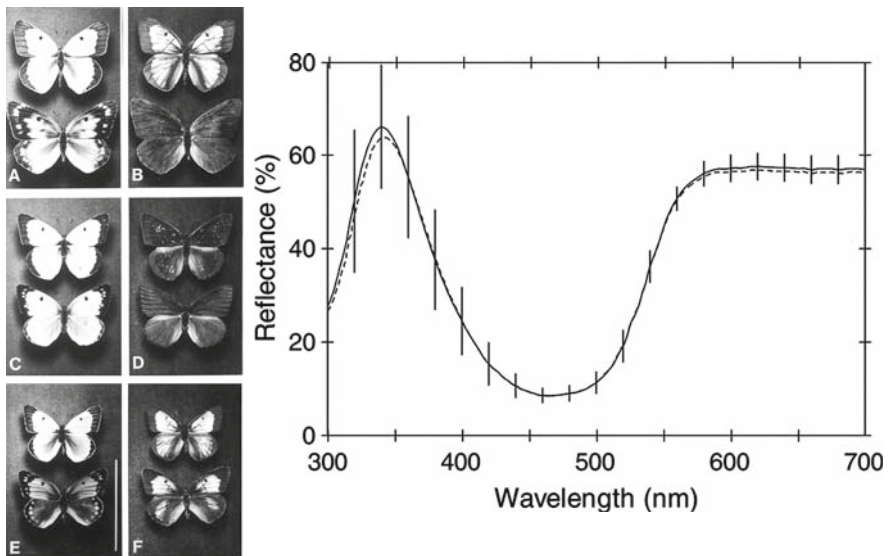
Fig. 7.5 Sending 'invisible' messages. Like semaphore flags, some courting butterflies flash UV-based wing patterns that are invisible to vertebrate predators. (*left*) Three species of pierid butterflies whose wings exhibit regions of high ultraviolet reflectance. The male is uppermost in each photograph and often exhibits a pronounced dimorphism with respect to the ultraviolet reflectance trait (right column, photographed in near-ultraviolet light, 300–400 mμ) which is not apparent to our visual spectrum (left column, photographed in visible light, 400–700 mμ). (**A**) and (**B**) are *Colias eurytheme* whose main visible color is orange; (**C**) and (**D**) are *C. philodice*, a predominantly yellow species; (**E**) and (**F**) are *C. chrysotheme*, another orange species. (*right*) Comparison of the average reflectance spectra for a group of in-copula males (solid line) and free-flying males (dashed line) of *C. eurytheme* from the same population shows no differences. Therefore such signals are probably not used by females to discriminate differences in male quality

   Knowledge of the color sensitivity of insects has significant implications for understanding and interpreting visual behavior. For example, to the eyes of a honey bee many flowers glow with color we can see only with the aid of special equipment. Many pale-yellow flowers, such as the evening primrose, *Oenothera,* or the cinque-foils, *Potentilla,* reflect ultraviolet light over the greater part of their petals but have patches at the petal bases that fail to do so; to honey bees, these latter *nectar guides* are sharply differentiated visually (Fig. 7.5). In addition, some red flowers such as poppies reflect ultraviolet light so strongly as to be conspicuous to the bees although the rich red so striking to us is totally invisible to them. Color vision probably also plays a part in the choice of backgrounds by cryptically colored insects, and such choices may be based on a quite different *Umwelt*—a useful ethological term for the perceptual 'self-world' of an animal.

   Some butterflies and dragonflies have particularly well-developed color vision. Courting butterflies may be especially sensitive to color patterns and iridescence on the wings of their potential mates composed of colors that are totally invisible to us (Fig. 7.5). The rhythmic flashing of these wing blotches during flight is of communicative significance during courtship but is invisible to vertebrate preda-tors. The combination of flight pattern and wing-beat frequency would seem to have the potential to produce sign signals analogous to the flashing patterns of male fireflies. Patches of closely appressed silvery hairs are commonly present on the bodies of various insects and in at least one case, the fly *Ochthera*, these patches reflect ultraviolet light and seem to serve as similar communicatory signals between the sexes.

7.4 Functions of Visual Communication

Visual systems would seem to have several advantages over other communicatory modes. The range of possible signal variations is theoretically almost limitless; one has only to vary, independently and in combination, such basic signal aspects as color, form or posture, movement, or timing. In addition, the rapid adaptation rates of insect visual receptors could be exploited in development of a wide variety of temporal patterns, developing a system that could be started or stopped immedi-ately. Thus, an insect sensing a predator could freeze and need not communicate its position by any lingering image such as those that might be left by a chemical system. But in situations where it would be advantageous to do so, the insect could make clear its exact position, so that the receiver could respond to it in terms of precise location as well as general presence.

   Functionally, any situation involving face-to-face interaction seems a potential candidate for visual signals. For example, many visual signs are employed in inter-specific contexts such as defensive behaviors (especially crypsis, threat displays, and mimicry) and in pollination. In intraspecific contexts, the great majority of currently known examples concern visual signaling associated with reproductive activities (see Plate 46). This may, however, simply reflect the disproportionate amount of scientific attention that has been directed toward courtship behavior as compared to other behaviors in which visual cues may be functioning (Fig. 7.6).

Fig. 7.6 Signaling status. Portraits of nest-founding females of the paper wasp, *Polistes dominulus*, illustrate some of the naturally occurring diversity in the shape and size of their conspicuous black facial spots. Experimentally altering spots with paints indicates that these wasps can use visual signals alone to assess quality differences among unfamiliar rivals, but there is some controversy as to whether they routinely use these badges to recognize and assess one another

It is not unreasonable to expect that many additional examples of visual signaling will be forthcoming as attention is directed toward other behaviors where frequent close-range interactions between conspecific individuals are commonplace.

The fact remains, however, that insects do not appear to rely upon visual signals for intraspecific communication to as great a degree as they do upon chemical and auditory ones. The same conspicuous patterns on an insect's body that aid in intraspecific communication can be a hindrance when it must hide from a predator. Thus, permanent intraspecific visual signals tend to be exploited most fully by those insects that are relatively immune to predators. In addition, except in unusual cases such as fireflies, visual signals are useless at night, in dark places, where blocked by the environment, and at long distances. The short visual range and limited capacity for detail possessed by the insect eye also restrict the importance of fine detail in insect releasers. Even within its useful range, a visual signal becomes simpler and bolder, consequently carrying less information, as distance increases. A visual signal normally cannot be increased by pumping more energy into it, as is possible with sound or chemical signals.

7.4.1 Aggregation and Dispersion

Behaviors involved in the distribution of members of a species in space have a crucial bearing on their exploitation of environmental resources and thus are of great importance. At close range, such behaviors would seem ideal candidates for visual messages. Aggregation by insects is relatively unstudied in comparison with such behavior in fish, birds, and many mammals, all of which have been demonstrated to utilize prominent visual signals in forming and maintaining such groupings. In bringing together large numbers of widely scattered insects from over large areas, it stands to reason, however, that auditory and chemical cues would be relied upon more heavily than visual ones. The habits of most insects are such that their environment simply does not permit long visual ranges. In addition, the fixed-focus compound eye is not well adapted to long-distance vision.

Dispersal through visual mediation is only slightly better known than insect aggregation using these cues but theoretically might be encouraged by visual signals of several levels of complexity. Insects might simply avoid other conspecific individuals at sight, or they might direct signals to one another, eliciting withdrawal. The signals could be simple ones generated by the insect alone, or compound visual situations involving perception of a complex of environmental factors as well.

Territoriality in dragonflies (see Plate 33, top and Fig. 7.7) provides a good example of visually mediated complex behavior. Perhaps the most striking features of the Odonata, aside from their two pairs of intricately netted wings, are their great protruding eyes. Combined with a head that can be rotated readily upon a slender neck, they allow a degree of motion perception (for some up to 40 yards away) that is most unusual for fixed-focus eyes. In addition, the antennae, so prominent in most
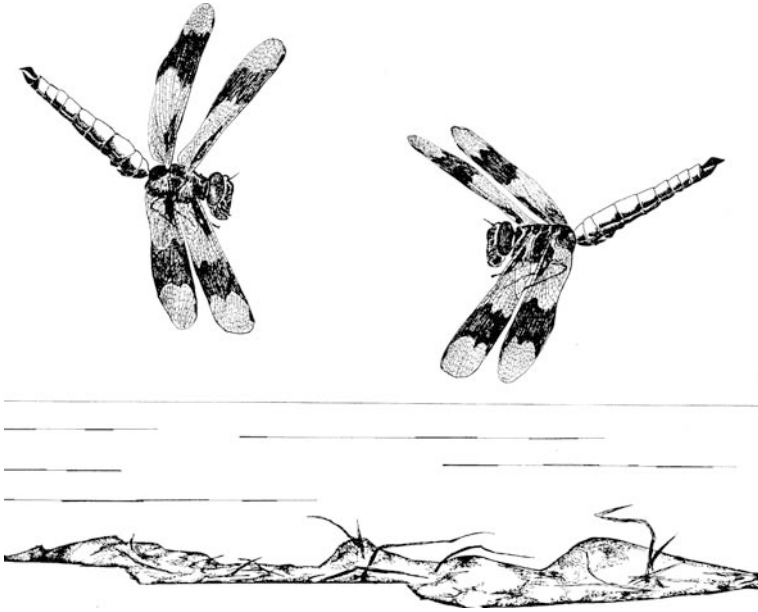
Fig. 7.7 Displaying aggression. Two males of the dragonfly, *Plathemis lydia*, mutually displaying over an oviposition site, their abdomens raised to display the white upper surface. Success in aggressive display is correlated with abdominal whiteness (which develops gradually with age) and therefore with sexual maturity. Males with abdomens painted black are sometimes ignored by other males

insects, are miniscule, and their removal appears to make no difference in navigation or prey capture. As these facts might suggest, dragonflies are indeed among the few insects in which the sense of sight is greatly dominant over the other senses. In fact, Odonata behavior is so visually mediated that some have facetiously dubbed them 'the bird watcher's bugs.'

All dragonflies are more or less selective in their breeding sites. In many cases the male, who generally arrives at the site before the female, confines his activities over a certain pond or stream area that he will defend against intrusion by other males. Within this area, he will court females. On a smaller scale, damselflies will often establish similar territories closer to vegetation or to the water surface. Sometimes several different species of different size classes will exhibit 'stacked territories' over the same pond.

As with most territorial animals, the dragonfly's territorial behavior centers upon certain ritualized *aggressive displays*, backed up by physical combat as a last resort. In aggressive display, two males of the same species recognize each other as such and then indulge in a formalized ritual that usually concludes with the departure of one of the pair. One example can be seen in one of the most common pond inhabitants in North America, a rather large dragonfly, *Plathemis lydia*. The males have abdomens that are bright silvery white above, and, as with the bright colors found

in many other male dragonflies, these play an important role in male interactions (Fig. 7.7) The two males alternately dash at one another, flashing their silvery tail patches in a pursuit display that continues until the new arrival finally restricts his movements to the vicinity of another site.

Unlike the redundant stereotypy of most sexual displays, visual displays that communicate aggression are often highly variable, ranging along a continuum from attack to flight. Such *graded displays* make it possible to communicate slight changes in motivation, an important advantage in facilitating the resolution of territorial and other conflicts.

7.4.2 Alarm

In marked contrast with auditory and chemical communication systems, specialized visual alarm systems have rarely evolved in insects. One explanation for this may be that most predators place great reliance upon their visual sense while hunting. It is most difficult for a potential prey to emit a visual alarm to its companions without also making itself more conspicuous to the predator. Thus, the commonest visual signals eliciting alertness, alarm, and flight tend to be provided not by specialized systems but by the very actions of flight.

Adult butterflies of several families congregate, sometimes in large numbers, around the margins of puddles of water or urine (see Plate 25) where they apparently obtain needed sodium. To a predator such concentration of brightly colored butterflies could represent a potential bonanza, but in fact it usually doesn't. Upon disturbance, masses of butterflies will suddenly fly up and around, surrounding the predator with a whirling cloud of butterflies moving in unpredictable and chaotic patterns, then gradually settle back again only as the source of disturbance wanes. A predator finds it much more difficult to single out particular individuals among the swirling cloud than to pursue an isolated individual flying away from the group. This holds true whether one or several species are involved. At the same time, greater protection might be expected in a larger crowd. Thus, there would be selective advantage in the convergent evolution of similar behavior among many 'puddling' butterfly species. (Thus although several individuals of the same species may be present, they are not necessarily closely related, and such behavior is better interpreted in terms of survival benefit to individuals that all respond similarly and simultaneously to threat of danger than as some form of alarm communication.)

True alarm–alert systems are characteristic mainly of group-living organisms such as social insects. Their evolution here forms part of the larger question of the evolution of all types of altruistic behavior, that is, actions that result in self-sacrifice of an individual benefiting others of its kind; this subject is covered in Chapter 10. Even among social insects, though, visual signals are not the most widely used channel for alarm communication, being upstaged by chemical and sound systems. One possible exception may be found in paper wasps of the genus *Polistes*. Close approach to a paper wasp nest will immediately alert some of the

Fig. 7.8 Alarming defense.
In response to the approach of
an intruder, resident *Polistes
exclamans* paper wasps
assume a characteristic
posture with raised wings and
front legs waving in the
direction of the source of
disturbance. Flight, attack,
and stinging will follow if the
intruder persists in disturbing
the nest, however some of the
participants are harmless
males

residents, which respond with a graded threat display in which front legs are raised
and wings are spread and vibrating (Fig. 7.8). Other workers detect this display
and respond by themselves showing an increased state of alertness and patrolling
activity, a mobilization to meet the potential threat. Although the possibility of
auditory and chemical cues being also involved in this system has not been ruled
out, to date no alarm pheromones are reported for any *Polistes* wasps. Moreover,
their relatively small colony size and their exposed comb nest environment make
it likely that visual and/or auditory alarm communication would be quite effective
here.

7.4.3 Sexual Signals

Perhaps nowhere else is the role of vision in insect communication as well studied
and amply documented as in sexual behavior, where visual signals often mediate a
chain of stimulus/response interactions between the partners (see Chapter 9). Such
signals are often highly redundant and stereotyped—there is strong evolutionary
pressure against making species-identification and sex-identification errors.

It is tempting to assume that Lepidoptera, with their wings of decorative colors
and patterns, are primarily visual communicators, making little use of odors and
touch in their sexual behavior. The validity of this assumption apparently depends
upon which species one is considering. The courtship of butterflies and moths ranges
along a continuum from those with distance responses in feeding and courtship that
are mainly evoked by airborne chemical stimuli and those responding mainly to
visual stimuli. The extremes are most easily recognized by differences in the behav-
ior of males. The 'chemical type' follows the scent upwind in a gradual zigzag flight
to find the female. The 'visual type' looks for the female and approaches quickly and

Fig. 7.9 Courting queens.
Stimulus-response reaction
chain in the courtship of the
queen butterfly, a species
closely related to the
monarch. Males may be
recognized by the glandular
pouch on either hind wing,
visible as a conspicuous black
dot. Resting males thrust their
unsplayed hairpencils into
them frequently, but the
pouches do not appear to be
essential to mating

COURTSHIP OF THE QUEEN BUTTERFLY
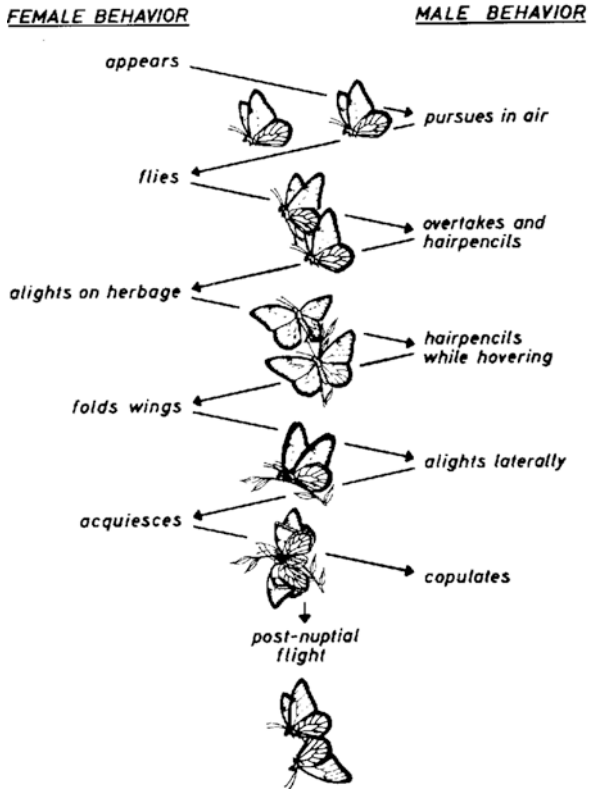
directly. An interplay of signal systems is common, however. In the common orange
queen butterfly, *Danaus gilippus berenice*, of southern Florida, courtship consists of
an aerial phase in which the male pursues the female and of a ground phase that
begins once the female alights (Fig. 7.9). During the aerial phase, males are first
attracted visually through a combination of female movement, color, and shape;
this attraction is quite general, and males often mistakenly pursue improper objects
such as falling leaves. Once the male has overtaken the female, however, a chem-
ically mediated phase begins. Hovering over the female with everted hairpencils
(see Fig. 6.8), the male disseminates pheromones that inhibit female flight and wing
movement. Males deprived of their hairpencils are capable of courting females but
find it impossible to seduce them.

What precise components in a visual signal are important to a courting male
butterfly? A classic study in the 1950s attempted to answer this question for the
silver-washed fritillary, *Argynnis paphia,* a spectacular spotted orange butterfly
common in Europe (Case Study 7.1). The question fairly begged for the use of mod-
els, the technique that has played an important role in so many areas of behavioral
study because of the ways that it allows variables to be controlled.

Case Study 7.1: Visual Communication in the Silver-Washed Fritillary, *Argynnis paphia*

This spectacular spotted orange butterfly, common in Europe, illustrates how knowledge of the nature and limitations of the insect eye can be profitably combined with the use of models to yield insights into an insect's Umwelt.

As with many other butterflies, male and female silver-washed fritillaries respond to blue and yellow when seeking nectar and to green when seeking a place to rest. Sexually active male fritillaries, however, actively pursue many different kinds of orange or yellow-brown moving objects. Only when within about 10 cm of the object do they discriminate further, turning away unless they encounter odor cues from a female.

In the 1950s, a German scientist, D. B. E. Magnus became interested in unraveling the factors behind this male response. Upon learning that many butterflies would court paper models dangled on a string from a wand, he built more sophisticated versions (Fig. 7.10). The concept was simple but effective—systematically varying different aspects of the model on each arm, then tabulating male choices, would allow him to determine the relative importance of aspects of the visual signal.
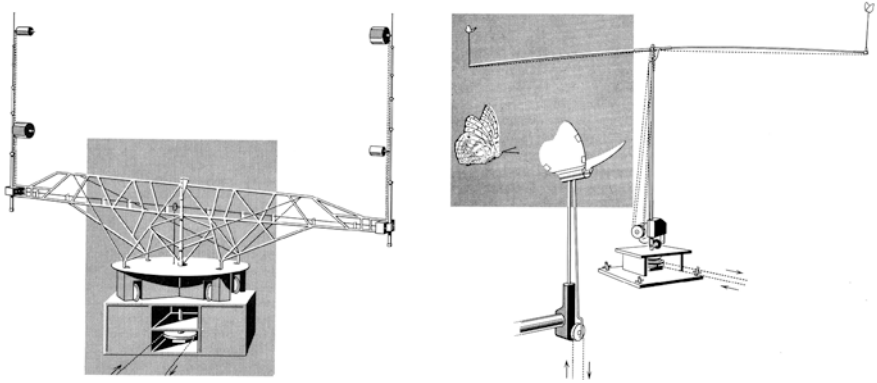
Fig. 7.10 Modeling courtship. Two of the several motor-driven carousel versions that Magnus used to present different stimulus patterns to wild male silver-washed fritillary butterflies, *Argynnis paphia*. The carousel arms carried either (*right*) a flapping butterfly model or (*left*) revolving cylinders with alternating colors

To test his initial apparatus, Magnus presented male fritillaries with models of the same general form and color as females and with flapping wings. Males readily followed the moving dummies and flew off only when they

were close enough to discover that the dummy did not smell like a female fritillary. Satisfied by this, Magnus methodically began to vary different visual aspects of the dummies on the two arms of the carousel. He soon confirmed that shape made no difference; a circle or triangle was just as effective as a 'butterfly.' A wide range of colors and patterns would elicit the first phase of male courtship. Evidently the object only had to be moving and colored somewhat like a female fritillary.

Size of the model mattered greatly, however (Fig. 7.11). Smaller models were followed less than those as large as a real female. Surprisingly, models that were twice the size of a natural female were even more effective; models four times natural size were better yet.

What about wing beat? When he varied the wing-flapping rate, Magnus discovered that the particular type of motion was less important than the rate of flickering perceived by the male butterfly. On the ends of the arms of his apparatus, he replaced the model butterflies with a much simpler type of dummy—a mere rotating spool with alternating bands of color. At first, he used segments of female wings on the spool but found that to a male fritillary, a pattern of pure orange and black was even more attractive.
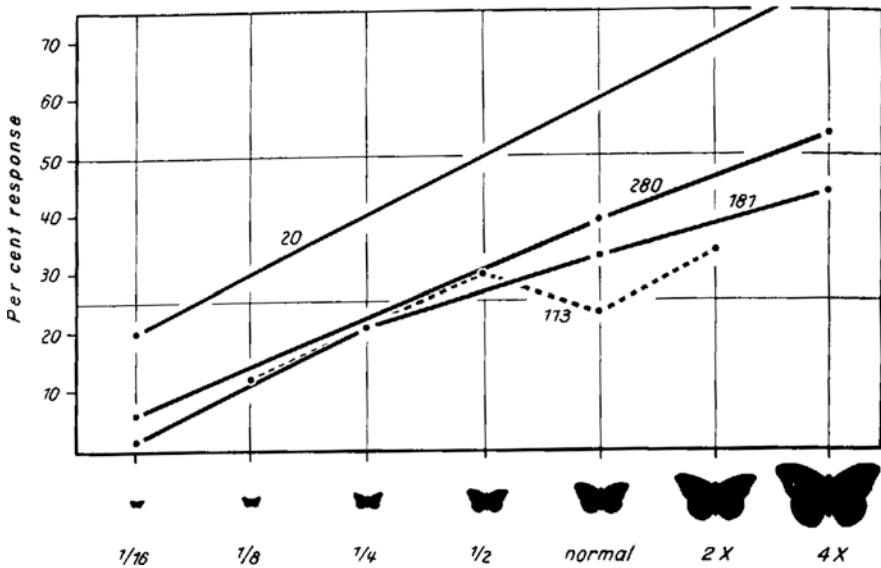
Fig. 7.11 Supersizing. Results of four different experiments comparing approaches of the male fritillary butterfly, *Argynnis paphia*, to nonmoving colored paper dummies of different sizes. The larger than natural size models are clearly more stimulating in each trial. Sizes were presented in different combinations in each experiment; for example, the *dashed line* trial shows percentages of 113 males that responded to each of four sizes: 1/8, 1/2, normal, and 2×

Modifying his apparatus once again, Magnus developed a way to vary the rotation of the spools on each carousel arm independently. When he charted males' choices between spools moving at different rates, he learned that increasing the rate of flicker above a female's normal wing-flapping rate also made the model more attractive. In fact, the improved attraction continued to increase even at flicker rates far greater than those that a flying female fritillary would be physically able to attain. Only when the flicker rate climbed above about 140 stimulus changes per second—the upper limit of resolving power of the butterfly eye—did the attractiveness begin to decline.

Thus, Magnus concluded, for a male fritillary the 'ideal' female would be up to four times his size, pure orange, and flickering her colors as rapidly as he was able to detect them.

Not only Magnus' work but a great many studies with models have shown that when it comes to attracting the opposite sex, 'size matters'. Of course, simple physical impossibilities and opposing selective pressures make it unlikely that a female like that in Fig. 7.11 would evolve. However, supernormal stimuli (see Chapter 2) have been demonstrated many times in behavioral studies, and their experimental use can be very helpful in interpreting the underlying physiological mechanisms involved in stimulus filtering.

Over the years since Magnus completed his work, others also have confirmed that visual long-range orientation of male silver-washed fritillary butterflies only serves to bring the potential mates together. At close range, female pheromones are necessary to initiate male courtship behavior, an apparently unusual situation in butterflies. Receptive *Argynnis* females release a pheromone and when males perceive it, they no longer respond to color. Furthermore, although receptive females react to approaching males by directing their abdominal glands toward them in what looks like a visually oriented response, this behavior might be strongly influenced by perception of male forewing pheromones.

7.4.4 Multimodal Signaling

Traditionally, studies of the impact of insect sensory systems on various behaviors have assessed the influence of a single trait in a single system. This is a very practical choice that limits the number of variables that must be considered. However, this approach has two problems. One is that it does not reflect the rich sensory input that an insect is receiving during that behavior. The other is that it does not address the evolution of multiple traits under complex selection regimes.

One of the themes of this book is that whenever a behavior is important to survival, it tends to rely on more than one type of signal. Consider the matter of insect courtship, a subject we'll be returning to in Chapter 9. Relying on many sources of information was once thought to be an unstable evolutionary strategy for females

engaged in mate choice. However, it now appears that mate choice may generate and maintain multiple secondary sexual traits in many animals, and that it is actually quite adaptive.

If female butterflies, for example, choose between males—and considerable evidence suggests that they do—then evolutionary theory suggests that they may be receiving some benefit from this choice. Benefits generally come in two types: material (or direct) benefits, and genetic (or indirect) benefits; examples of female choice on each basis have been found. In the case of many butterflies, the benefit is material, and comes in the form of a spermatophore; along with their sperm, males deliver accessory gland secretions that contain protein and nutrients a female is able to absorb and use for oogenesis and body maintenance. This is a significant gift, because butterflies are on a 'sugar high'; they are incapable of ingesting proteins as adults and must completely rely on reserves they packed away as larvae. Thus, for a female, receiving a spermatophore results in a higher oviposition rate and lifetime fecundity and longevity. For a male, it is a significant investment; recently mated males produce only about 40% of the quantity of material produced by males that have not recently mated. Thus, there should be considerable pressure on both sexes to 'get it right' by using every discriminatory tool at their disposal, not only during courtship but even before it begins.

Many studies of visual sexual communication in butterflies have agreed in finding movement to be universally necessary to elicit male butterfly courtship; *Colias eurytheme* is no exception. Like many other butterflies, males tend to be most responsive to the general color of their females' wings, but complex color markings and pattern details seem to have little effect, at least in this context. What are important, though, are bright iridescent ultraviolet (UV) patterns that are only found in males and can be seen over great distances.

Vision is not the only sensory modality, however. Pheromones are usually discussed in the context of night-flying moths, and wing displays in the context of day-flying butterflies, and while these are true, butterflies also produce cuticular hydrocarbon pheromones during courtship. Because UV signals can be seen over a distance and cuticular hydrocarbons require proximity, it has seemed quite reasonable to think that the ultraviolet signals of butterflies are used primarily to avoid interspecific mating encounters and contact pheromones are used for intraspecific female choice.

Newer evidence from several studies with *Colias eurytheme* suggests, however, that bright structural coloration in the form of high UV reflectance plays a major role in female mate choice. Under field conditions using free-flying males with naturally occurring individual differences in UV brightness, female *C. eurytheme* preferentially chose to mate with relatively younger males based on the greater brilliance of their structural UV coloration. (As another way of looking at the situation, the brightness of UV reflectance also was the strongest and most informative predictor of male courtship success.)

At the same time, many studies have shown that *C. eurytheme* males produce lipid-based cuticular hydrocarbons that they release when they brush their wings against the female's antennae. Individual males vary in both the quantities and relative proportions of the three chemicals that comprise the pheromone, and the

characteristics of pheromones from field-caught mating males differ from those of non-mating males. Moreover, there is considerable behavioral evidence that these pheromones increase female receptivity and ganglia activity.

How does this tie together? As a male butterfly grows older, his chances of having mated increase, and thus there is a greater chance that he will provide a spermatophore with fewer proteins; he will also mate more slowly, increasing a female's vulnerability and exposure to predators. However, his wings will also have become more worn, decreasing the brightness they reflect. Thus, in the parlance of the evolutionary biologist, ultraviolet brightness is an *honest indicator* of material benefit and females can, and apparently do, take advantage of this signal. Are the pheromones also honest indicators? Perhaps not; one component that has been investigated does not diminish with age. Is the pheromone a back-up system to the UV signal, or does it provide additional information about other aspects of a male? The question remains to be answered.

Possibly vision and chemical cues are still not the only systems employed. In a study of the Asian corn borer moth, *Ostrinia furnacalis,* a Japanese research team has discovered that courtship in this species includes extremely quiet ultrasonic songs produced when the male rubs specialized scales on his wing against those on his thorax, with the wing membrane underlying the scales possibly acting as a sound resonator. The song increases his mating success by suppressing the female's escape behavior. Such vibration-based communication, which seems to point to a whole undiscovered world of private messages, is the subject of the next chapter.

Chapter 8
Mechanocommunication

8.1 Introduction

Male grasshoppers and crickets stridulate, rubbing body structures against one another to produce their familiar clicking calls, to which female conspecifics respond. Death's-head hawk moths squeak a warning to interlopers by forcing air out of the pharynx through a short muscular proboscis. Male stink bugs challenge rivals and court females by drumming their bodies upon a host plant; females listen, then respond with their own species-specific calls.

Among all terrestrial animals, only vertebrates and insects have a rich sense of *hearing*—the ability to detect those time-varying changes in air pressure that we familiarly experience as 'sound' and to respond behaviorally in a biologically relevant context. If one restricts this definition further by requiring hearing must also involve ears—specialized organs sensitive to fluctuating airborne sound signals—hearing has evolved in at least seven insect orders, including all the major ones but Hymenoptera. However, expanding the definition to include detection of sound waves through water and solids, then the list of insects with hearing expands enormously.

Like the Russian nested dolls called matryoshkas, mechanocommunication keeps revealing new layers of complexity and subtleness as humans develop the technology to discern it. Since antiquity, people have known that many insects produce relatively loud sounds, but it has only been during the past 200 years or so that scientists have realized that many insects can hear. Detailed studies of insect ears and behaviors associated with hearing only began in the early 1800s.

The concept that insects produce and sense vibrations began, again, with rather loud and obvious examples, such as the tapping sound of deathwatch beetles in wooden beams. However, paralleling the trajectory of so many other areas of scientific endeavor, the development of new instruments for detecting and recording acoustic signals (particularly those outside the realm of direct human perception) has led to rapid developments in the field of insect bioacoustics. It is now clear that insects also communicate through very soft vibrations, a private language whispered at close range.

There is still much to learn, but already it is clear that insect acoustic communication is immensely more diverse than previously realized. It includes airborne and
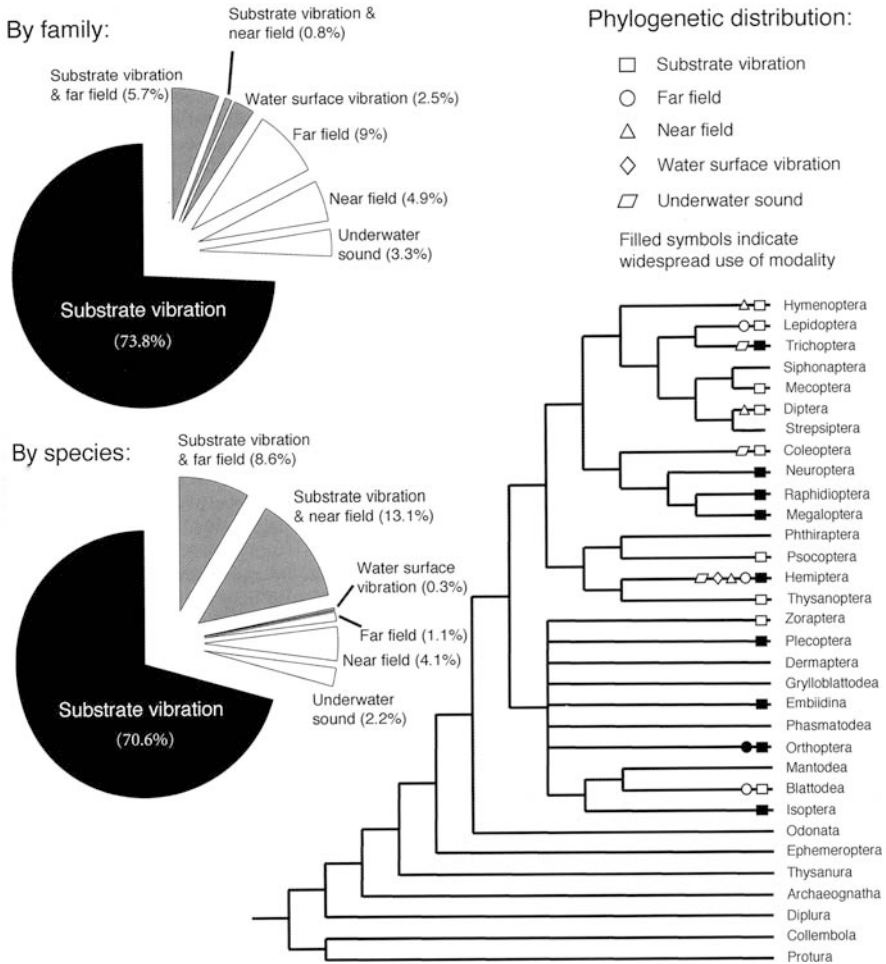
Fig. 8.1   Making sounds. Vibrational signaling occurs widely in the insects. The pie charts reveal that whether one tallies the occurrence of such signaling by number of species or by number of insect families, substrate vibration is by far the commonest modality. Members of the order Hemiptera display the greatest diversity in the use of different acoustic modalities

underwater sound, substrate vibrations, and water surface ripples. Current estimates are that over 195,000 described taxa use vibrational communication alone or in combination with other forms of mechanical signaling (Fig. 8.1); because it is based only on current published reports and named species, this number is probably low.

8.2 Producing and Sending Signals

The song of a single African cicada, *Brevisana brevis*, has been measured at 106 decibels at a distance of 20 inches (50 cm); considered the loudest insect sound on earth, the call is equivalent to hearing a gas lawn mower running three feet away.

Striking the tip of their abdomens against a tree branch, nomadic sawfly larvae make soft tapping noises that summon lone individuals back into the aggregation. The male waterboatman, *Palmacorixa nana,* strokes his peg-laden forelegs across a female's serrated mouthparts during mating, and she responds to the sound by remaining motionless during copulation.

Clearly, in examples such as these the insects are making sound on purpose, as a way to communicate. However, the first insect sounds undoubtedly were accidental. The noises made by a flying insect, the scratching of burrowing larvae, or the vibrations that occur when an insect crawls across a leaf all make sounds. Because insects have a durable elastic cuticle, chance sound production occurs during locomotion, feeding, or cleaning movements.

For communication to take place, however, there must be a sender and a receiver, and the way in which a sound is produced must relate in some way to the manner in which it is perceived. Many insects today produce sounds in the process of defensive behaviors, such as the explosive anal discharges of bombardier beetles (see Fig. 5.9) and the buzz of stinging bees and wasps. No one really knows whether these insects make such noises in order to add to the effectiveness of their other defenses, but such behaviors suggest a way in which some of the earliest sound communication among insects may have arisen.

8.2.1 Sound Creation

Moving their forewings back and forth, katydids sing their familiar choruses; one rainforest species sings in the extreme ultrasonic range, making the highest calling note of any arthropod. Booklice, lacewings, stoneflies and many other insects have taken a different route, tapping the substrate. Virgin queen honey bees produce a 'piping' sound by thoracic sclerite vibration; other queens still in their larval cells respond with their own piping in short pulses at a lower frequency.

In some insect or other, almost every body part has become modified to produce sound, and the majority of insect species produce communicative sound at some stage of their life cycle, using an enormous variety of mechanisms. Various ways to categorize these have been proposed. One is by the method by which they are produced (Table 8.1).

Clicking and buzzing insects seem to be everywhere, so it is probably no surprise to learn that friction-based methods of sound production predominate, particularly among the Orthoptera, Hemiptera, and Coleoptera (Fig. 8.2). Rubbing of one body part against another, or *stridulation*, is so common in fact that some authors have broadened their definition of this useful term to include any sound produced by an insect. One body part, the file, is usually a series of pegs, teeth or ridges; the opposing part, the scraper or plectrum, is generally a single edge or ridge. Associated with many frictional sound production devices are various types of resonating systems that impart distinctive features to the resultant sounds. Frequency and pattern may vary tremendously. Crickets produce some of the purest sounds known for any insects and, in general, the simplest patterns; each movement of their wings produces one pulse of sound. In other insects with more complex songs, such as

Table 8.1 Classifying insect air-borne sounds by the way they are made

Production mechanism	Selected examples	Use in communication
A. As a by-product of another activity		
Feeding	Wood-boring beetle larvae	Spacing individuals
Emergence	*Megarhyssa* wasps	Sexual attraction
Flying	*Schistocerca* locusts; *Heliothis* moths, many mosquitoes	Maintaining aggregation; sexual attraction
B. Impact against substrate (drumming)		
Head	Termites; deathwatch beetles	Alarm; sexual attraction
Abdomen	Booklice	Female mating call
Legs	*Ametrus* camel crickets	Sexual duets
C. Friction (stridulation)		
Many different body parts are used; mechanisms are essentially similar for all.	Widespread, especially in Orthoptera, Hemiptera, Coleoptera	Sexual and aggressive behaviors
D. Vibration of a membrane		
Muscle-driven tymbals	Cicadas, pentatomid bugs, arctiid moths	Sexual and aggressive behaviors, aggregation, predator confusion
Thoracic sclerites	Virgin queen honey bees	Identification
E. Pulsed air stream		
Epipharynx and pharynx	*Acherontia* hawk moth	Disturbance
Spiracles	*Gromphadorhina* cockroaches	Disturbance, courtship

tettigoniid grasshoppers, each wing movement can produce many sound pulses. Because of the mass and viscosity of water, the sound-producing structures of aquatic insects that stridulate tend to be heavier and more massive than those of terrestrial insects.

A second sound production method—using muscles to drive a vibrating membrane, or *tymbal*—is most common among Homoptera and also occurs in some Hemiptera (Pentatomidae) and Lepidoptera (Arctiidae). When the tymbal muscle contracts, the tymbal produces a single sound pulse; when it relaxes, the tymbal produces another. The mechanism is analogous to a rounded tin can lid pressed inward with one's finger and then released. The insect's tymbal muscle contracts with such rapidity (170–480 contractions per second have been recorded) that to human ears the sound output appears continuous. In a variation on this method, other insects vibrate still other body parts.

In a third common method, many insects make noises by striking some body part against the substrate. The death-watch beetle, *Xestobium rufovillosum*, attracts mates by bending its head down and banging it against the floor of its wooden burrow seven or eight times a second, creating a tapping or ticking sound that can be heard in old building rafters during quiet summer nights. Associated with quiet,

Fig. 8.2 Chirping. Males of the snowy tree cricket, *Nemobius fultoni,* produce their very audible chirps by scissoring the wings rapidly from side-to-side which rubs the stridulatory file, located on the underside of each wing on a thickened vein (between the *joined arrows*), against a scraper on the medial edge of the other wing. Sound is produced only during the closing stroke. The hearing organ or tympanum is visible on the front face of each fore tibia (*single arrow*)
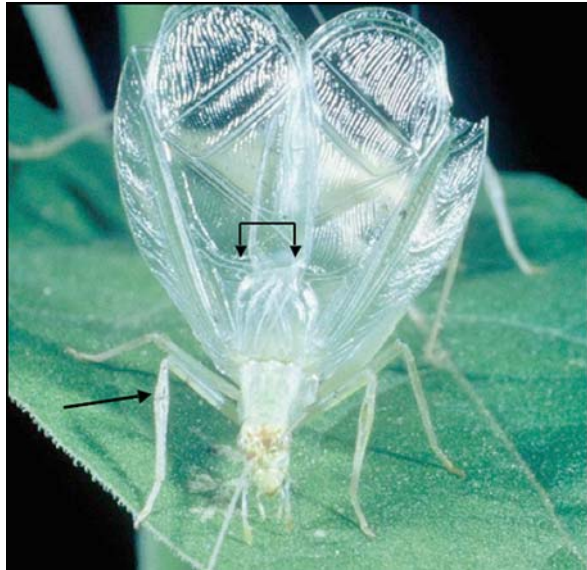
sleepless nights such as the vigil (watch) kept next to the dying or dead, they became an omen of impending death.

In addition to these three ways of producing relatively loud sounds, one must add the many methods by which insects produce a world of softer, closer-range sounds. This brings us to the matters of distance and substrate.

8.2.2 Distance and Substrate

The love song of tephritid and drosophilid flies depends upon short pulses of air that are only detectable at ranges of about 10 mm or less, driven by piston-like motions of their small wings. During courtship, males of the parasitoid wasp *Nasonia vitripennis* produce acoustic pulses that coincide with wing vibrations, but curiously, the wings are not the source of the pulses because altering their surface or removing them does not alter the signal. Crickets such as *Phaeophilacris* that dwell in cavities no longer use airborne sound for calling and courtship; their wings make soundless flicks that only fan the air, but conspecifics can detect these motions from ten centimeters away.

Another way to look at sound production is to consider the physics of vibration transmission. This results in three broad categories: near-field sounds, substrate-borne sounds, and hearing (or acoustic far-field sounds, which includes both airborne and waterborne sounds).

Near-field sound involves displacement waves in air or water that occur close to a sound (generally, a few body lengths from the sound source). At this short distance and small scale, sound production pushes air particles back and forth, making low frequency waves that do not travel very far. The particles that are displaced are

highly directional, and displacement occurs in the same direction as the radiating sound wave. Mechanoreceptive hairs are most often used to detect these particle movements. Near-field communication is probably more common than scientific literature would indicate, because technically, near-field communication is a difficult phenomenon to measure. Many good examples already have been identified. The antennae of many insects function as near-field sound detectors. Specialized dorsal hairs on some caterpillars can detect the near-field sounds produced by the beating wings of a flying wasp; in response, the caterpillars freeze or drop from a leaf, thus evading the potential parasite or predator. Similarly, cockroaches can sense approaching predators through particle-sensitive setae on their cerci (see Fig. 2.3).

Substrate-borne sound is vibration by its most restrictive definition. These signals have also been called seismic communication. Most insects can probably sense vibration, and thus in this wider sense, one could say that most insects can hear. (Section 8.3.1 returns to this subject.) However, airborne and waterborne sounds are the sort we are most accustomed to thinking of as hearing. They involve ears that are sensitive to traveling waves of changing pressure in air and water, known as the *acoustic far field*.

Combining communication by air and water vibration is somewhat artificial, because insects that produce sound under water must contend with the physical problems of sound transmission in a relatively dense, viscous medium with sharp boundaries. Aquatic sound fields also differ from those in air because the extent of the near field is approximately four times greater in water, extending to a greater distance than most aquatic insects communicate over.

8.3 Receiving Signals

In Kansas, great numbers of female cicadas are attracted to a tractor with its motor running. In France, another cicada species responds to whistling. Female corixid bugs of certain species come to the ultrasonic sound of a frequency generator. Parasitic wasps that lay eggs within wood-boring larvae can locate their prey with great accuracy even through an inch or more of bark.

What is happening? A simple answer easily comes to mind. These invertebrates are hearing, and responding to, sounds. Probably the sounds are very similar to those that would normally serve some communicative function for them. But if these examples seem to clearly involve hearing, what should one make of the following ones? When a noise is sounded near some types of caterpillars, they react by rearing up either the anterior third of the body or sometimes the tail end; decapitated caterpillars, or even isolated body pieces, show the same reaction. Whirligig beetles normally swim about on the water surface film in freely moving swarms; when their antennae are altered, individuals collide. Migratory locusts have hairs on the fronts of their heads; stimulation of these always results in flying. How many of these examples should be called hearing? Any? Some? All?

Table 8.2   A simplified functional classification of insect mechanoreception

Sub-sense	Information content	Receptors	Remarks
Gravity and pressure	Spatial relations	Displacement of various body parts	Cooperative with vision
Movement	Stabilization against disturbing forces, especially rotation	Halteres; mass of ear, head and hair plates in the neck	Surroundings as well as insect's own movements
Current	Orientation to currents	Johnston's organ; sensory hairs on head and antennae	Often linked with activation of sense of smell
Touch	Temporal and spatial distribution	Single hair sensilla	Most primitive expression of mechanoreception
Vibration	Alert; social and sexual messages	Sensory hairs on tarsi; chordotonal sensilla of legs; subgenual organs	Closely related to hearing, frequently using same receptors; very slow vibrations may be considered tactile
Hearing	Phonotaxis, phonokinesis; sexual behavior: attraction, alerting, localization	Auditory hairs and sensory spines; Johnston's organ; tympanal organs	Hearing and sound production often linked

Help in answering these questions can be obtained by briefly considering the whole of *mechanoreception*, the perception of any mechanical distortion of the body. This broad category includes any reaction to pressure. Whether the body is mechanically distorted by touching an object, being pulled by gravity, or being hit by vibrations traveling through the air, water, or substrate, the task for receptors is essentially the same—reaction to pressures of different sorts. Table 8.2 presents a simplified functional classification of mechanoreception. The range and sensitivity of all this equipment strikingly illustrates what an immense amount of information an insect actually has about the outside world; without a doubt, mechanical stimuli are involved in more behavioral activities than any other type of external stimulus.

At their most basic level, the majority of the sensory receptors of insects are quite similar in form, namely, a small structure with a single sense cell and a single nerve fiber. In fact, many of the tiny bristles or hairs that occur to one degree or another on most insects are sense organs. These 'little sense organs' or sensilla (see Fig. 6.2), provide the armor-encased insect with sensitive points of contact through its quite insensitive cuticle. On the front of an insect's head, sensilla perceive air movement. Between head and thorax, they perceive gravity and position. On the antennae and other appendages, many sensilla are touch receptors. On the tail filaments of some insects, they clearly serve as hearing organs. Furthermore, in places sensilla may join together to form a loose field or dense pad, functioning together as sense organs of higher order. Inside the body, homologous sensilla may also join to form still other types of mechanoreceptors.

In theory, these receptors fall into two general groups, those yielding information about an arthropod's position in space (the subject of Chapter 3) and those involved in communication with other living organisms, the subject of this chapter. In practice, however, the divisions are often less clear-cut. One reason is that the same set of information can be used for many purposes; for example, touch receptors function in such diverse activities as avoiding obstacles, fighting, and copulating. Another is that similar-appearing sensilla in different locations clearly serve different purposes.

All mechanoreceptors fall into two functional classes: pressure sensitive and velocity sensitive. Pressure-sensitive hairs show a repetitive neural discharge during a static deformation. In simpler language, they continue to fire all during the period of time in which they are bent. Most common on those body areas where position is important, they are the *proprioceptors*. Because they adapt slowly, proprioceptors are not suited to registering sudden stimulus change. However, they give an accurate measure of stimulus intensity, transmitting information about the state of muscles even when contracted for long periods of time. Proprioceptors help the insect to maintain its position, both the relation of various body parts to each other and the relation of its whole body with respect to gravity (see Fig. 3.6). Other receptors, particularly visual and tactile, assist in this capacity.

Velocity-sensitive sensilla, on the other hand, fire only while the stimulus is changing, such as when a sensory hair is deflected, moves back to its original position, and then is deflected again. Such waves of deflection are produced most commonly by oscillations—vibrations that cause ongoing alternate compression and expansion of the adjacent medium. Not surprisingly, tactile and auditory senses depend upon this class of receptors. Velocity sensitive mechanoreceptors usually have a very rapid adaptation rate and thus provide less accurate information about differences in stimulus intensity. They are well suited, however, to record temporal patterns of stimulation.

Because sound is vibrations spreading through a medium away from a source of mechanical disturbance, hearing is a mechanical sense much like touch. However, hearing and touch differ in the types of pressure alternations involved. Sound stimulation has a phasic nature, whereas touch stimulation has a non-fluctuating or irregularly fluctuating nature. More simply, the two senses differ on the basis of distance. *Touch* is mechanoreception that involves contact; *hearing* is mechanoreception that involves a distance between sender and receiver. The differences thus are akin to those between taste and smell in chemical communication.

8.3.1 Vibration

Water striders and backswimmers read the water's surface waves for cues to food and mate location (see Plate 26); they orient to the source of the pulsation through differences in arrival times of the waves at receptors located on different legs. Female *Ephippiger* bush crickets orient both to the audible songs of conspecific males and to the tremors they produce; if the songs halt but vibration continues, females are still attracted, but only if the male is close by. Some solitary

plant-dwelling stink bugs find and recognize their mates by quivering their abdomens to send signals through their host plants.

If the term 'hearing' is restricted to the detection of airborne sounds by specialized receptors, all other sound reception becomes relegated to a 'vibration sense' but in the insect world sound detection and vibration detection often overlap. As a good example, consider the *chordotonal sensilla* that are widely distributed in the insect body, occurring in mouths, legs, wing bases, halteres, antennae, abdomens, and tracheal systems. These sensilla are unique to the insects, but they have been found in every insect in which they have been sought. Subcuticular, with no external evidence of their presence, chordotonal sensilla were originally thought to be exclusively audioreceptors. However, it now appears that they are derived from proprioceptors, and at least some have a mixed function.

Upon the antennae, chordotonal sensilla are grouped into the *Johnston's organ* that detects movements of the shaft of the antenna. In culicine mosquitoes where it was first discovered, and in midges as well, the Johnston's organ is enormously developed and has a clearly auditory function. On the other hand, in most other insects where it has been studied, it appears to act primarily as a tactile organ that relays several sorts of mechanical information. In aphids it is used in the control of flight. Cutting off the antennal flagellum beyond the Johnston's organ causes an aphid's flight to become erratic, but when an artificial antenna is reattached, normal flight resumes.

Generally, insects also have chordotonal organs at various locations along their legs, located in bundles in such a way as to sense vibrations of the surface upon which they are standing. One set of particular importance are the 'below the knee' or *subgenual organs*. These are extremely sensitive at their optimal frequencies because the amplitude of displacement required to stimulate the organ is very small. Since they can localize a source of vibration that is not in contact with the insect, subgenual organs could be called organs of sound perception as well as touch perception. They may be particularly important among the wide variety of borers that stridulate, transmitting vibrations through their wooden tunnels.

The fact that insects can detect vibration does not necessarily mean that they communicate among themselves with it, of course. Most studies of *vibrotaxis*, movement in relation to a substrate-borne source of vibrations, have involved parasites and predators honing in on and exploiting vibratory signals given off by potential hosts, often unintentionally in the course of life activities. Thus, for example, larvae of the leafminer *Phyllonorycter* produce wriggling vibrations that differ in temporal pattern from the vibrations they make as they simply move through an apple tree leaf; their pupae wriggle as well. One of their parasitoids, the eulophid wasp *Sympiesis,* hones in on these signals to locate both life stages of their host.

Examples in which vibration is used for communication within a species have been reported less commonly, but seem particularly to include insects that exhibit some degree of sociality and regularly share some common substrate. Often, as in the honey bee dance language detailed at the end of this chapter, the vibration component of the communication is part of a larger picture that includes other communication modes. However, a particularly well-studied example of primary vibrotactic communication involves treehoppers, a group of membracid bugs that

feed on the sap of trees and shrubs (see Plate 27). Some inventive research with *Umbonia crassicornis* (Case Study 8.1) provides a useful model for studying natural mechancommunication behavior in the laboratory.

Case Study 8.1: Vibrotaxis in the Thorn Bug, *Umbonia crassicornis*

To find potential mates, capture prey, or avoid predators, it's not enough to just notice vibration; an insect needs to be able to locate the vibration's source. Can it be done? If so, how?

Shaped somewhat like little thorns, treehoppers spend most of their lives relatively motionless on host plant stems (a behavior that reinforces this resemblance), leaving only to disperse or find mates. Fascinating in their variation and complexity, treehoppers have become the subject of quite a bit of study. They exhibit the entire range of social behavior that ranges from asocial individuals, to aggregations of nymphs and adults, to highly developed maternal care with parent-offspring communication. The nymphs and new (teneral) adults of some gregarious and subsocial taxa are colored aposematically (see Plate 27); ant-treehopper mutualisms also are widespread.

Working with the thorn bug, *Umbonia crassicornis,* Reginald (Rex) Cocroft found that when he simulated a predator's approach, aggregated nymphal offspring of this little treehopper produce substrate-borne vibration signals that elicit their mother's anti-predator behavior. Vibration was, he showed, the primary communication mode; blocking vibration transmission between signaling nymphs and their mother abolished the mother's response.

The nymphs also communicated to one another, spreading the alarm throughout the aggregation. It was clearly a complex system rather than a simple response to random patterns of vibration because nymphs in otherwise undisturbed aggregations signaled only in response to signals coordinated into synchronized group displays. When signals from their siblings were played back to undisturbed nymphs, they reacted as though they had received an alarm. However, it was unclear whether they actually knew the direction from which the threat originated.

A full-grown *Umbonia* is only a centimeter long. Could animals as small as this send and receive vibration signals that encode location? To some scientists it seemed unlikely on theoretical grounds. They pointed out that vibration interactions take place at close range. Insect legs are close together anyway, and the high conduction velocity of vibration waves will further minimize arrival time differences between receptors. Cases of localization that had been reported were in relatively larger arthropods such as orb-weaving spiders, scorpions, and locusts, and in some cases, it also seemed that direction cues were being gained from amplitude differences along a gradient. Whether the same results would apply directly to smaller scales seemed questionable.

Experimental studies seemed to back up these theoretical concerns. When researchers placed large desert scorpions on substrates in which conduction velocities were five or more times higher than in their normal sand substrate, the scorpions' responses were no longer directional, apparently because of insufficient time delays between their receptors at this larger scale. Wouldn't similarly short delays be experienced in normal substrates by insects whose receptor distances were five or more times smaller?

Perhaps, Cocroft reasoned, insects detect vibrations by a mechanism that does not depend on large amplitude and time differences among receptors. Looking to other acoustic sound localizations in insects, he was struck by the case of another small insect, a parasitoid fly whose mechanically coupled ears react to the interaction of two modes of vibration. Might the treehopper's whole body be acting in an analogous way? Considering *Umbonia* from a mechanical viewpoint, it was like a mass (its body) resting on a set of springs (its legs). Whenever two or more modes of vibration might rhythmically swing the body about, its mechanical response would differ in ways that would depend on the direction of wave propagation.

Earlier studies had shown that that bending waves are transmitted along a plant stem that is mechanically vibrated in a plane perpendicular to the stem's long axis. By extension, it seemed logical that the signals of insects that vibrate the stem also would be transmitted in the form of bending waves. However, before he could examine the influence of vibration direction, Cocroft need to show that thorn bugs actually were communicating with bending waves.

A straightforward way to test this would be to measure the propagation velocity of signals the insects produce, and learn whether the measured values were proportional to the square root of frequency, as expected for bending waves. Cocroft collected adult *U. crassicornis* and placed them on potted host plants in his laboratory. Then he attached two accelerometers with wax onto the underside of a horizontal stem and placed female treehoppers individually on its upper surface. By amplifying and digitizing the signals, he confirmed that this was indeed the case.

When he tried to examine the influence of direction on the biomechanical response to substrate vibration, however, Cocroft ran into problems. Natural stems vary in filtering properties and identical sources would be difficult to obtain; he would also need to present each stimulus both in front of and behind the insect. Alternatively, between each pair of stimulus presentations he would need to remove the treehopper, turn it 180°, and replace it in the same location and posture on the stem. Both approaches seemed destined to introduce too many unknowns. Clearly what he needed was an artificial plant stem where propagation direction could be switched electronically between measurements. With colleagues, Cocroft designed a simulator consisting of a

short length of dowel and two piezoelectric actuators (see Fig. 8.3). The actuators were driven with two time signals that created the relationship between slope and displacement that are characteristic of steady-state bending wave motion. This would allow him to precisely control the frequency, intensity, and direction of the vibration stimulus without moving the free-standing, stationary bug.

Fig. 8.3   Picking up vibrations. A female *Umbonia* rests upon Cocroft's artificial stem. To mimic the properties of bending waves and allow their propagation direction to be switched electronically between measurements, one end of a pair of piezoelectric actuators was attached with epoxy at each end of a short dowel and the other was mounted with epoxy on a fixed metal plate. As the actuators were driven with two random noise signals, a laser opposite the dowel's center measured motion in the plane of the long axis of the actuators and the dorsal-ventral axis of the treehopper

With laser-Doppler vibrometry, the researchers measured points on the substrate and on the treehopper's thorax and middle leg. Transfer functions showed that vibrations resonated in the insect's body at lower frequencies but attenuated at higher frequencies. The measurements differed substantially depending on whether the stimulus came from in front of or behind the insect, and in addition to two modes of vibration along the length of its body, in some cases the treehopper also experienced a side-to-side rocking. Although behavioral directionality and the neural basis of vibration perception remain to be investigated, Cocroft's research demonstrated a means by which straightforward comparison of signal amplitude, probably by the subgenual and chordotonal organs, could provide a simple way for a small insect to determine the direction of a vibrational signal.

   To what degree can results like those in Case Study 8.1 be generalized? Treehoppers have a very expanded pronotum, but it does not appear necessary for generating a basic pattern of resonance and attenuation. The transfer function for the legs and for the thorax was similar, and when Cocroft removed most of the pronotum from three treehoppers, mechanical directionality remained unchanged. Therefore, it seems as though other insects with different morphologies would show similar patterns in mechanical response to vibration.

   The bigger problem with generalizing lies in the many ways that environmental constraints on vibrotaxis can occur. For a treehopper on a plant stem, orienting to a vibration source is essentially a one-dimensional problem. However, for other insects such as a beetle searching for a mate on a leaf, localization is a two-dimensional problem; results of studies on two-dimensional surfaces have given mixed results, leading some scientists to question vibrotaxis as an explanation. Alternatively, they say, insects may triangulate, sampling and comparing vibrations at multiple points before orienting. Another possibility is that they may follow a simple searching rule, making large turning angles whenever the amplitude of the vibratory signal drops below a certain threshold. Further research will be needed before all this can be straightened out but there is no reason, of course, to make such explanations mutually exclusive; all insects need not follow a single rule.

8.3.2 Hearing

Some hawk moths have hearing organs in their mouthparts; while feeding on flowers at dusk, they can listen for bat echolocation calls by inflating their palps. The South African bladder grasshopper, *Bullacris membracioides,* has six pairs of ears running along its abdomen.

   A diverse group of specialized auditory organs has arisen in insects from organs serving originally for proprioception. These organs are the ones most similar to what most people might call insect ears. They show a great deal of morphological diversity, and from one taxon to another, they can be found in many different body locations (Fig. 8.4). Sometimes they are conspicuous; many other times, they are not. Vertebrate ears are always on the head, behind the eyes and above the jaw. How can insect ears appear in so many places? The answer seems to lie in evolutionary and developmental differences. Vertebrate ears arise from the gill arches, neural crest, and optic capsule, which confines them to the head. Insect ears, of the other hand, have arisen through a few simple modifications to existing proprioceptors and their surrounding cuticular tracheal structures. Because the chordotonal proprioceptors are widely distributed, ears can be as well.

   Despite this great diversity, each ear typically consists of the same three units: a tympanal membrane, a tracheal air chamber, and a chordotonal sensory organ.
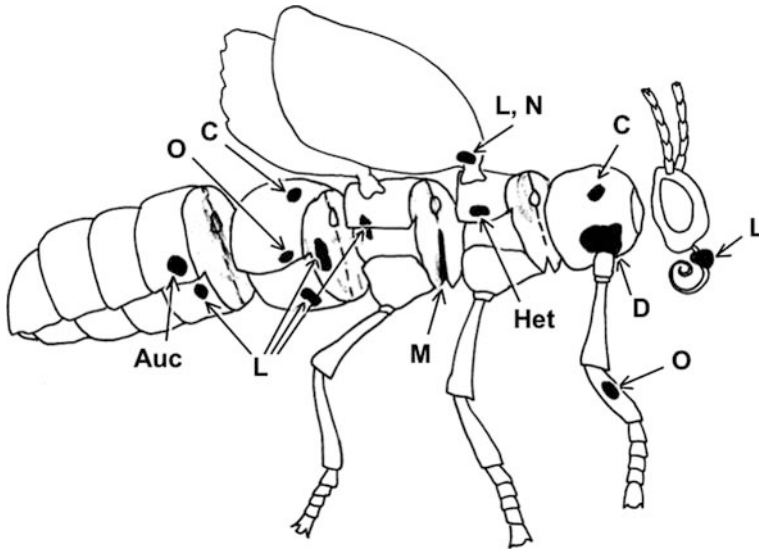
Fig. 8.4 **Finding insect ears**. A generalized insect showing 15 body locations where tympanal organs have been identified as evolving independently among members of seven different orders. Key: Auc = Hemiptera: Auchenorrhyncha, C = Coleoptera, D = Diptera, Het = Hemiptera: Heteroptera, L = Lepidoptera, M = Mantodea, N = Neuroptera, O = Orthoptera. Locations of hearing organs of Lepidoptera are most diverse, but all tympanal organs probably evolved from proprioceptors

With the development of ears, the chordotonal sensilla have increased in number and become attached to a thin, taut membrane that is set into vibration by waves of airborne sound. This membrane, or *tympanum*, functions as a sort of eardrum. In many nocturnal Lepidoptera that are ultra-sensitive to sounds, the typanum is so thin that it is transparent and occurs in a protected location. By contrast, many Orthoptera have a much thicker tympanum conspicuously positioned on the cuticle surface (see Fig. 8.2). Tympanic organs are usually paired and they often interconnect through a series of tracheal chambers.

In still another variation on insect hearing, hair sensilla that are primarily used for tactile purposes often react to high-intensity airborne sounds. As a result, many insects that lack tympanic organs are still quite sensitive to sound waves in air. Most if not all caterpillars, for example, can detect sound and will react by becoming immobile or thrashing as a protective response. It does however appear that those sensilla types most highly developed for airborne sound reception differ from tympanic organs in several ways. Compared to tympanic organs, these hair sensilla respond over much lower frequency ranges and fatigue fairly rapidly. They exhibit only limited frequency discrimination, responding synchronously with stimulus frequency over certain ranges. Finally, they tend to habituate or equilibrate, that

is, as a sound continues through time, the amplitude of the massed spikes in the responding nerve declines.

8.3.3 Communication by Touch

The very large and complex nests of many social insects present an enigma. No single colony member can oversee more than a small piece of the construction work or envision the nest in its entirety. Sometimes, a nest may require a number of worker lifetimes to complete, and each new part must be brought into balance with the old. How can the workers communicate so effectively over such a long time period? Who has the nest blueprint?

In the 1950s, termite researcher Pierre Grassé suggested a key to this puzzle. Perhaps the insect nest-builders were responding to previously accomplished work on the nest itself rather than to direct communication from their nest-mates. Then, even if one could constantly renew the work force, the nest would be completed 'according to plan' because the nest structure already finished would determine what further work should be done. In the years since, many researchers have challenged the completeness of Grassé's explanation, but not its basic insight. The most durable signals that communicate information between insects of the same species are those incorporated in structures built by the insects such as nests. In his groundbreaking book *Sociobiology,* Edward O. Wilson termed such communication *sematectonic*, from the Greek words for sign and builder, and defined it as the evocation of any form of behavior or physiological change by the evidences of work performed by other animals, including the special case of the guidance of additional work.

Sematectonic communication is not limited to social species. For example, in the nests of many solitary bees and wasps the cells are arranged end to end in a linear series. At emergence, adults always chew outward in the direction that they are facing, which is almost invariably toward the nest entrance. In general, the nest tunnel is not broad enough to permit the adult to turn around inside should it emerge from its cocoon facing the wrong way. How does the mature larva correctly orient itself with an accuracy that far exceeds that expected by chance alone?

As the wasp nest is constructed, the mother builds partitions between successive cells. As a result of the techniques of construction, the inner and outer faces of each partition differ in texture and concavity. The mother wasp works from the outside, and the partition tends to become concave on the outer surface. It is also smoothed on the outside, while the inner surface has an irregular, bumpy texture on its convex face. By testing independently the effects of the four possible cues on larval orientation, Kenneth Cooper was able to clearly show that concavity was the primary cue used by the spinning larvae (Fig. 8.5); they always oriented their heads away from the concave surface. Moreover, Cooper found that completely unrelated

Normal Nest

All Partitions Reversed

Some Partitions Reversed
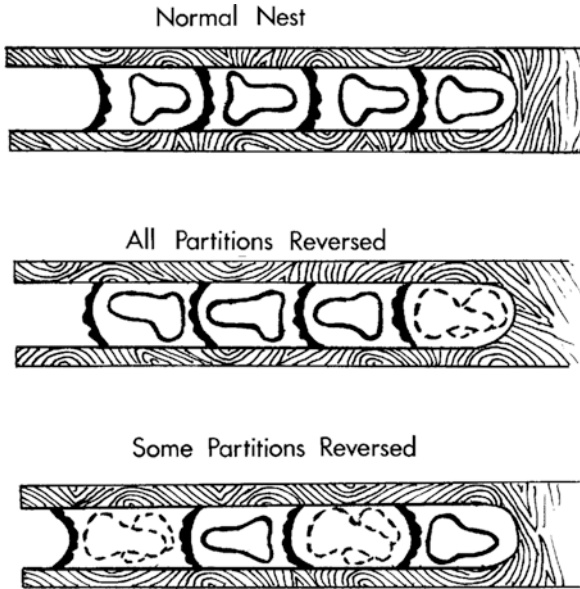
Fig. 8.5   Getting cues from mother. The orientation of a solitary-wasp larva when spinning its cocoon depends upon the way its mother built the linearly arranged cells. By facing the rough convex side of the partition, when its development is complete the offspring will leave the nest in the right direction. Artificially reversing partitions was the key to understanding this behavior; the swollen end of each cocoon contains the head

wasps, including some parasitic species, orient correctly by the same cues. In twig-nesting solitary bees, where the cell partitions tend to be rather amorphous walls of resin or chewed leaves, the significant orientation cues seem to lie in the placement of the pollen mass. Spinning larvae always orient cocoons facing away from the pollen mass.

Theoretically, touch could form the basis for a complex and important communication system, transmitting a great variety of messages by varying frequency, pressure, and time of contact. However, tactile communication appears to be relatively unimportant in comparison with the other communicatory modes. Most tactile systems have one overriding limitation: the sender must be in contact with the receiver. As a result tactile methods are usually restricted to close-range situations such as courtship, mating, and occasionally alarm.

Except for the special case of sematectonic cues, touch communication as a whole among insects is quite poorly known. The sense of touch is one of the most difficult modalities to investigate in a communicatory context because it is hard for an observer to interpose himself or his instruments in such a way as to register the signals in the form that they are actually received without disrupting the system. And because of this difficulty, even in cases where tactile signaling is involved, other communicatory modes tend to receive the first attention.

8.4 The Acoustic Channel

Among insects hearing had seemed to be the exception, not the rule. This disconnect was probably only because hearing had been defined too narrowly. For insect sounds the human ear has little to recommend it as an analyzing instrument. Its frequency response range is too small, and its time constant is too long. However, as noted above, to compare, contrast, or even properly describe insect songs, the use of various instruments is essential, and with this continually improving technology the extent and scope of insect mechanocommunication has turned out to be surprisingly broad. Continued use of such technology promises to breach the gap between the known occurrences of insect sound and the relatively little known significance of them. It also promises fuller recognition and understanding of insect communication that is occurring in near-field and vibratory modes, which is undoubtedly going on all around us, but unaided human ears have almost completely ignored.

8.4.1 Parameters of Insect Song

People hum melodies and whistle bird songs. But have you heard someone sing along with an insect? Probably not. Why? One reason stands out—insects cannot carry a tune. Most also appear to be tone-deaf; different tones are indistinguishable to them.

Melody involves variations in pitch (the level of sounds in the scale, as defined by their frequency), and insects sing in a monotone. The dominant frequency of most air-borne insect songs stays at a more or less common pitch. Most insects produce sounds that are in the upper part of the auditory range detected by their sound reception organs, where frequency discrimination appears to be rudimentary or absent. The chirp of the domestic cricket is comparatively unusual, occupying a narrow band of frequencies having a nearly pure tone that we recognize as a definite pitch. Most insect sounds are noise-like, covering a broad band of many non-harmonically related frequencies. These sibilant sounds are commonly below 18 kHz, but many range into the ultrasonic.

If melody is a weak point for singing insects, rhythm is their strength. The basis of insect acoustic communication lies in sound intensity and timing. Many (and maybe most) insect songs occur as a nested pattern of time-related groupings of individual sounds at various volumes. The scale on which these elements occur is normally hidden to us because the time constant of unaided human ears is too long to discern and analyze them. For example, what we hear as a simple buzz is actually a set of individual behavioral song components (*phonatomes*) and their first- and second-order groupings. Were the phonatome rate to be slowed down enough, we could hear the individual phonatomes as countable 'ticks' or 'smacks' or, if they occurred slightly too rapidly to count, as a 'rattle'. Because temperature has a substantial effect on phonatome rate, the same song component that is identified as a rattle at one temperature may be called a tick sequence at

a lower temperature. Sometimes this relationship to temperature is quite precisely known. For example, snowy tree crickets (see Fig. 8.2) are well known to naturalists as 'thermometer crickets' because by counting the number of chirps heard over 15 seconds and adding 40, one can fairly accurately calculate the Fahrenheit air temperature.

One phonatome includes all the sound produced during one cycle (one complete stroke of the scraper over the file and return) during stridulation. Because it is a behaviorally defined term, the phonatome label is difficult to apply precisely in cases where the behavioral basis of sound production is not known. In contrast, a *pulse* is the simplest element of amplitude that is convenient to recognize—a wave train isolated or nearly isolated in time by a substantial amplitude modulation (frequently, an interval of silence). With some simple sounds a pulse may be equivalent to a phonatome, as in a single cricket chirp or one squeak of a restrained velvet ant. In other cases, such as the meadow katydid, *Orchelimum*, the simplest sound element is a pulse lasting a fraction of a millisecond, and the travel of the scraper along the file generates a whole train of pulses that collectively are equivalent to a phonatome.

Analogous to the way that a prism can separate the colors in light, special electrical equipment can separate the components in a sound. The resultant images are of two types, spectrograms and oscillograms (Fig. 8.6). A sound spectrogram, or *sonagram*, records the frequency spectrum of a sound as a function of time; this is commonly used to study bird songs because it permits one to distinguish pitch differences. On the other hand, an *oscillogram* shows the volume of a sound; the greater the deflection, or amplitude, of the tracing above and below the abscissa baseline, the louder it is. This is important because insect songs often show rhythmically alternating loud/soft patterns through time. Equally important, oscillograms can resolve phonatome sequences that occur too rapidly for unaided human ears to separate.

8.4.2 Song Synchronies

The alternating songs of crickets, the long raspy choruses of katydids by nights, and the intense shrill buzzes and rattles of cicadas by day—these are some of the most familiar and conspicuous insect sounds that humans recognize. Their precise choreography in space and time often gives rise to striking alternation or synchrony between neighbors, and one cannot help but wonder how and why they evolved and are maintained.

Of all the acoustic responses an arthropod may give, the most widely observed and easily demonstrated is the *phonoresponse*—upon hearing a noise, the insect replies by making one. Acoustic stimulation may produce two different types of phonoresponse, depending upon the species. In some, the responding insect alternates its emission with that of the stimulus. Such alternation is frequently displayed between two males, either at the emission of the calling song or of the rivals' song; it is also observed in species where a male and female emit an agreement song.
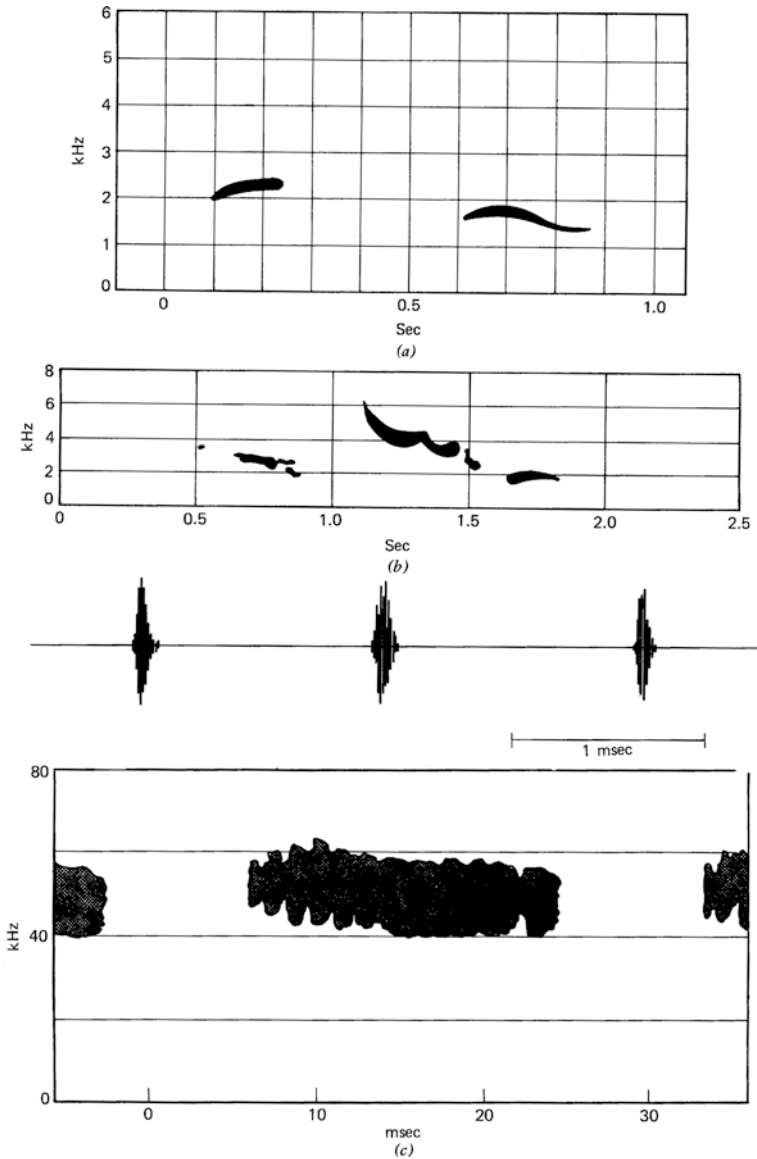
Fig. 8.6   Measuring songs. Sonagrams and oscillograms enable a viewer to appreciate song characteristics and differences at a glance. Sonagrams show the carrier frequency on the vertical axis (ordinate) and time on the horizontal axis (abscissa). Oscillograms also represent time on the abscissa, but the ordinate expresses fluctuations in the pattern of sound intensity (loudness), without specifying the frequency; the degree of blackening correlates with sound intensity. (**a**) Sonagram of an easily recognized human 'wolf whistle'. (**b**) Song of the long-horned grasshopper, *Phlugis*, displayed on an oscillogram (*top*) and a sonagram (*bottom*)

Phonoresponses involving two or more individuals of the same sex are the most common type.

Among other insects, particularly species living closely packed together, sound emission by one individual may set off a collective and synchronous song of all the population. Like their counterparts among bioluminescent species, these *chorusing* displays of acoustically signaling insects are recognized as some of the great spectacles of the living world. Chorusing most commonly involves males, and it may result in large numbers of insects coming together in dense aggregations. In some cases, individuals may synchronize or alternate calling phrases for indefinitely long periods of time, as do Cicadidae and some Orthoptera. The forces that drive such synchrony are undoubtedly many. The role of sexual selection has been a matter of particular interest. Many play-back sound studies with various species have shown that when females are presented with two male calls that are out of phase, they preferentially orient toward the earlier call, a type of *precedence effect*. The importance of this effect on mate choice in actual choruses and natural populations is still poorly known, but there is some evidence that males strive to adjust their singing so as not to lag behind others.

Studies of chorusing insects point to the powerful role of the social context in influencing acoustic signaling, an area of research receiving increasing attention in the context of communication networks. Chorusing of vertebrates has been most thoroughly studied in various frogs and birds; chorusing of invertebrates, in periodical cicadas *(Magicicada)*. In the latter, a three-species complex shows extraordinary chorusing behavior. In each species, a calling or aggregating song produced individually but sung in chorus activates and assembles both males and females. Not only do the songs of each species differ in their acoustic parameters, but each species has a different time of peak chorusing activity as well (Fig. 8.7). These two factors result in a slow but clearly defined grouping of each species in its habitat. In their first few days of adult activity the three species may be intermixed, but after a week or two the grouping has become so intense that a tree may contain hundreds of cicadas of one species and only one or two of the other two species. Such sorting undoubtedly helps female cicadas find a mate of their own species.
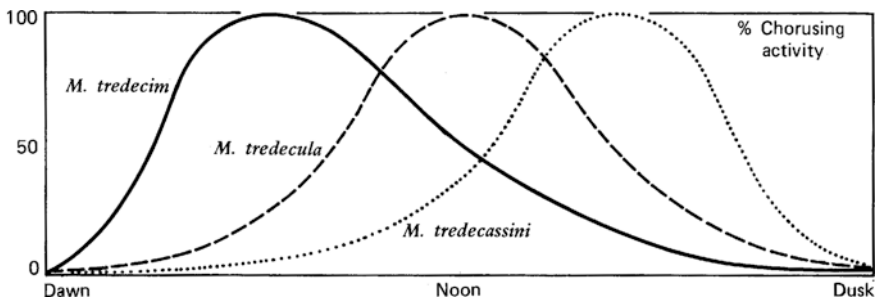
Fig. 8.7   Singing one's species. Approximate diurnal times of maximal chorusing activity in the three sympatric species of *Magicicada* found in the southeastern United States

Do female cicadas also choose between the males on some basis of some quality difference signaled by the songs? Periodical cicadas have seemed to be strong candidates for participating in lek mating systems (see Chapter 9). However, a study of patterns of mating success in actively chorusing males could find no consistent differences between mated and unmated males on the basis of size and song pitch, and the patterns of mating success in actively chorusing males were indistinguishable from random mating. Whether other insect choruses are leks is a matter of ongoing debate.

A chorus is an extremely complex acoustic scene. What kind of information do males and females acquire amidst this cacophony? How do they respond to these signals? The reception of unintended signals—in a word, *eavesdropping*—has become a particularly interesting area of theoretical study. Key conceptual questions concern how listeners might use overheard information to their own advantage, and how signalers might strategically direct their signal production to minimize possible eavesdropping in certain contexts.

8.4.3 Active Acoustics

Based on early studies, hearing was thought to be a basically passive process. In fact, Georg von Bekesy won a Nobel Prize in 1961 for showing that mammalian hearing is place-coded; specific frequencies of sound excite hair cells corresponding to their location on the basilar membrane in the cochlea. While this basic idea still stands, more recent discoveries are causing a major paradigm shift in scientists' perception of auditory processing. At the level of cellular mechanisms, it is becoming increasingly clear that acoustic reception is not a basically passive process it was once believed to be. Instead, hearing involves active processes that take place as hair cells acts like molecular micro-machines to enhance auditory sensitivity and tuning. These active processes occur only in living organisms, and for this reason they have only come to light as newer technology has allowed such advances as laboratory culture of vertebrate organs, tissues and cells *in vitro* and noninvasive cellular-level studies of hearing in intact, living insects under relatively normal behavioral conditions.

In retrospect, active hearing in vertebrates seems perfectly obvious because of a phenomenon we have all experienced: *selective attention*. Consider the situation in a crowded room; many conversations may be going on simultaneously, but at the mention of your own name, instantly your attention zooms in on that conversation. Probably nearly ever animal has some type of similar response that momentarily heightens perceptual acuity when confronted by an important stimulus such as a social signal or an environmental noise that might indicate a predator's presence. However, whereas in mammals, selective attention seems to be mostly brain-centered, in the few insects where it has been studied, selective attention is ear-centered.

Given the extraordinary auditory world of mosquitoes (see the case study later in this chapter), it is probably unsurprising that the best-studied example of active

acoustics in insects involves a non-bloodsucking mosquito, *Toxorhynchites brevipalpis,* that occurs in Tanzania. Like other mosquitoes that have been studied, adult males of *T. brevipalpis* detect the presence of females on the wing by ear. When they hear a nearby female's flight tones, they pursue her. It sounds like a simple system—cruise, catch, mate—but studies have shown that there's significantly more to it than this. For one thing, the wings of a female mosquito are very small compared with the wavelength of the sound they make. For the male mosquito, this means that if a female is flying more than a few tens of centimeters away, he should not be able to hear her, yet he does.

To investigate this puzzle, Joseph C. Jackson and Daniel Robert turned to Doppler laser vibrometry, a powerful technique that allowed them to study intact mosquitoes in a completely noninvasive way. Painstakingly, they measured mosquitoes' antennal responses to the sounds of real mosquitoes, tethered and untethered, and to simulated mosquito sounds played through a loudspeaker. When the results were analyzed, they showed that male responses were nonlinear; rather than a straight-line response to female wing-beat sounds, the male antennae showed three distinctly different levels of mechanical excitability, depending on the female's location. Significantly, after a female flew on by, the male's antennal cells continue to be at heightened sensitivity for a while. (The scientists likened it to the lingering scent of perfume, which briefly persists even after its owner has passed by.) This mechanism would sustain and amplify the normally weak and transient female signals.

The study revealed a remarkable twist to the mosquito auditory system—a mechanism that changes a male's sensitivity to a biologically relevant sound. Because all the responses occurred within the range at which female mosquitoes are well within earshot of a male, it appears that this is a mechanism not so much for improved detection as for focusing the male mosquito's attention by making a female appear closer than she is. Similar nonlinearities have been known in mammalian ears (where they also enhance acuity) for some time. However, this is one of the first indications that the adaptive imperatives of functional hearing have resulted in similar biomechanical processes in invertebrates.

Sensory tuning and selective attention will probably turn out to be quite widespread. In 2006, James Windmill showed that the yellow underwing moth changes its sensitivity to a bat's calls when the moth is being chased; even after the calls stop because the moth has escaped, its ear remained tuned in for several minutes in case there is another attack.

It is also worth noting that one American field cricket species has been shown to have an abruptly lowered auditory threshold at just the frequency (pitch) of its song, about 4.5 kilocycles/second. If other crickets also have their auditory organs so precisely tuned to their own frequencies, the songs of different genera might be rendered almost inaudible. Then rhythm patterns of each could evolve without reference to one another, and songs could be rhythmically quite similar without confusion. Some weight is given to this theory by the observation that ground crickets (Nemobiinae), which often live with field crickets, have songs usually pitched quite differently from them (about 8–10 kilocycles/second). In a region such as

North America, where 40 or 50 insect species often may be stridulating simultaneously in the same locality, such a development would obviously be a great advantage.

8.4.4 Sound as a Communication Method

Acoustic messages are an unusually complete and efficacious way to impart information. They diffuse easily, resist disturbances, and exhibit the potential for creating a vocabulary. They convey information instantaneously but they leave no lingering traces to alert a predator or parasite. In many cases, an insect would not even need to suspend other activities in order to transmit or receive sound signals.

Sound can be distinguished at very low levels; it also may be raised above environmental noise by pumping energy into the system. Sound waves can travel at any time or day or night, and not only through the air but through solid surfaces, thick vegetation or muddy water. Sound also can be transmitted over long distances. If one considers the distance at which signals are no longer physiologically perceptible, chemical messages have perhaps the widest range and visual messages probably the shortest; acoustic messages fall somewhere in between.

If audible sound is such a good way to communicate, why don't more insects use this method? One set of reasons has its roots in insects' relatively small size. First, for mechanical reasons small size generally results in the production of relatively high-frequency signals. These attenuate and degrade more quickly than low-frequency signals, and this limits communication range. To get around this problem, some small insects increase their broadcast range by behavioral tactics such as using plants as acoustic baffles, calling from elevated positions, or calling from within burrows that act like horns; others have structural modifications that allow them to produce sounds at lower frequencies than others of comparable size.

Second, sound production may be energetically more costly and inefficient for a small invertebrate organism. The density and elasticity of insect cuticle differs significantly from that of air, so it takes a great deal of effort to convert the muscular energy controlling a vibrating structure into airborne sound. Thus, it probably should not come as a surprise to find that many insects have taken the route of producing vibrations in the substrate instead. The energetic costs of tapping on a surface are much lower than the costs of calling through the air. Tubular structures such as leaves and stems allow information to be transmitted as bending waves, which can travel efficiently for some distance.

Third, the narrow separation of insect ears makes it difficult to nearly impossible for most insects to localize the source of an airborne sound by using differences in sound wave arrival times at their ears. Some insects have gotten around this problem by adopting a different mechanism, pressure-difference receivers. However, this has other consequences for acoustic communication, such as limiting the frequency ranges that can be effectively used, as well as interacting with mechanisms used in sound pattern recognition.

Another set of reasons arise from the ease with which potential predators and parasites can home in on sounds. For example, Mediterranean house geckos orient to locations where male decorated crickets, *Gryllodes supplicans,* are calling. Even though the male crickets call from burrows where they are protected from the geckos, this behavior enables the geckos to intercept and consume female crickets that also respond phonotactically to the cricket calls. Eavesdropping can occur with any sensory system, of course, but acoustic messages are particularly apt to provide clues to location.

Unlike bird songs that often feature a learned component, the song of arthropods appears to be totally hereditary. What plasticity is present is preformed; it cannot be modified through learning. Thus, song can be considered to be a species-characteristic feature very much like morphological features. While external factors, especially temperature, may considerably modify the song, these modifications are only simple responses to changes of environment much like changes in pigmentation or ornamentation. This means that with even a simple mutation, song may become an important reproductive isolating factor. When new arrangements arise (a rare but not impossible circumstance), they are capable of producing instant isolation of these individuals from other members of their species. Sometimes, this isolation may lead to speciation; more often it does not. Two sympatric grasshopper species, *Chorthippus biguttulus* and *C. brunneus*, produce hybrids in the laboratory, but few hybrids are found in nature. Because hybrid males produce hybrid songs that are intermediate between those of either parental species, the females of both species shun them. Thus although hybrid males are reproductively fertile, they are behaviorally sterile.

8.5 Functions of Insect Communicative Sounds

To develop a complete functional classification for insect sound would be a gargantuan task, but a relatively simple system covers most acoustic behavior in four basic (but sometimes overlapping) categories. All of these fall naturally into two groups, depending upon whether the sound shows any repetition of some basic element, that is, whether the song is *patterned*.

Unpatterned sounds, while they might serve as simple behavioral releasers, cannot transmit complex information. Signals between species tend to be characterized by their high intensity and lack of pattern; they are the type of sounds often released when an insect is touched, and most alarm and warning sounds are of this type. Patterned sound, on the other hand, is found in all cases of complex intraspecific behavior mediated by sound, and pattern is their most constant feature.

8.5.1 Protest, Alarm, and Aggression

When threatened, both sexes of the velvet ant *Dasymutilla occidentalis* (Fig. 8.8) stridulate with enough volume to be readily detected by the human ear a meter
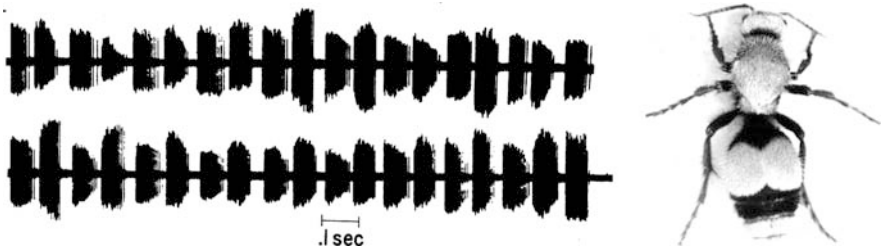
Fig. 8.8   Making a ruckus. Oscillogram of the stridulation produced by an unrestrained adult female velvet ant, *Dasymutilla occidentalis*, when disturbed. The unpatterned sound is produced by an in-and-out movement of the abdomen segments; this rubs a series of transverse striations (the file) on the dorsal anterior margin of some abdominal segments across raised ridges (scrapers) on the posterior dorsal margins of the preceding segments. The *top* recording represents one direction of abdominal movement; the *lower* trace represents the opposite direction

away. After an encounter with the stridulating carabid beetle *Cychrus*, the common shrew will not attack this insect again.

Insects of almost every order are known to react with some noise when picked up, pinched, probed, restrained, or otherwise disturbed. In fact, more descriptive papers have been published on this general kind of sound communication than on any other aspect of arthropod acoustical behavior. For most arthropods, the only known acoustic communication is such a *protest sound*, a high-intensity unpatterned sound of a broad frequency spectrum. These signals are elicited primarily upon tactile stimulation. Their function is still unknown, and whether they are even primarily airborne acoustic signals is open to question. It has been suggested that the effective stimuli are tactile or vibratory and the air-transmitted portions of the signal are incidental.

The emission of protest sounds is so widespread in the Arthropoda that it is most tempting to consider these as predator-escape mechanisms. However, after actual observations one finds it at least as easy to persuade oneself that such signals do not upset predators at all; the literature is certainly full of documentary notes on insects being eaten while emitting such sounds. Of course, failure in a certain proportion of cases does not necessarily mean that a protest sound does not have a defensive function. Some startled predators may still release the prey. Even if it only worked to the prey's advantage some of the time, such behavior would still have positive selective value.

Another suggestion has been that these protest sounds should be regarded merely as displacement activity, an outlet for the intense nervous excitement involved in capture or cornering. A variant of this theory states that these sounds have no meaning at all. Why, it is asked, does the possible meaning of this acoustic display even have to be considered when no one thinks of giving equal consideration to the role and efficacy of the cries of a mouse captured by a cat? Of course, on this subject one is truly unencumbered by the facts. Until some perceptive experimental work is undertaken, the situation will remain so. It is likely that various hypotheses may
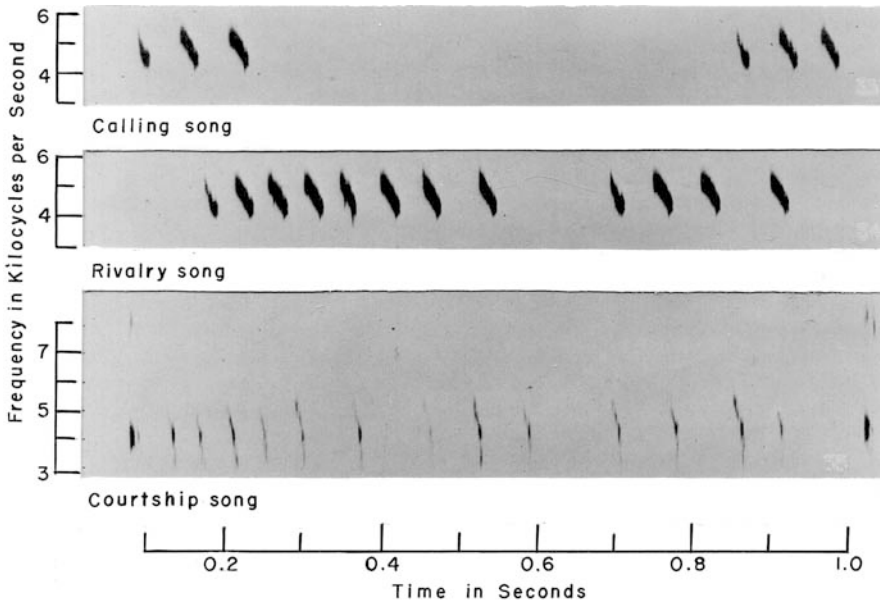
Fig. 8.9   Performing the play list. Sound spectrograms of a domestic cricket, *Acheta domesticus*. The loudest and most commonly heard song is the calling song sung by males to attract sexually receptive females to them. Once the sexes are together, a new song—the courtship song—facilitates mating. A quite different song, the rivalry or aggression song, is sung when two males encounter one another and serves to determine the relative dominance of an individual. In other species, the male may sing a post-copulatory song that keeps the sexes together for a period after sperm transfer

be supported in different situations. Furthermore, in still other situations, the very novelty of an unfamiliar acoustic signal may be enough to elicit predator avoidance.

Actual acoustic *alarm signals* differ from protest sounds in some important ways. Their sounds are almost always patterned, though they may range from simple to (often) complex. Most operate within a species rather than between species. Alarm signals also are characteristic of social insects and show a wide range of intensities. Releasing stimuli are often elaborate. On theoretical grounds an effective alarm should have a very wide frequency range and be of high intensity, and indeed these characteristics do typify most sounds in this category. Such sounds are both easily heard and readily pinpointed as to source.

The termite *Zootermopsis angusticollis* provides a good example of an acoustic alarm. When suddenly exposed to bright light or an air puff, soldiers and workers tap their heads on the roof and floor of their tunnels. They often also produce substrate vibrations when they meet other termites, and they will respond to an alarm vibration by producing one. The vibrations are received through subgenual organs on the tibia; these appear to be tuned somewhat to the frequency and pulse rate of their particular disturbance response.

In human biology, it is common to speak of a 'fight or flight' response to perceived danger. The two reactions are behaviorally linked in insects, as well. Thus, a second type of intraspecific disturbance sound is the patterned aggressive signal or *rivalry song* that is used to settle competitive interactions between individuals an example of which is shown in Fig. 8.9. Another example among bark beetles was mentioned previously (see Chapter 5). However, the role of aggressive acoustic signals has been most thoroughly studied in crickets (Case Study 8.2).

Case Study 8.2: Aggressive Singing in Two Crickets, *Acheta* and *Gryllus*

He who fights and runs away, lives to fight another day.

Over the years at least since the Tang Dynasty (618–906 AD), cricket fights have been a popular sport in China. If two adult male crickets are caged together with just one burrow to hide in, they will fight over it until a winner is established. Escalating battles involve fencing with their antennae, flaring their mandibles at one another, and finally, grappling with each other (see Fig. 8.10). As the two males approach each other or engage in battle, they also produce an aggressive rivalry song quite unlike their sounds in other situations (see Fig. 8.9). When a winner is decided, actual physical combat declines. The subordinate cricket becomes unusually quiet, and repeatedly avoids encounters with the dominant one. Meanwhile, the winner continues to stridulate aggressively, as though boasting of his success.

What determines the outcome of these fights? How is this outcome maintained? In the early 1970s, two Princeton University biologists, L. H. Phillips and M. Konishi, decided to attack the question experimentally in each of two common cricket species, the house cricket *Acheta domesticus* and the field cricket *Gryllus pennsylvanicus*.

First, Phillips and Konishi marked adult males of each species with various combinations of silver enamel dots. Two previously unacquainted conspecific crickets were introduced at a time into a very small cage. Under these conditions, they encountered each other frequently and fought or demonstrated clear dominance. The procedure was repeated many times until a statistically sufficient number of encounters was recorded. Then, the losers in these matches were anesthetized and the tympana in their forelegs carefully torn. By electrophysiologically monitoring the responses of the tympanic nerve to recorded chirps, the investigators satisfied themselves that the crickets were deaf, their tympanal organs unable to respond to sounds of the frequency involved in aggressive chirps. Monitoring of the cerci and the subgenual organ in the foreleg showed these unable to register the stridulatory sounds as well. While the subgenual organs in the middle pair of legs responded to the chirps when they were played at supernormal intensity, control experiments ruled out any behavior effects of such responses under normal situations.

Having thus carefully established the subordinates' deafness, the researchers re-matched them with the previous winners. In all cases, the deafened losers immediately became extremely aggressive! They initiated combat and engaged in sustained battles, and often came to clearly dominate their former superior rivals. In a second series of experiments, the researchers chose sets of three or four crickets that had already established a dominance hierarchy in an empty aquarium. The lowest-ranking individual in these sets was then deafened and rematched in tournaments with all the higher-ranking individuals. In every rematch, the deaf cricket significantly increased the proportion of winning encounters.
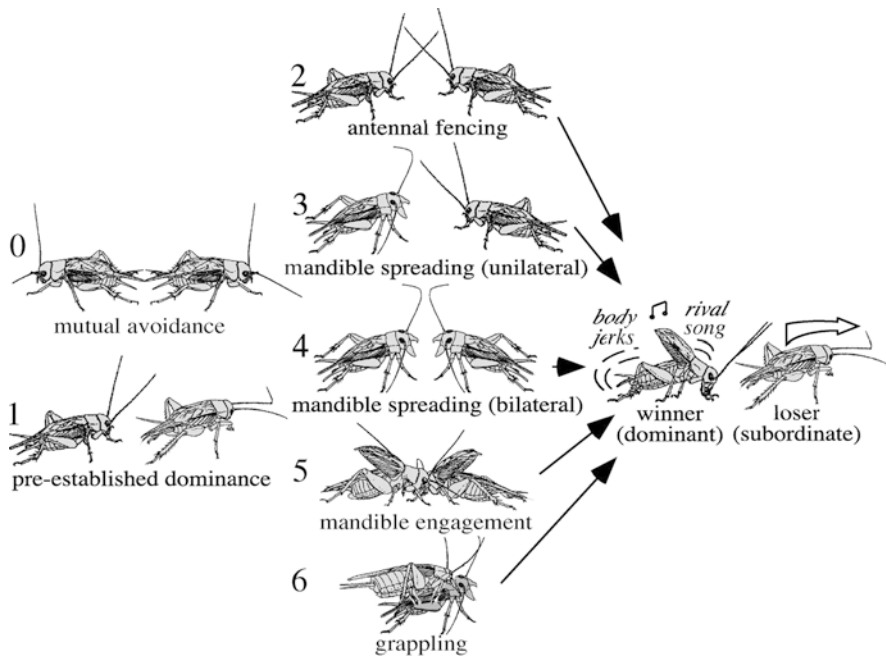
Fig. 8.10   Fighting for dominance. The stereotyped sequence of escalating performances characteristic of aggressive encounters between male crickets, moving from mutual avoidance (level 0) through to all-out fights with biting and grappling (6). At any point in the sequence, the fight halts if one opponent retreats. This establishes the winner, who typically bounces around singing a rival song

Figure 8.10 outlines the interactions that occur when two male crickets encounter one another. How can they be explained? One might assume that the acoustic signals of the dominant cricket's song inhibit the aggressive tendencies of the subordinate cricket and that inability to hear these signals frees a deafened cricket from this inhibition. This would account for the increased aggression that Phillips and Konishi's

deafened individuals displayed. However, in the rematches, the deaf individual did not *always* come out on top. Therefore, it seems likely that the probability of a cricket *winning* an encounter is additionally influenced by the existence of other factors as well. In fact, tactile antennal stimuli are also important. Research has shown that a dominant male can be 'defeated' by repeatedly exposing him to artificially produced aggressive sounds while lashing him with bristles simulating cricket antennae. Other studies with staged fights indicate that crickets use such antennal fencing to assess the fighting readiness of an opponent, and high willingness to fight may help crickets win fights even when they actually may have inferior fighting ability because they are younger, less experienced, or weigh less than their opponent. This is in line with game theory prediction that at least some behavior patterns displayed during aggressive encounters are used to assess asymmetries in variables that indicate fighting ability and resource value.

Territorial behaviors often involve aggressive/alarm sounds and vibrations. As is the case with many vertebrates, ritualized signaling seems to allow contestants to resolve contests without physical harm. For example, caterpillars of the hook-tip moth *Drepana arcuata* defend their silk nest sites from conspecific intruders by drumming and scraping their mandibles and specially modified anal 'oars' against the leaf surface in a ritualized display that sometimes goes on for several hours. As acoustic communication has come under closer examination, it is becoming clear that not only the hook-tip moth but a great many other Lepidoptera larvae (and probably many other insects as well) use acoustic signals to settle territorial disputes.

8.5.2 Aposematic Sounds and Acoustic Mimicry

Small insectivorous birds called tits will not approach stridulating *Nicrophorus* carrion beetles. Unless they are one of the few who are aware that male Hymenoptera cannot sting, most people will not go near a buzzing male carpenter bee. Syrphid flies hum like the bees and wasps that they mimic visually. Bats will avoid palatable mealworms shot into the air if the sounds of unpalatable arctiid moths are played concurrently.

It has long been noticed informally that many insects make warning sounds that indicate some sort of special capacity for defense such as noxious secretions, an offensive taste, or possession of chelicerae or a sting. A predator might, after one or several experiences, associate protest sounds with earlier painful feelings. Once thus conditioned, the predator would treat the sound as a warning to keep its distance. The ultrasonic clicks of certain moths (see Chapter 2) appear to serve as such a device.

A major theme in evolutionary biology is the use of visual signals that warn of special capacity for defense and the mimicry of these signals by other organisms, both protected and unprotected (see Chapter 5). By comparison with the extensive research attention these visually based phenomena have received, acoustic aposematism and mimicry remain almost uninvestigated but both may be more common than scientists have recognized.

A particularly well-designed study of acoustic aposematism included not one but three normally stridulatory taxa: mutillid wasps (*Dasymutilla*), water scavenger beetles (*Tropisternus*), and round sand beetles (*Omophron*). At night in the field under natural conditions, W. Mitchell Masters presented predatory wolf spiders with individuals of these three species that had been either surgically silenced or sham-operated. In all cases, the spiders gave up their attacks more quickly when attacking phonic insects. More of the silenced insects were killed, and more quickly. Then he constructed an artificial insect—a vibrating probe that mimicked the cuticle of a stridulating insect. When this was presented to the spiders, they also attacked it longer when it was silent than when it was vibrating.

Two maxims run throughout insect behavior. One is that whenever a behavioral outcome is really important, there will be back-up systems. The other is that whenever an organism invests in an important behavior, there will be others that attempt to exploit that investment. An excellent example of both maxims in practice involves night-flying moths and their major predators, the bats (see Chapter 2). As back-ups go, the tiger moth family Arctiidae has a particularly well-developed array of defenses and displays. Many retain distasteful or poisonous chemicals acquired from their host plants, and some species also have the ability to make their own defenses. Most advertise their multimodal defenses with bright coloration, unusual postures, odors—and in many of the adults, ultrasonic vibrations produced by vibrating the membranes of a tymbal organ on the metathorax. These signals interfere with the bat's ability to precisely locate flying moths, and they also help these nocturnal predators learn to avoid them. The tiger moth *Bertholdia trigona* goes even further, actively jamming bat radar with loud and steady broadband sound above the range of human hearing. Experiments show that when the moth's noise-making organs are disabled, bats easily catch and consume them; however, bats are almost never able to nab intact moths.

With such an effective array, it probably is unsurprising to find that other insects seek to take advantage of it. Acoustic aposematism is a defensive strategy that is clearly open to mimicry. Seeking definitive experimental evidence for it, William Conner and colleagues trained naïve laboratory-raised bats of two species to hunt tethered moths. Then each night they presented the bats successively with various combinations of noxious and palatable moths in varying order (see Plate 28). The bats fed normally on palatable non-mimics but within five nights, they had learned to avoid the noxious model. When a sound-producing Müllerian mimic was introduced starting on night six, bats avoided it for a full five days more. On day 11, to determine whether the bats were generalizing on the basis of the clicks, the researchers removed the moths' tymbals and presented the silenced moths. The percentage of tiger moths captured returned to control levels, but all of the moths were subsequently dropped rather than being eaten. Apparently other signals such as vibration or chemical cues were still active. To investigate possible Batesian mimicry, Barber and Conner conducted similar trials, this time introducing a sound-producing but totally palatable mimic on day six. Again, the bats avoided the mimic initially. However, a few bats of one species subsequently discovered its palatability, showing again what a powerful selective force bats are capable of exerting on mimetic

resemblance. Interestingly, some tiger moths also fly during the day where they are exposed to visually hunting bird predators. In the spring when birds are very active and bats less so, tiger moths tend not to produce their ultrasonic clicks, and those species active during the day are visually conspicuous, where their multimodal defenses also serve them well.

Acoustic mimicry can occur in contexts other than predator-prey interactions, of course. Courtship and mating provide another important set of behaviors open to exploitation. For example, males and females of the Australian bush cricket *Caedicia* normally sing in duets. However, when they cannot find a duet partner, some males perform an extensive repertoire of acoustic mimicry tricks instead. They make short-click calls that mimic the female's reply within a duet. They disruptively over-sing other males' song elements that are critical for the female's conspecific recognition. Sometimes they even make a call that mimics the entire duet. As they perform all this deception, they also search for the calls of any unmated female that might be tricked into a response.

8.5.3 Sexual Signals

Males and females of the Neotropical stink bug *Euschistus* communicate by alternating vibratory songs transmitted through plants. When male *Aphodius* beetles encounter a female in dung, they begin vibrating the substrate in a complex song that consists of a series of different patterns displayed in a specific order over a considerable time; females rarely stridulate, but seem to use the information within the song in the context of mate choice.

Acoustic sexual signals come in two types: long-distance acoustic signals (pair formation and calling sounds) and close-range signals used after the two sexes have come together (courtship and copulation sounds). Close-range acoustic courtship signals have received less attention than the louder and more obvious long-range calling. By definition, close-range courtship signals would include any sounds or intentional patterned vibrations that occur after pair formation and before copulation. Responses to acoustic courtship signals have not been widely confirmed experimentally; often, they are described only in terms of a female 'allowing' the male to copulate. However, most cricket species have both a calling song that attracts females from a distance and a courtship song that is given only when a female has come in contact with a male (see Fig. 8.9).

The acoustic behavior of more than half of the 1000 or so species of Orthoptera and Homoptera in North America and Europe has been studied to some extent, and pair-forming or calling signals have been experimentally demonstrated more frequently than any other kind of intraspecific acoustic signal. In no case has identical or confusingly similar sound signaling been discovered between sympatric species singing at the same time and place. However, closely related but geographically and/or temporally isolated species often have identical or very similar sounds.

In general, the evolution of these two aspects of sexual signaling appears to have proceeded quite independent of each other. It seems likely that the long-distance

signals are used mainly for species recognition, whereas the courtship song may contain information about an individual male's quality. If so, a calling song might be expected to be more stereotyped and less variable than a courtship song. Such a difference has been demonstrated in the field cricket *Teleogryllus oceanicus*; the higher variability in courtship songs did not depend on the response of the female being courted, because similar results were obtained when males courted dead females.

In long-range acoustic pair formation, one usually thinks first of a direct loco-motory response of a silent female to a single sedentary male's calling song, such as occurs in most crickets (Fig. 8.11). Such oriented movements in response to acoustic signals are called *phonotaxes*. Many variations in pair formation exist, however. Some involve elaborate visual/acoustic displays by both sexes. Others
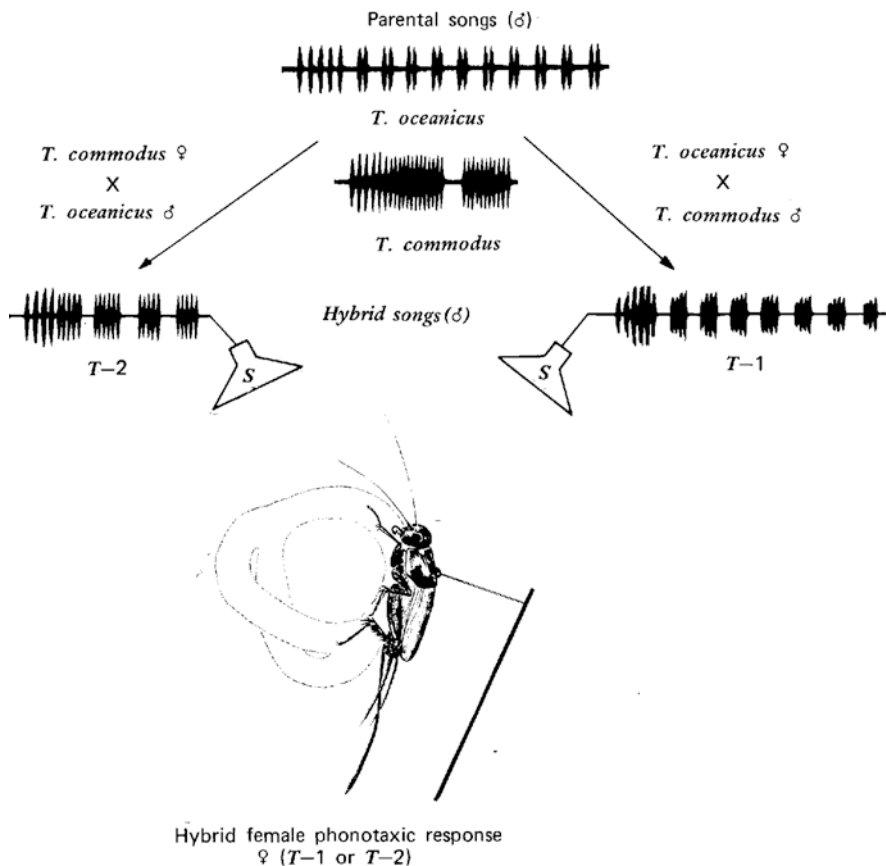
Fig. 8.11 Finding the singer. Positive phonotaxis used in experimental studies on the inheritance of song in hybrid *Teleogryllus* crickets. Walking along a featherweight Y-maze, tethered receptive hybrid adult females listened to different hybrid male calling songs played simultaneously by equally distant speakers, and revealed their preference at fork points in the maze

depend upon alternating and distinctive songs between males and females. Habitat ecology is undoubtedly a major determinant of the type of system that can be employed. For example, diurnal desert grasshoppers that live in open habitats can use visual–acoustic systems with ease, but tettigoniid grasshoppers that live in visually restricted habitats and have nocturnal and/or cryptic habits must rely more heavily upon strictly acoustic elements.

During long-distance pair formation, one also usually thinks of each species stridulating its own specific sex-related messages. If they do not, one immediately assumes some other clear-cut isolating mechanism, but sometimes the case is less well defined than this. One of the best examples of acoustically based reproductive isolation involves two sympatric grasshoppers, *Chorthippus brunneus* and *C. biguttulus*. Morphologically they differ only by a very few small, nonoverlapping characters. Although they have different songs, the two species are not separated ecologically. Studies by A.C. Perdeck showed that the two species would cross-mate and produce viable offspring in the laboratory, but very little hybridization occurred in the field. How could this be? Careful field study revealed that the major difference between the species lay in the degree of stimulating and orienting influence that their songs possessed. In the presence of its own specific song, a male moved faster and made more copulatory attempts; a female was also more ready to copulate in the presence of the song of her own species. Hybrid females would answer the songs of both hybrid males and parental males, but pure females of either parental species would not respond to the song of hybrid males, which was intermediate between the parental songs.

Long-range acoustic courtship signals are best known in cicadas, in some male Orthoptera (Acrididae, Gryllidae, Tettigoniidae), and in some Diptera, but there is suggestive evidence for their occurrence in males of many other arthropods. In the classic case, a male insect stridulates sex-related messages and the female receives them through her tympanal organs. However, sound production may also arise as a by-product of other activities such as flight, and in some species the sounds used in communication fall within the sensitivity range of hair sensilla and antennal receptors. These sounds could, and do, also attract the opposite sex. Predictably, the significant properties of these sorts of courtship sounds are rather different than for the songs of Orthoptera.

Mosquitoes are a case in point. Many mosquitoes produce an audible hum during flight, often so distinctive that some people can identify mosquito species solely by their sound. Astute observers have long known that mosquitoes react to sounds as well. Swarms of various species have been seen to alter their behavior following acoustic stimuli as varied as pistol shots, locomotive whistles, musical instruments, and the singing human voice. Furthermore, the antennae of male and female mosquitoes of many species are structurally quite different. The female antennal flagellum is about 2 mm long; the male flagellum, only about 1.6 mm. The flagellum of the male antenna is plumose, with many more hairs of varying lengths, and intriguingly, these hairs are absent in the males of some mosquito species for which acoustic communication has not been demonstrated. As though to underscore the hairs' importance, males that have them can change their positions relative to the

antennal shaft; most of the time the hairs lie flat, but they are raised erect during the period of swarming and mating.

Despite such circumstantial evidence for mosquito hearing, however, some careful studies were needed to prove its existence and unlock the details. The first researcher to elucidate the basis of mosquito sexual communication in detail was Louis M. Roth. Case Study 8.3 presents a few aspects of Roth's complex, wide-ranging investigation; the interested student may wish to peruse his original 1948 study for further detail.

Case Study 8.3: Sexual Attraction in the Mosquito, *Aedes aegypti*

Do mosquitoes listen to one another? If so, how? And what do they actually hear? Before some perceptive research, the acoustic basis of mosquito sexual communication was a matter of dispute.

In 1855, Christopher Johnston, a medical doctor in Baltimore, Maryland, discovered a sensory organ in the second segment of the mosquito antenna, and suggested it might play a role in mosquito hearing. Although the organ was subsequently named after him, until about sixty years ago, scientists were unwilling to give his observations a pivotal role in a behavior as vital to survival as sexual attraction. Instead, one researcher claimed that males were drawn to females by odor. Another postulated that the female's motion alone was sufficient for male recognition and attraction. A third suggest that knoblike projections (halteres) behind the wings of the female produced attractive 'birdlike' sounds both at rest and in flight.

As an entomologist in the U.S. Army during World War II, Louis M. Roth had his own hunches. Observing yellow fever mosquitoes, he had noticed that when a female mosquito was resting, she sometimes was surrounded by males, with some so near that they touched her, but he never observed them mating. It therefore appeared unlikely that odor or constantly produced sounds were involved. It seemed more likely, he thought, that male mosquitoes were attracted by the buzzing sounds produced by a female's wings during flight and that males received this sound through their enlarged antennal bases, which have conspicuous Johnston's organs. But how best to prove this?

Beginning with careful behavioral observations, Roth established that once male *Aedes aegypti* became sexually responsive 15–24 hours after emergence, they remained in a constant mating state through the rest of their lives. When he forced caged females to fly continuously, males attempted mating with them repeatedly; after a time, the females tended to resist further mating attempts but as long as they continued to fly, males continued to be attracted. However, when he killed female mosquitoes and presented them, the same males that had readily mated with flying females were indifferent to these freshly dead bodies.

Next, Roth exposed mosquitoes of both sexes to some mechanically produced sounds. He found no evidence that female *A. aegypti* were attracted to any, though they sometimes gave shock reactions to certain frequencies. Males, however, showed their characteristic phonotaxis and mating response to any sound in the range between 300 and 800 vibrations per second. This was true whether he produced the sound by a recording of another mosquito, by an audio oscillator, or by a tuning fork.

His hunch further strengthened by this, Roth fastened fine wire loops about the necks of female mosquitoes. Then he suspended them in a cage full of males. As long as a female hung with motionless wings, the males flying near her remained indifferent. Even when Roth swung the female to and fro upon her tether, they did not respond. As soon as she began to vibrate her wings, however, the males flying nearby immediately seized her and began to mate. To put the theory of attractive birdlike sounds from the halteres firmly to rest, Roth repeated the experiment again after surgically removing the halteres from some females and removing the wings from others. Males responded to the haltere-less females that still had wings and vibrated them. However, males ignored wingless females that still had their halteres.

What sets the range of sounds within which the male is attracted? Measuring the wing-beat rate of mosquitoes of different ages and sexes, Roth found the key in the sexual maturation of the mosquito. Mature females and freshly emerged males beat their wings at about the same rate and are pursued by older males, but young, freshly emerged females have a different wing-beat rate and are not pursued. Evolutionarily, it is a sensible system. By setting response limits such that only mature females are pursued, the likelihood is increased that the female has ingested a blood meal and that a mating will produce viable progeny. Young males avoid sonic misidentification and pursuit by older males by simply remaining quiescent until they complete their sexual maturation. By the time a male begins to fly, the sound he makes in flight is sufficiently high in pitch to be beyond the range that will stimulate older males.

Is the female mosquito's buzz simply a byproduct of normal wing flapping during flight? When Roth cut off greater and greater portions of their wings, the sound progressively decreased in volume while the pitch rose progressively. Yet males were attracted to and mated with females that had only part of their wings, even stumps, vibrating. This suggested that some basal organ might be the principal sound producer; subsequent morphological studies confirmed the presence of a stridulating organ at the base of the female's wings.

Spurred both by intellectual curiosity and by mosquitoes' obvious medical and economic importance, generations of researchers have continued to build on the

work of Johnston, Roth, and others. Their studies have revealed a very complex system, and the mechanical sensitivity of the male mosquito's antenna has been shown to exceed that of all other arthropod movement receivers studied so far.

Research on physiological aspects of mosquito acoustic communication was hampered initially by technical limitations and the antennae's morphological complexity and small size, but in the last decade or two, new technology has allowed new analyses. Studies show that because the antennal hairs are stiffly coupled to the shaft of the antennal flagellum, at the appropriate frequencies, the flagellum moves like a stiff rod rocking about in its socket. This stimulates the Johnston's organ at the flagellum's base. In both male and female mosquitoes, the antennae are resonantly tuned mechanical systems that move as simple forced damped harmonic oscillators when they are stimulated. The tuning of female antennae does not match the flight sounds of males or of females, but male antennae respond to a range of attractive frequencies that brackets the fundamental frequency of female flight sounds for their species. This bracketing occurs because hairs of different lengths have different best frequencies, with the result that males respond to a wider frequency band than would be possible if all the hairs were the same length. This may be an advantage in that it assures that females remain attractive even if they produce slightly different sounds because of such uncontrollable factors as size, wing damage, or extent of distension of their abdomen with food.

Is the resonance of the hairs themselves essential for mosquito hearing? Probably not. These same studies have shown that the hairs resonate at frequencies much higher than the best frequencies not only of female flight sounds, but of all arthropod sensory hairs known to serve as near-field sound receivers. For this reason, some researchers contend that the main function of the hairs may just be to increase the antennal surface. At this scale, they may also increase the drag force of air passing between the hairs on the antenna, much like a boat paddle dragged through water.

Earlier we mentioned acoustic tuning by males of *Toxorhynchites brevipalpis.* Despite the fact that the Johnston's organ is only slightly less sensitive in female mosquitoes than in males, most studies have investigated ways in which males are attracted to female flight tones. Gabriella Gibson and Ian Russell have done some of the first work to show that the auditory attraction phase of sexual recognition in mosquitoes involves interactive behaviors, just as in sexual behaviors of other insects. When they flew opposite-sex pairs of tethered *T. brevipalpis*, each mosquito altered its wing-beat frequency in response to the flight tone of the other, so that within seconds their flight-tone frequencies were closely matched or completely synchronized (Fig. 8.12). The behavioral thresholds in both sexes are about ten times greater than neural thresholds, differences that could be explained by neural processing (see Chapter 2).

Before leaving the subject of mosquitoes, it should be noted that once again, a vital activity such as courtship relies upon more than one sensory mode. Swarming *Aedes aegypt*i males have been shown to produce a volatile pheromone that stimulates the flying activity of females at a distance. Females also produce a volatile attractant that appears to act as an aggregation pheromone. The resultant pheromone-mediated swarm has been described as a 3-dimensional lek (see
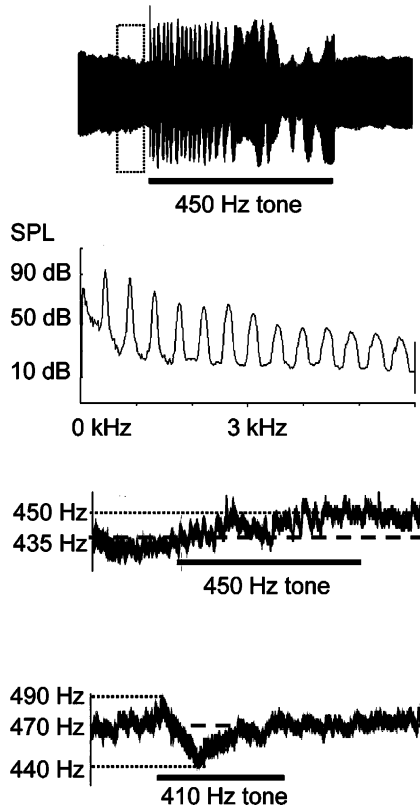
Fig. 8.12   Flying in tune. Responses of tethered flying *Toxorhynchites brevipalpis* mosquitoes show that males and females interactively synchronize their wing-beat frequencies to one another. (*above*) The flight tone of a flying male is shown as an oscillogram, with the frequency spectrum of the sound pressure levels (SPL) for the area outlined in the rectangle directly below. (*middle and below*)The lower two graphs depict spectrograms of a flying male and a flying female, respectively, over a 10-second recording; each shows fundamental components of flight tones before, during, and after a pure stimulus tone (*solid line*) was played. The male's spectrogram illustrates that his flight tone first exceeds and then converges with the stimulus tone. The female's spectrogram shows that her flight tone first drifts upward, then decreases without reaching the stimulus tone, and finally returns to the original frequency. Numbers on vertical axis indicate flight tone at onset of record, peak frequencies during the record (*dotted lines*), and final frequency. The *dashed line* indicates the flight tone in the second before the stimulus

Chapter 10), though there is still some question as to whether female choice is involved in these swarms.

8.5.4 Social Sounds

Pogonomyrmex harvester ants trapped in a small landslide stridulate loudly, attracting other workers who dig them out. Sibling groups of the sap-feeding treehopper

Calloconophora forage cooperatively; scouts that locate a new feeding site vibrate the leaf, and newly recruited individuals signal in concert with those that have already arrived. Hornets produce and are sensitive to a variety of sounds inside their nests. Honey bees initiate swarming in part in response to a contagious buzzing sound started by a few workers running excitedly through the hive.

Group-living insects range from those existing in simple aggregations to those that cannot survive outside of their complex societies (see Chapter 10). To be social necessitates having a way to integrate the cooperative behaviors of group members. Social communication is rarely restricted exclusively to one particular mode. Most often such integrative communication is primarily chemical, but sound also serves as an effective avenue of communication in social insects, often as a back-up and sometimes as a primary channel.

The interlocking combination of odor, sonic, and tactile signals that character-izes the communication system of the Douglas fir bark beetle (see Chapter 6) is a case in point. However, one of the classic and best-studied examples of the interac-tion of communicatory modes is provided by that classic social insect, the common honey bee. The behavior involved is recruitment to food, one of the most important adaptations of nearly all social insects. Case Study 8.4 outlines the story.

Case Study 8.4: Communicatory Interaction in the Honey Bee, *Apis mellifera*

Honey bee dance language remains one of the most striking, best-studied examples of mixed channel communication and of a highly complex transfer of symbolic information.

Beginning in 1919 with a few paint-marked bees and a flower enriched with a drop of sugar syrup, Austrian biologist Karl von Frisch began a series of thorough observations of honey bees that has culminated in what is proba-bly the best known example of complex insect communication in the entire world. In recognition of his pioneering work, von Frisch shared a Nobel Prize in 1973, the only entomologist to date so honored; behaviorists Niko Tinbergen and Konrad Lorenz received it with him. He continued to research honey bee communication for many decades and in the 1960s, published an outstanding summary of the work he and his students had conducted. The story continues to excite new research, and has become part of the shared human experience as the premiere example of symbolic communication aside from human language.

What was it that excited people so? Von Frisch had learned that a forager bee that found a good food source would bring back a full load of pollen and nectar to the hive. It would then fly out again to the food, thus establishing the most direct outward route. Back in the hive upon its second return, the suc-cessful forager communicated its vital information to others by performing specific, repeated, stereotyped behaviors, which von Frisch termed 'dances', upon the vertical face of the honey-comb inside the hive (see Figs. 8.13
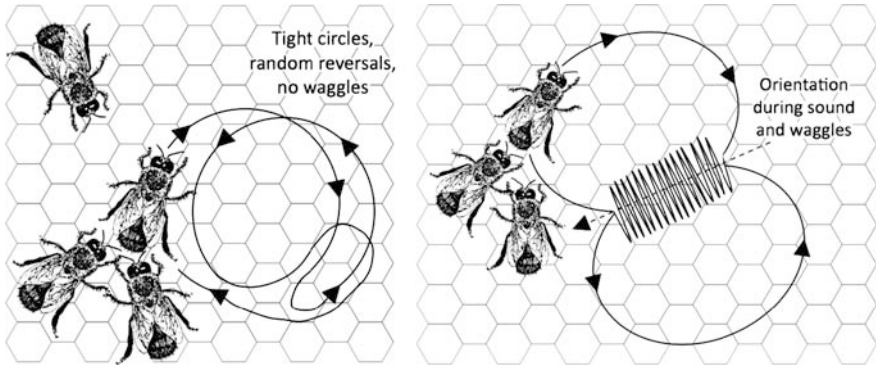
Fig. 8.13   Sharing good news. The dance language of a successfully foraging honey bee. *(a)* A forager locating a source of food close to the hive (within a distance that varies among strains) moves in circles of alternating direction, performing a *round dance*. Followers of the round dance obtain information that food is near. As the distance to the food increases, the round dance performance gradually changes to an open figure-8, then to the *waggle dance* (*b*) performed by foragers discovering food sources far from the hive. As the bee passes through the straight run portion of the dance, she waggles her abdomen rapidly from side to side. At the end of each straight run, she circles back to the beginning, to the left one time and to the right the next, so that the dance takes a figure-eight shape

and 8.14). In response, other foragers accurately flew directly to the food. The discovery captured the common imagination and excited the scientific community. Although observers had repeatedly noticed that a bee in a colony sometimes would perform repeated circular movements, no one had firmly established the connection between these movements and recruitment, and few had guessed the complexity of the communication.

One aspect of the forager's message was distance, which correlates with the type of dance the forager displays. Relatively short distances evoked a *round dance*; longer distances, a waggle dance. Within the *waggle dance*, a number of features also correlate with food source distance. Von Frisch's standard measure was tempo, which he measured as number of circuits (a waggling run plus the loop that returns the bee to the beginning of the next waggling run) per 15 seconds. Correlations also occur with the speed or length of the wagging run, the duration of the semicircular run, the duration of a single tail-wagging phase, and the number of tail wags during the straight run. How did the bee know how far it had flown? For a foraging bee, distance could be assessed in various ways. To von Frisch, the most important aspect seemed to be the energy that the bee had expended in covering it, because if a bee had to fly into a headwind or uphill or if it was forced to walk, it would report a distance farther than what was actually involved.
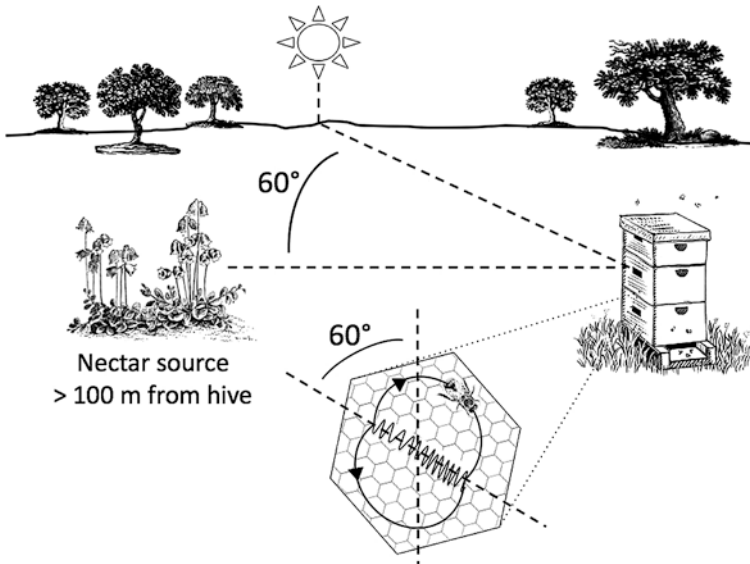
Fig. 8.14 Translating directions. When a forager waggle-dances to recruit others, her dance velocity and number of figure-eight shapes per unit of time indicate distance to the food source. Direction is more complex; whereas she learned the flight directions horizontally relative to the sun azimuth, her dance takes place inside the dark hive on a vertical comb. To translate this to her followers, the forager uses the direction upward as a reference for sun direction, and orients the waggle portion of her dance at the same relative angle. Thus, a cross-run angle of 60° to the left of the upward vertical axis as she dances means that the food was on a path 60° to the left of the sun-hive line, going toward the sun. Interestingly, on sunny days a forager will sometimes dance at the hive entrance; in this horizontal position, her tail-wagging run points directly toward the food source

The other aspect was direction. The angle of the tail-wagging run in the waggle dance with respect to the vertical is equal to the angle formed between the sun's position and the food source. Communication of this aspect is theoretically complex, because the dance is performed inside the hive out of sight of the sky and (because it happens on a vertical comb) it must be translated to occur with reference to gravity (see Fig. 3.6) rather than directly to the sun itself. Furthermore, using the sun as a directional reference is complicated by two problems—it moves, and sometimes it hides. Thus, both a celestial compass and perception of polarized light are involved.

Some returning foragers do not dance at all; others may dance a hundred circuits. As this would suggest, honey bee recruitment seems to be regulated in a way that allocates outgoing bees to the resources that most benefit the colony. The number of waggling runs a forager performs seems to indicate the overall value of the resource, and bees dancing to good patches seem to circle and dance more rapidly. Bees perform more dances to more sources of

nectar that are more highly concentrated or closer. When a colony is heat-stressed, they perform more often and more vigorously to water sources than to nectar sources.

A returning worker also changes her information in response to the activities of nest-mates with whom she interacts. When a successful forager returns home, other workers greet her and, if she is carrying nectar, they induce her to regurgitate her load to them. If many workers greet her enthusiastically, she begins to dance a round or waggle dance. If, instead, she perceives a long delay in unloading nectar or a shortage of receiver bees, she will perform a lesser-known variant called a *tremble dance*. Although von Frisch described this dance in the 1920s, it has received less attention, and its function was unclear until 1993 when Wolfgang Kirschner discovered that the tremble dance stopped nearby workers from flying to gather more nectar and switched them to unloading nectar.

How do followers sense the dance? Given that the dance language is communication, it is surprising how much remains undecided about this aspect of the system. One reason is simply the complexity involved; the dances provide such a rich variety of potential information that it remains difficult to know which information is actually being used and how it is being passed on. Another reason is that the dance features help followers find and stay with the dancer may differ from the features that carry the location signals.

Von Frisch emphasized the role of odors, specifically odors from flowers and other environmental chemicals that might cling to the bees' hairy bodies and be detected by dance followers. He suggested that the dances got bees into the flowers' general vicinity, then odors from the forager guided them in. In support of this idea, he noted that a powerful odor can even lead bees to ignore dance information and instead find the food that the odor signals. Foragers have in fact been found also to release an attractive pheromone as they return to a familiar feeding place.

Might hearing also be involved? One of the first to tackle that question experimentally with the aid of scientific instrumentation was Harald Esch, who had spent some time studying bees with von Frisch. In the 1960s, Esch built an artificial motor-driven bee capable of doing a waggle dance. When it was introduced into the hive, bees clustered around it just as they would a genuine forager, but no bees left the hive to search for food. Why? Perhaps the robot didn't sound right, Esch reasoned. So he placed a microphone in the hive to record actual dancing bee sounds. To his surprise, not only did the dancing bees produce strong sound signals with vibrations of their wings, but the period of sound production coincided exactly with the duration of the straight run of the dance. Since von Frisch had already found a correlation between the latter and the distance to the food source, a logical conclusion was that the bees might equally well be using sound as the cue to distance rather

than using the visual or tactile cues of the waggle itself. About the same time, Adrian Wenner independently discovered that sound was produced during the bee's dance. Produced mainly at 250 cycles/second, the sound occurs in bursts and the number of bursts correlates directly both with the distance and with the sugar concentration of the food. The pulse rate of these sounds is directly related to the rate of waggling, but they are approximately 2.5 times as fast.

Because the followers can be seen to have antennal contact with the dancer, other researchers noted that it is also likely that tactile cues are important. The speed of waggling could be sensed this way as a measure of distance. Contact could also be necessary in another way. By following the dancer and closely imitating the path of her dance, as many potential recruits do, they might obtain information on direction as their proprioceptors monitored this imposed movement. Von Frisch also showed that foragers could orient their dances either to celestial clues or to gravity through proprioreceptive bristle fields between the major body segments and the segments of the legs.

In general, as one moves closer and the insects involved become smaller, hearing grades into vibration and near-field signals, and finally to touch. Many studies have now provided evidence that dancing bees produce sound with their wings and followers detect these with their antennae. They also produce vibrations in the substrate that could be detected via the subgenual organs. At very close inter-bee distances, near field airflows are generated by the dancer's vibrating wings and by its waggling abdomen. Observations show that most follower bees place their heads directly into this zone of intense airflows. During the waggle run, there is substantial physical contact between dancers and followers. However, at all these levels, questions remain unsettled as to whether the information is precise enough and/or is used beyond some restricted circumstances.

What about vision? Though humans find it natural to describe what the dances look like, in the total darkness of the hive bees could not observe the dance and visually interpret its tempo. However, von Frisch recognized that vision might have an important role at an earlier stage: foraging bees might measure distance by monitoring *optic flow*, the streaming of visual texture across the visual field as an animal moves through the environment. He noted that bees flying to a feeder over calm water (which provides a weak optic flow) signaled a shorter distance in their dances than bees that had flown over more visually textured surfaces such as a wind-disturbed lake. Von Frisch was never quite convinced that optic flow was as important as his energy hypothesis as a way to encode foraging distance. However, through an extensive series of studies, Esch and others have shown that optic flow is probably not only the most important, but perhaps the only, odometer for foraging honey bees. Furthermore, they have shown that many of the experimental results that von

Frisch interpreted as supporting the energy hypothesis are also consistent with the optic-flow hypothesis.

With so many senses interacting, one finally must ask what systems are not involved in the honey bee dance. Even though bees can orient to magnetic fields in other contexts, so far there is no evidence that they use magnetic orientation in their dance. The evidence for orientation via landmarks is also equivocal; honey bees can use landmarks if they were first given the opportunity to see them in conjunction with celestial clues, but the role of this ability in nature remains to be shown.

When Karl von Frisch showed that bees could use waggles and circles to tell other bees where to find forage, he moved honey bees and their close relatives to front and center as a model of animal communication and social behavior. Ever since, biologists have been trying to figure out the details of how bees communicate this information and attract recruits in the darkness of the hive. Probably the most important lesson learned in that search for answers has been that important communication nearly always involves *redundancy*—more than one sensory modality acting simultaneously and generally reinforcing one another's messages.

Failure to consider such possibilities when analyzing communication systems can be a pitfall, as was illustrated by the so-called *dance language controversy* that arose in the 1960s when some researchers (particularly Adrian Wenner, Patrick Wells, and Dennis Johnson) directly challenged von Frisch's theories. suggested that even though the dances might contain spatial information, it was irrelevant to honey bee recruitment. No interplay of sensory systems was needed; odors alone were sufficient to explain the phenomenon. In fact, the entire concept of bee communication was unnecessary. Wenner, for example, asserted that bees are recruited solely by a conditioned response to food or odor. He felt that bees lacking experience with a particular food source have great difficulty finding it. Only a relatively few seem to be successful, and these take much longer to arrive than would be expected if they were flying a straight line between the hive and the source. Inexperienced foragers, Wenner suggested, locate the source simply by dropping downwind of the hive and then searching for the right combination of odors from food, locality, and other bees. Johnson and Wenner's experiments, done with strong scents and short distances, seemed to confirm their expectations.

Some of von Frisch's experimental results couldn't be readily reinterpreted in terms of an odor-only hypothesis, however. For example, when a hive is turned on its side so that bees cannot use gravity as a reference, they do disoriented dances. Under these conditions, recruits are less well oriented, even though odor cues have not been affected.

Normally, odor information and dance vector information are highly correlated. To settle the controversy, scientists knew they must tease these factors apart. In the 1970s, James Gould did this quite successfully in a set of experiments that

unlinked the location and odor of the foragers' food source from the directional information in their subsequent dances. He knew that if one shines a bright light from the side, dancing bees will use the position of this light as though it were the sun, and recruits will interpret it that way. However, if a bee's ocelli are coated with opaque paint, the bee becomes less sensitive to light, and this shift in reference does not occur. Gould set up a situation in which dancing recruiters with painted ocelli (and a reference of up, toward the sun) were followed by recruits with unpainted ocelli who were reading those dances relative to whatever angle the artificial light produced. In this way, he was able to show that recruits could interpret a direction from the dance that was independent of the direction to the food source. When given the opportunity to hunt for the forager's nectar source, these recruits searched principally in the direction predicted by the modified dance information. By the odor-only hypothesis, they should have still gone toward the true direction of the feeder.

Many other imaginative investigations also took place as the scientific community subjected these two varying interpretations to critical examination and experimental test, including development of a series of mechanical models and robots capable of mimicking various aspects of honeybee dances (Fig. 8.15). One of these was a computer controlled robot developed by Axel Michelsen, Martin Lindauer, and Wolfgang Kirchner that mimicked the behavior of a dancing bee; although it recruited rather imprecisely, changes in its dance caused significant shifts
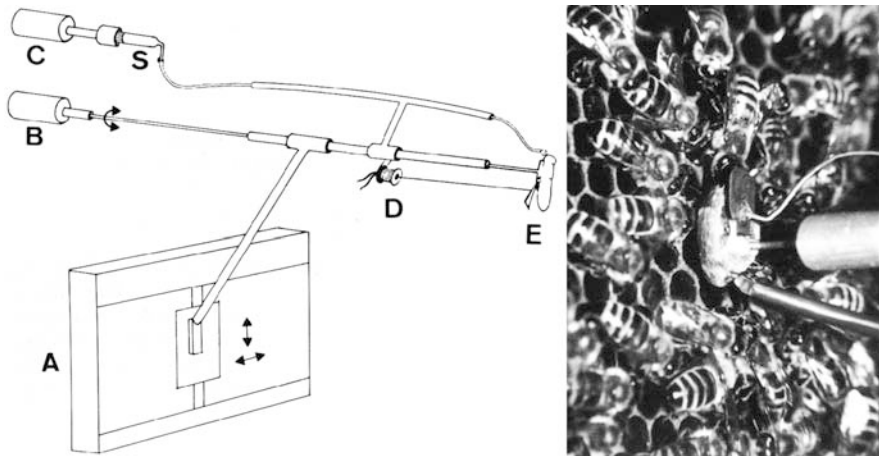
Fig. 8.15   Mimicking a forager. An example of a complex model developed to simulate honey bee foraging communication. *(left)* As an X-Y recorder (*A*) drives the model's figure-eight and wagging motions, a stepper motor (*B*) turns the model. Another motor (*C*) connected to a syringe (*S*) pumps scented sugar water through a soft tube to the front end of a beeswax-covered model, and an electromagnetic driver (*D*) from a bone-conduction hearing aid moves a wing (*E*) made of a tiny piece of razorblade. (*right*) Potential recruits surround the mechanical model as it performs a wagging run

in the search distribution of recruits in just the way that von Frisch's dance language theory predicted.

The odor search hypothesis has not yet been abandoned by its most loyal adherents, and unfortunately some philosophers and science sociologists have greeted the 'dance language controversy' as a welcome example of what they see as severe limitations of the scientific method. However, it is now clear that honey bee recruits can use either the dance language and odor information or odors alone, and they most probably can and do use other sensory inputs as well. The relative importance of these various inputs undoubtedly varies from one situation to another. Furthermore, as Gould has pointed out, the controversy might not have arisen but for the fact that while von Frisch and Wenner were both studying situations involving exploitation of an abundant food source, they focused on different stages of this process: von Frisch on the early stages of discovery, Wenner on later stages.

The general consensus now seems to be that sounds, comb vibrations, tactile cues from touching antennae, and odors all play roles in this elaborate transfer of information, and that additional signals will probably continue to be discovered. A study by Corinna Thom and associates in 2007 has added another component, semiochemicals (see Chapter 6) in the form of four cuticular hydrocarbons emitted by wagglers. Interestingly, the most energetic waggle-dancers produced the most copious quantities of these compounds.

How did such a complex communication system evolve? Seeking an answer, researchers such as Esch, Lindauer, and Kerr were among the first to focus on related stingless bees (Meliponini) that occur in the tropics. All 11 species of these social bees that they studied show some means of alerting their colonies to food, but the efficiency and degree of development of these communication systems vary greatly. In the simplest case, *Trigona iridipennis* workers that have found a food source simply fly back to the comb and excitedly run about, thus alerting other workers to the existence of food but not to its location. In the most complex case, a *Trigona postica* worker constructs a trail system of marks left at short intervals by rubbing her mandibles on convenient objects such as leaves to deposit mandibular gland secretions. Back at the comb, the bee then runs noisily about, giving out food samples. When a number of other bees have been acoustically and chemically alerted, the forager leads these bees along the scent trail. Such a system is of special advantage to these forest-dwelling species, because when living among trees vertical movements may be as important as horizontal ones.

James Nieh has shown that another stingless bee, *Melipona panamica,* sends and receives acoustic signals that allow inexperienced workers to communicate foraging information. Foragers trained to a feeder at the top of the jungle canopy make short pulses of sound while sharing food inside the nest, whereas those trained to a feeder at the forest floor make much longer sound pulses. Immediately after unloading, the forager dances briefly; sounds produced during this phase correlate with distance of the food, with longer pulses given for greater distances. Nieh did various studies in which he trained bees to a feeder, let these experienced foragers interact with inexperienced bees, then released only the inexperienced bees to find a new feeder

placed at the training location (Fig. 8.16). In this way, he showed that both distance and height of the food source are communicated inside the hive, but direction appears to be communicated outside, perhaps by following the foragers outside the nest for a brief distance.

Honey bees represent a very tiny fraction of the approximately 20,000 known species of bees. Among the present members of the genus *Apis,* the more basal species make single, exposed combs, while the more recently evolved species nest in cavities and have multiple combs (a development that has greatly facilitated their domestication). Martin Lindauer's pioneering study of three *Apis* species that differ in their nesting habits seemed to indicate a progression in complexity that appears to correspond to the phylogenetic development of the dance during *Apis* evolution (Fig. 8.17). On a horizontal surface, both *A. florea* and *A. mellifera* orient similarly (Fig. 8.17a). However, on a slope, differences are apparent. Dwarf honey bee dancers invariably orient to the sun's azimuth by using the sky horizon as a reference; placed on a slope, they compensate by head rotation (Fig. 8.17b). In contrast, true honey bees on a slope rotate both their body and head (Fig. 8.17c), so that the slope's plane serves as an apparent horizon reference for orienting to celestial cues. To Lindauer this suggested that dancing first evolved in an ancestral bee that built a single comb in the open and oriented to celestial cues but could not yet substitute gravity for the sun, much as *A. florea* still does today. Perhaps the earliest dances were simply excited, disorganized movements, but other bees were aroused by the excitement and thus were more apt to leave and search for food. In a later evolutionary stage, still on an open nest comb, dancers began to translate their solar flight angle into a dance angle relative to gravity and added acoustic signals. Over time, bees became able to use celestial cues when they were available and gravity cues when they were not, setting the stage for bees to begin moving their nests into the protection afforded by cavities. As intriguing as Lindauer's theory may be, however, there have been a number of objections to it, based both on taxonomic uncertainties as to ancestry of the various bees and on behavioral studies that have revealed more plasticity than Lindauer observed. Researchers' hopes for discovering 'missing links' in the shape of simpler forms of honey bee dance language so far have not been fulfilled, but however the story plays out, it promises to be an interesting one.

Before leaving the subject, it is interesting to note that elements of the bee dance also have been uncovered in a diversity of insects outside of the Hymenoptera. For

Fig. 8.16 Communicating food location. The tropical stingless bee *Melipona panamica* uses a wide range of communication techniques including sound. Some aspects of the information are shared inside the nest; other aspects, outside. In the three types of trials shown here, bees were trained to a feeder, then allowed to interact with inexperienced bees inside the nest. When the inexperienced bees were released to find food, (**a**) more found the training feeder high in the forest canopy than found the control feeder at the base of the trees; (**b**) many more went to the training feeder than to the control feeder that was closer to the nest; and (**c**) equal numbers went to the control feeder and training feeder when they were at equal distances but in opposite directions from each other
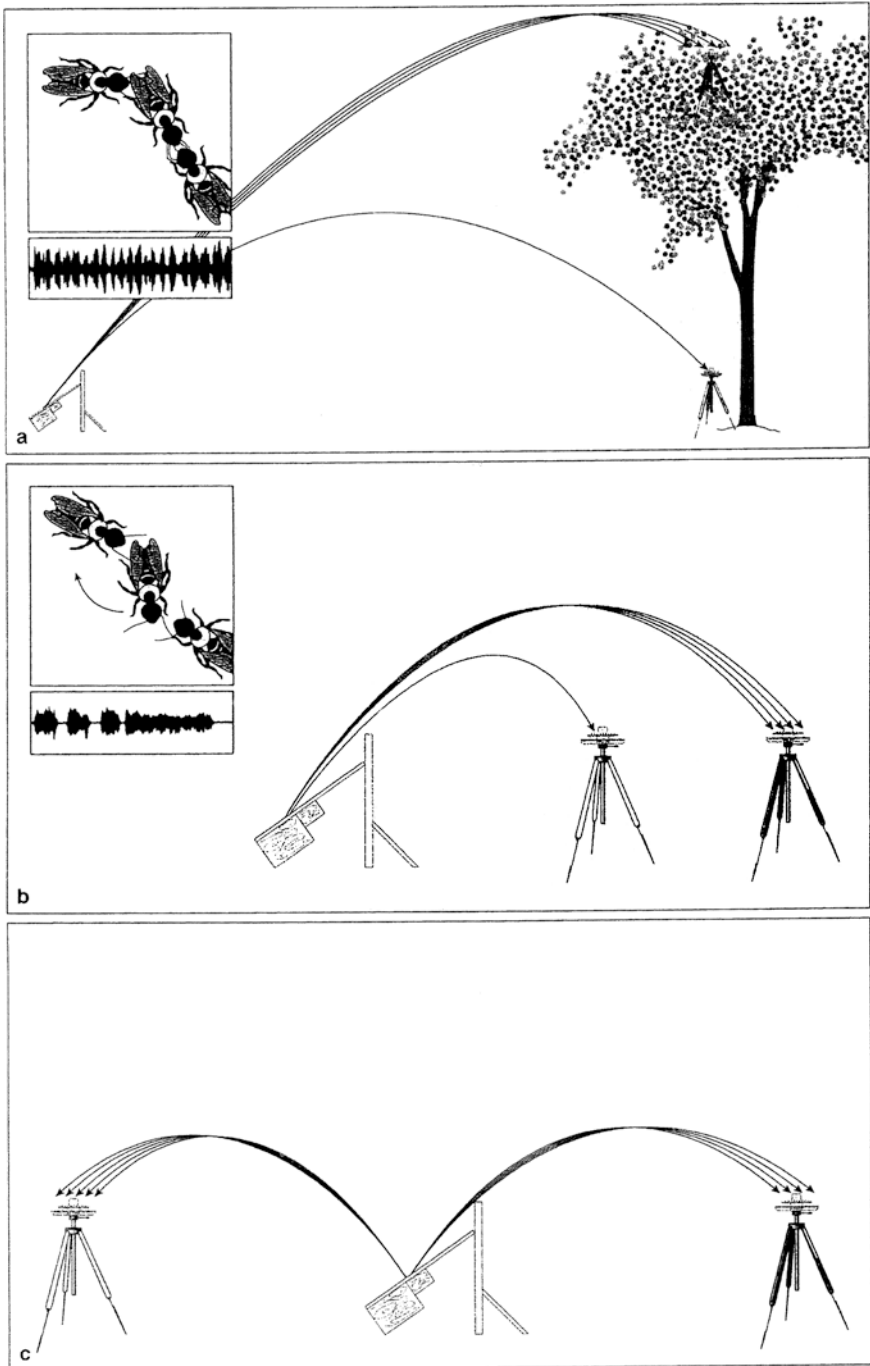
Fig. 8.16 (continued)
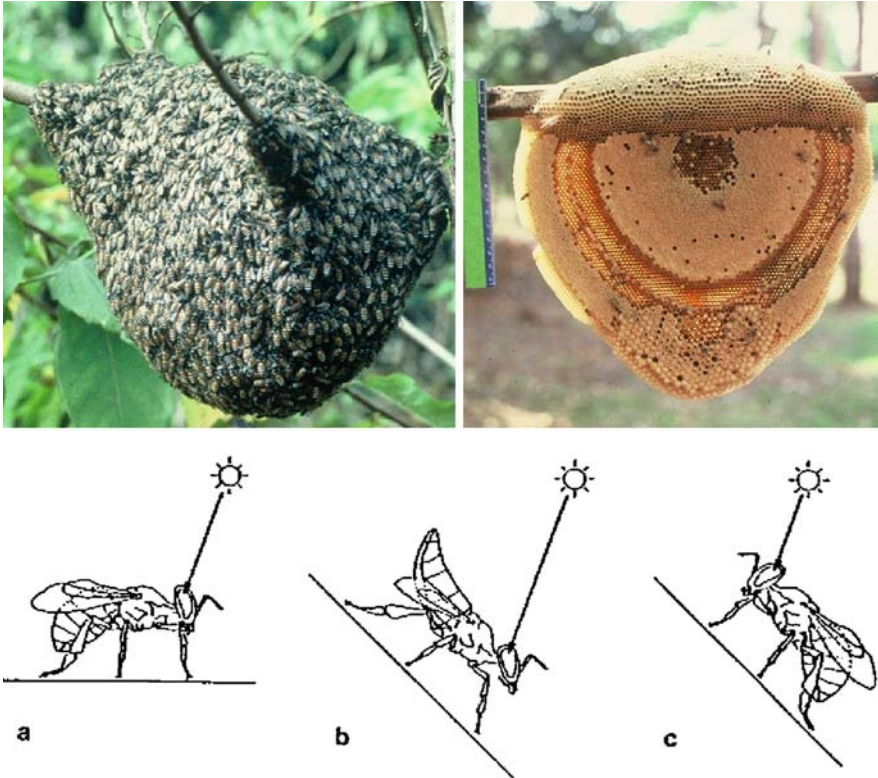
Fig. 8.17   Translating the sun. (*above*) The exposed nest of the dwarf honey bee, *Apis florea*, (*left*) with and (*right*) without the curtain of bees. Dances are performed on the upper horizontal surface of the comb and are oriented directly toward the source of the food. (*below*) Various bee species orient differently on horizontal and sloped surfaces (see text)

example, blowflies will perform a crude sort of dance after eating, with a vigor and persistence related to the distance the fly has flown after feeding. Some saturniid moths rhythmically sway upon settling down after any movement; the number of oscillations is closely correlated with the distance they have flown before settling. Of course, there is no evidence that these activities have any communicative function; they may be simple by-products of the physiological state of the insect concerned. But they do share the important characteristic of persistence, that is, they continue to be performed for a considerable time after the cessation of the activity that produced them. Such persistence is of paramount importance in communication, especially in recruitment of foraging bees. If such by-products were to come to signal the sender's state to another animal, then they would be ideal materials for the construction of a communication language. However, recruitment to food is considered primarily an adaptation to social life. Why should this be so? Sociobiologists point out that being able to recruit nest-mates to food sources allows insect colonies to capitalize on one of the major advantages of living in groups—the ability to harvest food

that would not be readily available to an individual foraging alone. At the same time, recruitment overcomes an inherent disadvantage of group life. Were it not for the compensation that recruitment provides, solitary individuals would have better access to food if they did not have to compete with and share with other group members.

Chapter 9
Reproductive Behavior

9.1 Introduction

'Lovebugs Menace Florida's Tourists' a recent newspaper headline declared. Not a bug at all but a fly, the lovebug (Fig. 9.1) does not bite or transmit diseases, nor is it a pest at picnic outings. How could such a poetically named insect constitute a 'menace'?

Aspects of insect sexual behavior already have appeared in several contexts in this book, from long-distance olfactory signals emitted by night-flying moths to visual attraction by fireflies and dragonflies. The use of sequential cues from a number of sensory modalities—a characteristic of the majority of courtship systems—was illustrated by the interaction of pheromones and acoustic signals in
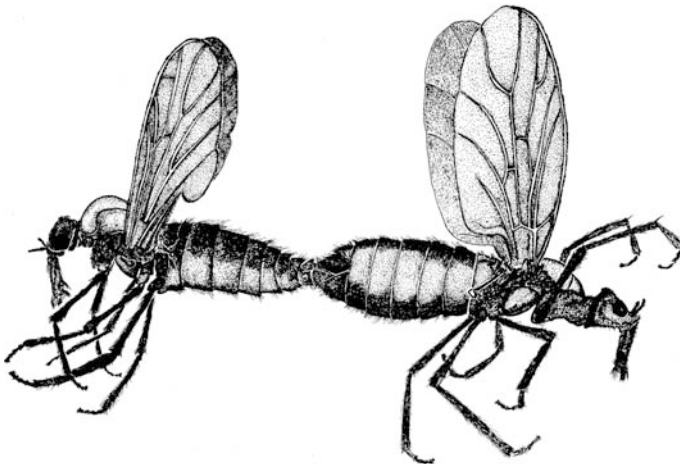
Fig. 9.1 Going to extremes. Lovebugs, *Plecia nearctica* (Diptera: Bibionidae), in typical copulatory position (female on the *right*). Attracted in large numbers both to car engine exhaust fume components and to engine warmth, mating pairs can be a serious problem for motorists in the southern United States. In the laboratory, lovebug pairs copulate for an average of 56 hours

Douglas fir bark beetles and the tactile, visual, and olfactory interplay involved in butterfly courtship.

These examples left several questions unanswered, however. Why are the courtship rituals of some species so intricate, even bizarre, whereas many others mate with apparently only minimal preliminaries? What factors influence the choice of a mate? Why are some species territorial? Why do individuals of some species mate but once, whereas others promiscuously?

Insect reproduction has been one of the most intensively studied aspects of insect biology in the past century. One reason is quite practical, based on the intersection between insect populations and our own interests in agriculture and human health. Learning about the reproduction of problem insects offers the promise of disrupting that reproduction and reducing the number of those insects in the next generation. The other reason is more theoretical, based on the diversity in insect reproduction, which provides a rich source of material for discovering underlying rules of biology. As intensively studied model systems in both field and laboratory, insects are ideal for addressing questions like these.

9.2 Courtship and Mating

After an extensive aerial courtship, a male butterfly places a packet of sperm into the female's genital opening. Bed bug males inject sperm subcutaneously into the female's blood-filled body cavity. A male damselfly transfers sperm away from his abdominal tip, freeing its claspers to grasp a female by the prothorax; the pair may fly about for hours in this tandem position (Fig. 9.2, Plate 33).

Sexual reproduction, nearly all biologists agree, has evolved because of the much greater speed with which new genotypes are assembled under this system. Such diversity, they argue, is highly adaptive. Sexually reproducing populations are more likely than asexual ones to adjust to changed environmental conditions through the creation of new genetic combinations. Thus, sexual reproduction has increasingly become the mode. In sexually reproducing animals, reproduction includes all those events surrounding insemination (the transfer of a male's sperm to a female) and fertilization (the fusion of a sperm and egg to create a diploid zygote). We are accustomed to the two events being closely linked, but in insects they often are not, because insemination can be either internal or external and can either be direct or through an intermediary step that involves a transfer container, or spermatophore (see Plate 29). In addition, fertilization can occur as much as years later because long-lived sperm can be stored in a special female pouch called a spermatheca. Thus, rather than spanning all of reproduction, the narrower term 'mating behavior' is used to describe the more immediate actions that surround insemination itself, from pair formation through courtship and copulation to the final breakup of the mating pair.

The reproductive behavior of the primitively wingless (apterygote) insects has received relatively little attention. In those that have been studied, an almost complete dissociation of individual males and females occurs, each sex reacting to a
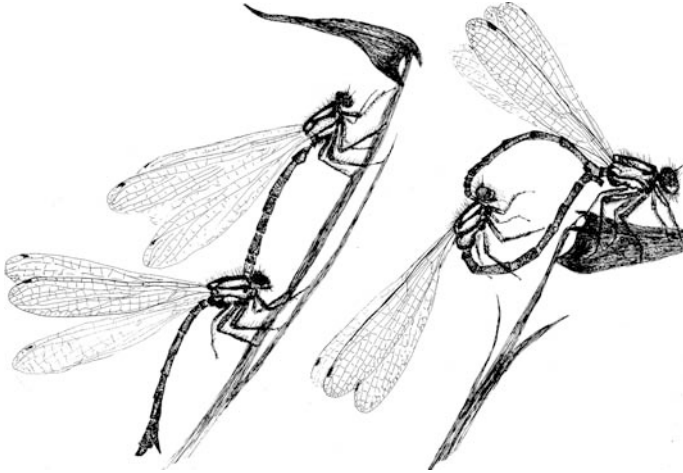
Fig. 9.2 Indirectly transferring sperm. Prior to copulation, the male of dragonflies and damselflies transfers sperm into a pouch-like structure on the underside of the second or third abdominal segment. During copulation, the female bends the tip of her abdomen forward to contact the male's accessory genitalia. The male (*above*) uses claspers at his abdominal tip to grasp the female's prothorax, thus completing the "wheel position" characteristic of this group (*right*). Pairs of damselflies or dragonflies often fly about for hours in tandem, the male holding the female by his anal claspers (*left*); in some species the female oviposits during tandem flight

spermatophore rather than to each other. Such indirect sperm transfer seems to characterize Archaeognatha, Thysanura, Collembola, Protura, and Diplura. In contrast, in most winged (pterygote) species, sperm transfer is direct, through copulation. For these insects, mating almost always involves chain-like interactions (see Fig. 7.9) that begin with searching for mates, move on to pair formation and courtship, and progress to copulation. For many, post-copulatory male behaviors culminate the reaction chain.

Given the human interest in courtship and mating, it is perhaps no surprise to find an enormous amount of published information on this aspect of insect behavior, nor is it unusual that different approaches to the subject have arisen. The field has become far too large to review comprehensively, but a brief overview can suggest some of the directions that are being taken.

Early research on insect mating behaviors was almost solely descriptive. As would be expected in a taxon as large as Insecta, the biological diversity in mating behavior is enormous. Just to chronicle variation in the manner in which copulation is accomplished has begun to produce an insect Kama Sutra. That task is still far from finished and it is still a useful approach, not only in its own right but also in providing the raw materials with which other analyses can proceed. Despite tremendous diversity in the ways they may accomplish their goal, however, most insects must solve a strikingly similar set of problems. They must find a partner, recognize it as such, comport themselves appropriately so that insemination will occur and be successful, and—for males—counteract potential sperm competition. Thus,

mating behavior studies increasingly are focusing upon broader and more theoretical questions of causation and organization, fitness consequences, evolution, and sexual selection in the context of costs and benefits to the individuals involved.

9.2.1 The Physiology of Mating Behavior

Females of the polyphemus moth, *Antheraea polyphemus,* start their distinctive calling behavior only after exposure to a volatile chemical, trans-2-hexenal, that is present in the leaves of their host plant, and then only at a specific time during the photoperiodic cycle. Allatectomized females of the Cuban burrowing cockroach, *Byrsotria fumigata,* fail to produce their sex pheromones and do not attract males; when active corpora allata are implanted or synthetic juvenile hormone analogs are injected into these females, their pheromone production ability is restored. Aging male *Nasonia vitripennis* wasps court more and more slowly.

For something as vital as attracting a mate, it is not surprising to find that insects use every sensory modality at their command, but chemical sex attractants certainly predominate (see Chapter 6). For indicating the location of a receptive potential sexual partner, the specificity and long-range effectiveness of pheromones are unexcelled. These may function as attractants, excitants, arrestants, identifiers of species and/or sex, or releasers or have several of such effects serially or concurrently. Either sex may produce them, and sometimes both sexes have their own, each with a distinctive role.

Neuroendocrine control of insect reproductive behavior tends to occur in those insects that have a long adult life, a life history that includes repeated reproductive periods, and a life span that includes time periods when mating is inappropriate or even impossible. Cockroaches are an example. For most insects that feed as adults and require neuroendocrine factors to mature oocytes, some type of neuroendocrine sexual regulation is the rule. In insects that do not feed as adults, such as many Lepidoptera, females from which the juvenile hormone-producing apparatus has been removed can still lay fertile eggs; in at least some species, however, neuroendocrine factors are still necessary for proper environmentally cued release of sex pheromones. For other insects that are very short-lived as adults—mayflies being an ultimate case—mating and oviposition must happen quickly before they die. With a premium on efficiency, mating is more efficiently built into the developmental process, appearing automatically with adulthood and divorced from extensive endocrine controls. Most insects fall between these extremes, of course. A common female reproductive pattern includes a single adult period of feeding and oocyte maturation, followed by mating and then by an oviposition bout (or bouts interrupted by additional feeding and often additional matings as well).

Not surprisingly, a great deal of research has focused on the triggers that switch insect reproductive behavior on and off, because such knowledge promises both theoretical and enormous practical benefits. Just as for much of the rest of the animal world, the triggers are usually different for males and females.

Male sexual behavior usually matures along with the metamorphosis of the nervous system; following ecdysis, expression of full copulatory behavior awaits only suitable stimuli. In most such cases, the corpora allata are not involved, although sometimes juvenile hormone lowers the male's behavioral threshold to the female. The endocrine control of male sexual behavior has been best studied in the grasshoppers and locusts, where some species require the corpora allata for the maturation of male sexual behavior. For example, allatectomy of newly ecdysed males of the desert locust, *Schistocerca gregaria*, and the red locust, *Nomadacris septemfasciata*, completely prevents the onset of male sexual behavior; if, however, several pairs of active corpora allata are transplanted into an allatectomized male, sexual behavior reappears.

Particularly among longer-lived insects that have a restricted breeding season, male sexual behavior often is modulated through an interaction between the corpora allata, the brain's neurosecretory system, and environmental parameters such as photoperiod. For example, under long-day conditions, males of some locust and grasshopper species show little or no sexual behavior, apparently due to cessation of neurosecretory activity in the brain. Sexual behavior resumes, however, when these uninterested males receive active corpora allata implanted from other locusts reared under short day conditions.

Female insects usually pass through three distinct behavioral states: young virginity, unreceptive to courtship; mature virginity, responsive to male advances; and mated, typically unresponsive toward males but showing intense oviposition behavior. The switch from one state to another is often abrupt and often hormonally induced. Hormones regulate pheromone production and release so that mating will occur at the appropriate stage in the reproductive cycle of the emitter and/or in the proper environmental context. Though chemical systems have received the most attention, neuroendocrine control of sexual signaling should apply equally to nonchemical communicative modes.

Cockroaches provided some of the first evidence that hormones mediate the onset of insect sexual behavior. About fifty years ago, Franz Engelmann reported that when he allatectomized newly emerged females of *Rhyparobia (=Leucophaea) maderae*, 70% of them never displayed sexual receptivity. When he reimplanted corpora allata, normal receptivity ensued. However, when other researchers attempted to duplicate Engelmann's results, to their surprise their allatectomized females became receptive and mated normally. To resolve the conflicting results, the researchers repeated their experiments together, this time both using Engelmann's cockroaches. Nearly all the control roaches mated, usually within a few minutes after the introduction of males. Allatectomy, on the other hand, once again led to a high percentage of non-mated females, and those that did mate required over an hour before males could induce them to copulate. The different experimental results were due to differences in the two laboratory populations, underscoring both the importance of heredity in behavioral studies and the dangers of generalizing from a single strain of laboratory animal.

In many species of insects, females will no longer accept courtship advances after successful mating. Female grasshoppers, for example, show secondary defensive

behavior rather than receptivity toward males once a spermatophore is placed in the genital tract. For some species, such refractory behavior is temporary; in others it lasts for life. A great variety of mechanical or chemical stimuli may be responsible. In some cockroaches that respond to mechanical stimuli, inserting a glass bead into the bursa of a virgin female will stimulate refractoriness. Other insects respond to chemical cues such as juvenile hormone withdrawal or the release of chemicals from the maturing ovaries. In many cases, secondary reproductive structures such as male accessory glands or female bursae release agents that trigger the switch.

An interaction between mechanisms is probably common, as has been shown in some Diptera; mating first results in a rapid neurally mediated refractory state, then is followed by a more slowly developing but more persistent hormonally induced response. As the bursa copulatrix of the yellow fever mosquito, *Aedes aegypti,* fills with seminal fluid, an immediate (probably neural) switch-off of receptivity occurs. However it is the action of a chemical (matrone) from the male accessory glands passing through the bursa walls into the hemolymph that keeps females behaviorally unreceptive to further mating for the rest of their lives. In fact, injecting matrone into the haemocoel is an equally effective way to produce refractoriness.

The implicit assumption that 'mated' equals 'inseminated' should be carefully evaluated in each case, because the two are different events. For example, although new adult female *Aedes aegypti* mosquitoes appear to mate readily as soon as they begin to fly, they actually are unable to accept the transfer of sperm for at least 24 hours after they eclose. Certain tiny parasitic wasp females will mate only once; thereafter they rebuff the overtures of the males that nevertheless persistently attempt to court them; an occasional virgin female, having been intensely stimulated by male courtship, reacts as though inseminated and thereafter behaves like a mated female even though her actual physiological status is still virgin. Such examples underscore the importance of using insemination rather than copulation as the criterion for a successful mating.

9.2.2 Reproduction Modes

The ways in which insects reproduce vary in three important aspects: whether eggs are fertilized, whether eggs are provisioned, and where embryonic development takes place. The most common method of insect reproduction is by yolked eggs, fertilized internally and laid outside the body. However, as one might expect in a taxon as large as Insecta, other means are not uncommon, and some species approach the task in quite unusual ways.

Take the matter of where embryonic development occurs. In Chapter 1 we considered oviparity, ovoviviparity, and viviparity among cockroaches, and it seemed quite straightforward. Oviparous insects, by far the numerical majority, lay eggs. Ovoviviparous insects do the same but retract their eggs back into a brood pouch to develop, extruding them into the world again once they become nymphs. Going a step further, viviparous insects 'feed' their developing young within the brood pouch with nutrients and water.

The overall picture is not quite this simple, however, because discrete terms cannot adequately describe a continuum, and insect reproductive modes clearly form a continuum. For example, several chrysomelid beetle species have embryos that develop in the ovary so quickly that they hatch a few minutes after deposition. Should they be considered oviparous or ovoviviparous? They do not differ essentially from close relatives in which the embryos hatch within the genitalia just a few minutes earlier. Furthermore, in addition to the reproductive modes mentioned above, insects also show a wide variety of more unusual types of development.

In a smattering of insects (and quite regularly among endoparasitic ones) each egg develops into a number of larvae rather than just one. This process, called polyembryony, theoretically would have the effect of increasing the reproductive potential of the insect involved, but because polyembryonic forms tend to lay fewer eggs than related 'normal' species the actual net effect is not always much greater. However, the metabolic costs are lower.

In other cases insect eggs develop without being fertilized, a situation known as *parthenogenesis*. Because it has been recorded as an occasional event in nearly every insect order, sporadic parthenogenesis is probably widespread when a female fails to find a mate. Clearly the phenomenon should have short-term advantages. When only female offspring are produced, a mother's immediate reproductive potential is much greater than if half the population is male, and a parthenogenetically reproducing female can spend all her time and energy in feeding and reproduction, without having to locate a mate and/or court.

Then why is sexual reproduction the rule, rather than the exception? The classic argument has been that over the long run asexual reproduction has an important drawback—it lacks the genetic recombination that normally occurs at mating. Sexual reproduction is favored because it allows selectively advantageous intergenomic recombination that promotes adaptation to and persistence in novel and rapidly changing environments; it also purges weakly deleterious mutations from the genome.

Debate arises, however, with certain predictions that arise from this cost/benefit theory. One is that the transition from sexual to asexual reproduction should occur frequently because of the short-term success of asexual lineages. The other is that asexual lineages should suffer rapid extinction as the disadvantages play out. From a phylogenetic perspective, this means that obligate asexual lineages should be polyphyletic and young. However, ancient asexual lineages clearly exist, and in a number of species, parthenogenesis has become the normal method of reproduction.

This is where cyclically parthenogenetic taxa fit in. A life history of alternating parthenogenetic and bisexual generations looks like an evolutionary compromise, and a successful one at that, for over 15,000 species in three animal phyla have been discovered to utilize it. Cyclical parthenogenesis suggests that there must be a short-term advantage to maintaining a sexual generation. If not, such taxa would be expected to rapidly move to obligate asexual reproduction.

In most of the cyclically parthenogenetic arthropods that are known, multiple asexual generations are punctuated by occasional sexual generations, with male production often triggered by a change in environmental conditions. Among *Andricus*
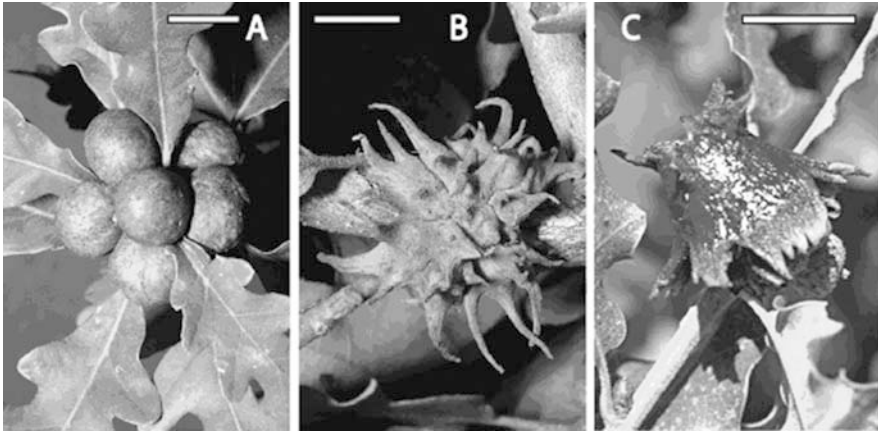
Fig. 9.3 Alternating diversity. Some cynipid wasp species produce galls on two alternate host plants at different stages of the wasps' life cycle; among other cynipids, asexual and sexual generations produce different galls on the same host plant. In some species of *Andricus*, a large genus of oak gallwasps, the adults of the sexual generation are morphologically quite similar, and the galls they produce are small and structurally simple. However, asexual generation adults are morphologically distinct and produce large, complex, structurally diverse galls such as those shown here for (A) *A. glutinosus*, (B) *A. coriarius*, and (C) *A. pictus*. Scale bars are 1 cm

oak and sycamore gall wasps (Fig. 9.3), however, sexual and asexual generations are produced in strict alternation. However, the adults and galls of the sexual and sexual generations are so different morphologically that historically they have often been placed in different genera. Furthermore, whereas the galls of the asexual generation are large, complex, and long-lived, those of the sexual generation are small, cryptic, and short-lived. Thus, it is not surprising that the sexual generations have been under-sampled and misidentified, and many fewer species are known only from a sexual rather than an asexual generation.

New light was shed on the debate in 2008, when an international team of researchers led by Graham Stone used molecular techniques based on analyses of allele frequency data to test for cryptic sexual generations in eight apparently asexual European species in the gall wasp genus *Andricus*, and found that cryptic sexual generations were widespread. Their results led support to the side of the debate that suggests either that selection acts against the loss of sex or that constraints make loss of sex difficult. The research team also found four *Andricus* species that appeared to reproduce only sexually; because no known oak gall wasps have such a life cycle, these discoveries imply the existence of unknown asexual generations in a genus that scientists had thought were quite well known.

Aphids provide another example of relatively well-known taxa that continue to yield surprises. Some aphids lay eggs. Others give birth to their young (see Plate 30). Still others are some of the few cases among insects in which immature insects are able to reproduce. Apparently as a result of a hormone imbalance, development of the offspring usually begins while the parent is still a larva itself. Most insects that

show such *paedogenesis* are also parthenogenetic and viviparous. When all of these phenomena converge into a single life history, the situation can become incredibly complex.

In tropical regions, most aphids are continuously parthenogenetic, but in temperate zones they have developed a complex alternation of generations. Throughout the summer, generations succeed one another so rapidly that while embryos are developing in a mother's egg tubes, they already have embryos developing in them. Thus, the female aphid is not only an expectant mother but an expectant grandmother! In autumn, males appear and normal sexual and oviposition behavior are resumed. Eggs overwinter and, upon hatching the following spring, resume rapid-fire parthenogenetic reproduction once again.

Overlaid upon this system there are usually also two other seasonal cycles: the occurrence of several aphid morphs (physiologically and morphologically distinct forms of the same species) and an alternation of host plants. For example, in Europe members of the first spring generation of bean aphids, *Aphis fabae* (see Plate 10), emerge from overwintering eggs on spindle trees, a species of *Euonymus*. This generation is entirely female and parthenogenetically produces either a winged female generation or several wingless generations of females which themselves give rise to winged forms. These migrate to bean plants, there to produce another series of wingless morphs. Ultimately, these produce both winged and wingless sexual forms. The winged aphids return to spindle trees and produce females; the wingless ones go on to produce winged males that then join those females to mate and produce winter eggs.

9.2.3 Complexity and Plasticity

Two closely related sympatric species of *Melittobia* parasitoid wasps differ strikingly in the occurrence and sequence of different elements of their courtship. In *M. australica*, males pump the female's antennae slowly maintaining continuous contact and only periodically lift their middle legs; complete courtship requires an average of ten minutes. Males of morphologically similar *M. megachilis* pump the female's antennae discontinuously in rapid alternation with an up-and-down movement of the hind pair of legs; courtship duration for this species is slightly less than two minutes. The two ecological homologues may parasitize the same host in a single back yard, but the different courtship patterns will not permit them to cross-mate.

As this example illustrates, insect courtship displays have at least three common functions: to promote the meeting of solitary individuals, to facilitate species and sex identification, and to stimulate and maneuver females into copulation. Among predatory insects such as robber flies and scorpionflies, an important additional function is appeasement, the inhibition of the normal predatory instincts of the participants, especially the female.

The traditional view of insect courtship and mating has been that these behaviors are relatively constant within a species and that, by differing from one species to
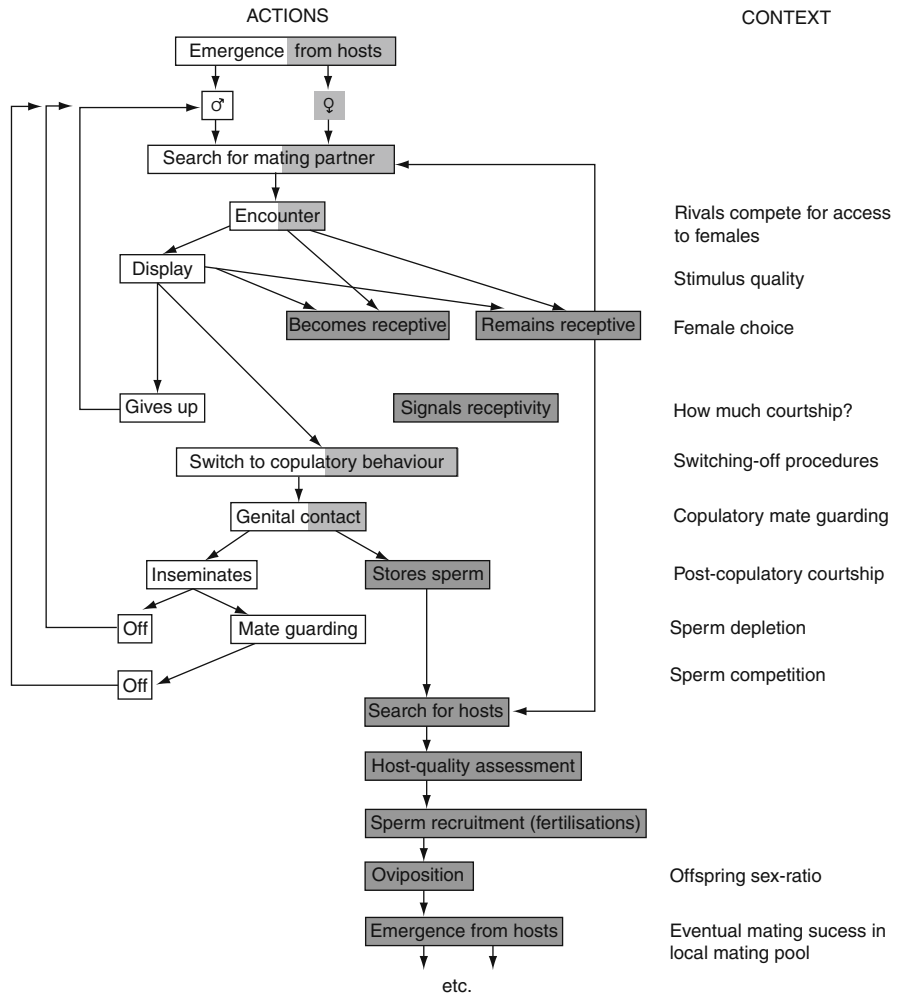
Fig. 9.4   Seeing the big picture. A schematic representation of the course of events in a typical mating behavior sequence. Shaded and unshaded parts of the boxes denote the contributions of the female and male, respectively

another, they serve as isolating mechanisms that effectively maintain and define discrete species. An attractive analogy (Fig. 9.4) states that insect courtship operates like a ratchet regulated by innate releasing mechanisms or physiological filters; at each stage, some signal on the part of one participant elicits a response in the other. This in turn elicits a new action by the initiator, and so on. Thus, the pair clicks along toward copulation while the ratchet mechanism precludes inappropriate mating or steps being performed out of sequence. Reproductive isolation is generally assumed to be a principal function of such a reaction chain.

Does courtship actually perform this function? To answer such a question, one must turn to analytical analyses of individuals reared in isolation in order to exclude learning or imprinting. As an example, consider the investigation in Case Study 9.1, which detailed the courtship reaction chain in crane flies.

Case Study 9.1: Courtship in the Crane Fly, *Tipula oleracea*

Crane flies generally look alike and tend to occupy the same sorts of habitats. What courtship cues do conspecific males and females rely upon?

Crane flies, which look rather like delicate, fragile, oversized mosquitoes, include a great number of species that are generally similar in appearance and tend to occupy the same sorts of habitats. While the males mate repeatedly, females typically mate but once. Under such conditions, a complex series of reciprocal signals would be predicted; in what specific ways might this be accomplished?

In the early 1960s, a Canadian researcher, H.J. Stich, raised crane flies in the laboratory and kept them isolated from one another as adults. When the adults were five days old, he began mating trials. The crane flies mated readily, in a rapid series of actions and reactions that sometimes took as little as 15 seconds and usually lasted only 90 seconds. Though the female often began the courtship by touching a male's long threadlike legs, it was apparent that the male took the most active role in courtship as a whole. True to the ratchet analogy, when Stich interrupted the courtship pattern by removing the female, reintroducing her never allowed the pattern to resume. Each time, the males began courtship anew from the beginning.

The first detectable step of the crane fly courtship occurs when two individuals happen to contact each other's legs. A male's response was to grab the leg with his own. Stich began amputating legs before introducing live females to males; six, five, four, three, two, or one leg—it made no difference to sexually active males. Only when a female had no legs at all did males fail to respond.

Next, Stich picked up amputated legs in his tweezers and offered them. Males immediately grabbed them. Was any discrimination occurring at this step? Apparently not in relation to sex, because dead males or their legs evoked the same grabbing reaction as females did. In fact, any leg-like tactile stimulus seemed sufficient—males even readily grabbed paraffin-stiffened threads dangled near them. But when stiffened threads of different thicknesses were presented, those of the 'wrong' diameter were immediately released. Stich repeated the experiment again, this time using legs of different diameters from other species of *Tipula*. Male *T. oleracea* grabbed at them all but immediately let them go. Here was Stich's clue to an initial discrimination that probably helped to ensure that the potential mate belongs to the proper species.

Stich observed that receptive females respond to the male's grasp by lifting one or more of their legs upward, and that afterward, the male assumed a mounting position above the female's body. What exactly was the female signaling with this behavior? To answer this question, Stich constructed a number of models. He found that males refused to mount the model made from a dead female with artificially stiffened legs, but they would mount a variety of movable models, even a simple 1 mm long wire if it were fashioned into a pair of movable legs. So, if to a male moving legs signify a female, what signifies another male? Stich repeatedly caged pairs of males together and watched their behavior. Males grabbed each other whenever their legs touched, but in over 100 trials neither of them ever responded by upward leg movement nor did they ever exhibit a mounting reaction.

After male leg-grabbing and female leg-lifting, a male crane fly tries to pin down the female's raised legs. Sometimes, this is accomplished in less than 3 seconds; at other times, the female may resist, and the ensuing struggle over leg position can extend over a period of 3 minutes. On the hunch that this great variability might be associated with sexual receptivity, Stich presented males with previously mated females; these readily elicited the males' grabbing and mounting reactions, but all their attempts at pinning down the females' legs failed. Sexually unreceptive females kept at least one leg continually raised, eventually causing the male to leave. Thus, previously mated or otherwise unreceptive females effectively terminate courtship attempts at this point.

After successfully pinning a female so that she remains motionless, a male begins to locate her head, by contacting her with his mouthparts while he moves progressively forward over her body. When he reaches her head, he touches his mouthparts to the back of it and stops his search. To determine the stimuli for this particular element in the courtship sequence (which Stich anthropomorphically called 'kissing'), the researcher exposed males to variously altered females (see Fig. 9.5). Male reactions to these models clearly indicated that both the female's body and her head were necessary as a stimulus at this point in the courtship.

Fig. 9.5 Searching reactions. Male crane fly behavior toward experimentally altered females. (**a**) Decapitated female: searching extends beyond the body until male contacts substrate. (**b**) Female head glued onto paper strip: male uses strip as guide to reach head, but percent completion declines as strip length increases. (**c**) Female head attached to end of abdomen, model presented so that male and female heads point in same direction: male orients toward head, attempts copulation through neck cavity
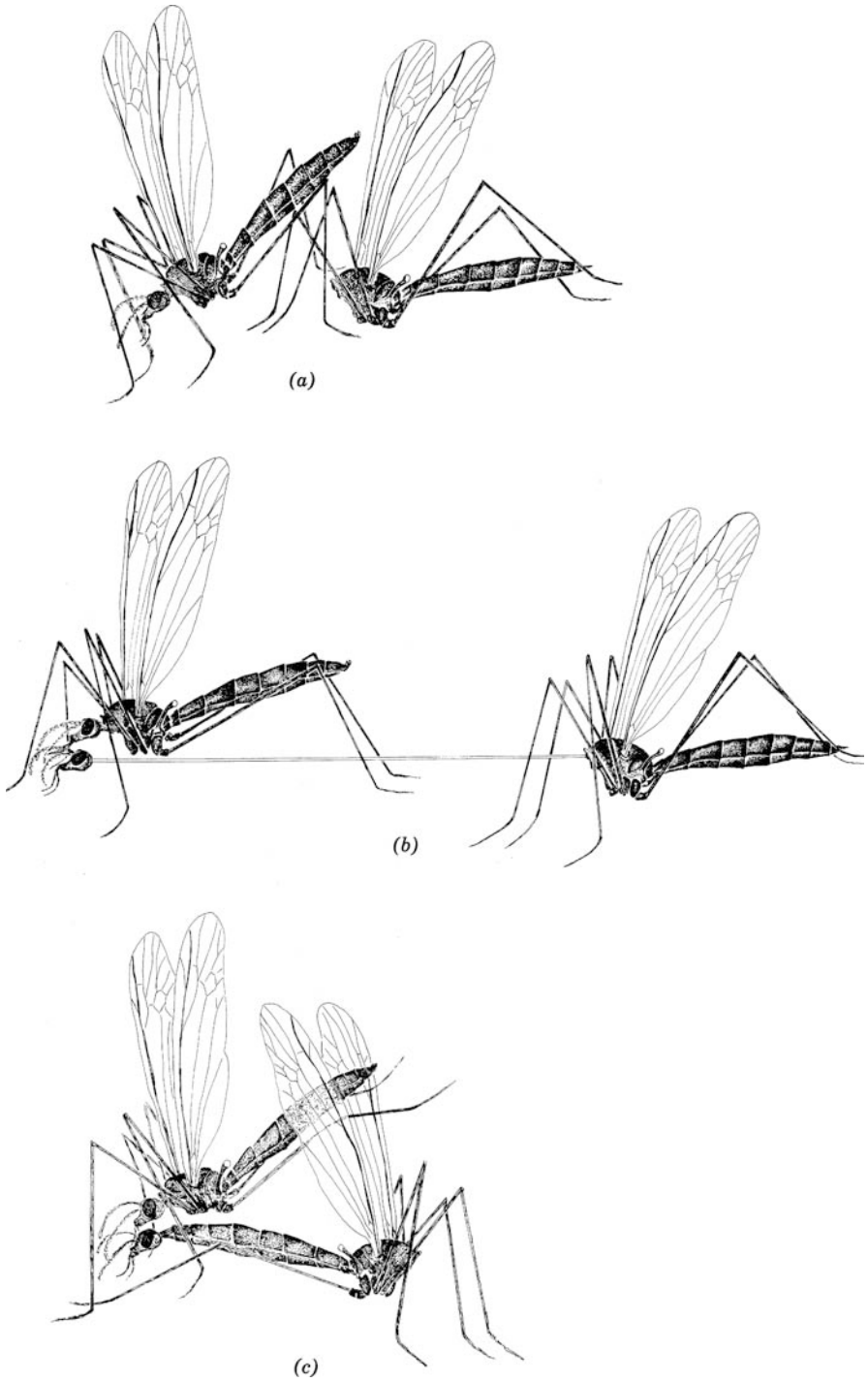
Fig. 9.5   (continuted)

The final step in the courtship sequence occurs when the male slowly steps backward, sliding his abdomen back over the female's, and bends his abdomen in such a way that the male genitalia come into contact with the female's. Does the female head or the 'kissing reaction' release this behavior? Or does the abdomen function as the sign stimulus? To answer, Stich removed the heads from females and attached them in various ways. Male responses to reversed-head females showed clearly that the head, not the abdomen, was the sign stimulus.

Thus, Stich was able to show that crane fly courtship facilitates discrimination with respect to sex, species, and physiological condition of the participants. At each stage of their courtship, different behaviors and different body parts are employed as specific signaling devices in a touch-oriented chain ideally suited for such weak-flying, drab denizens of the woods, and courtship proceeds like a rigid sequence of filters excluding all but conspecific sexually active males and receptive unfertilized females.

As this study illustrates, the use of experimental models can be particularly helpful in teasing apart the roles of individual behaviors in the complex interactive chains that characterize many cases of insect courtship.

9.2.4 Pollination and Male Reproductive Behavior

Approximately 65% of all flowering plant species are known to be insect pollinated. As a group, insect-pollinated plants generally have relatively showy and conspicuous flowers (which may however appear quite different to an insect's eye than to our own; see Plate 24). They produce pollen over a period of time and characteristically produce nectar as well. In contrast, wind-pollinated plants have rather small and inconspicuous flowers, generally lack nectar, and produce copious amounts of pollen in concentrated flushes. Corn is a familiar example; most grasses and their relatives are pollinated by wind, a not surprising fact since grassland habitats tend to be relatively windy and open. An exception to this rule, certain bamboo-like grasses that grow deep inside tropical forests where wind circulation is nil have secondarily evolved insect pollination systems, an example that serves to reemphasize the importance of ecology and especially population and community structure in understanding insect–plant coevolution.

Pollination is often closely interwoven with other aspects of insect behavior, and coevolved adaptations are common. One particularly striking case, the fig wasp, was examined in Chapter 4. A few other examples will illustrate some of the variety that occurs in the interrelationships between pollination and reproductive behavior.

Some of the strangest cases of insect pollination involve orchids. One of the two largest families of flowering plants, the Orchidaceae includes some 880 genera; there are said to be over four times as many orchid species as mammal species on this earth. Although most are found in the tropics of Asia, South America and

Central America, orchids are cosmopolitan, and occur in almost every habitat but deserts and glaciers.

While some orchids are self-pollinated and a few reproduce vegetatively, most require cross-pollination. However, orchids have developed highly specialized pollination systems and the chances of being pollinated are often scarce. In addition, orchid seeds are generally almost microscopic and very numerous, in some species over a million per capsule. After ripening they blow off like dust particles or spores. They lack endosperm and must enter symbiotic relationship with various mycorrhizal fungi that provide them the necessary nutrients to germinate, so that all orchid species are reliant upon fungi to complete their lifecycle.

In response to such long odds, orchid flowers usually remain receptive for very long periods and most orchids deliver pollen in a waxy mass called a pollinium (plural, *pollinia*) Each pollinium is connected to a stalk-like filament that ends in an adhesive pad (viscidium) that sticks to the body of pollinators; taken together, the entire apparatus is called a pollinarium (plural, *pollinaria*). In functional terms, this means that the whole pollen content of a flower is removed during a single pollinator visit and each time that pollination succeeds, a great many ovules can be fertilized, making pollination a high-stakes game.

In orchids that produce pollinia, pollination happens as some variant of the following. When the pollinator enters into the flower, it touches a viscidium, which promptly sticks to its body, generally on the head or abdomen. While leaving the flower, it pulls the pollinium out of the anther, and the springy stalk bends, moving the pollinium forward and downward into a (generally orchid species-specific) position such that when the pollinator enters another flower of the same species the pollinium will stick to the stigma of the second flower, pollinating it (Fig. 9.6). Bees, wasps, flies, ants, and moths are all exploited for orchid pollination in this manner.

Orchids go to great lengths to attract pollinators, guide them into the proper positions, and assure that pollinia attach to an insect body location where they will successfully be removed during the insect's next visit to their particular orchid species. The strangely contorted flower shapes that humans find so interesting are actually adaptations that guide insect visitors in ways that promote pollination. Sometimes, such promotion can grade into coercion. The bag-shaped bottom petal of one group of orchids traps visiting insects; the only exit leads to the anthers that deposit pollen on the visitor. *Catasetum*, a genus discussed briefly by Darwin, actually launches its viscid pollinia with explosive force when an insect touches it.

For nearly 700 specialized orchids in the Neotropics, the pollinarium system is carried even further. These flowers lack nectar, the usual reward for bees that visit flowers, but produce such strong species-specific fragrances that they are often called 'perfume orchids.' A bee attracted by the odor approaches a blossom from downwind and upon landing, alternately brushes the surface of the basal flower petal with his front legs, then hovers in front of the flower while scrubbing his legs together as if to transfer some substance to his hind tibiae. Individual bees may stay with a given blossom for up to 90 minutes, with repeated bouts of brushing and hovering–transferring. Toward the end of prolonged visits the bee becomes much less wary and its overall behavior suggests nothing less than increasing intoxication!
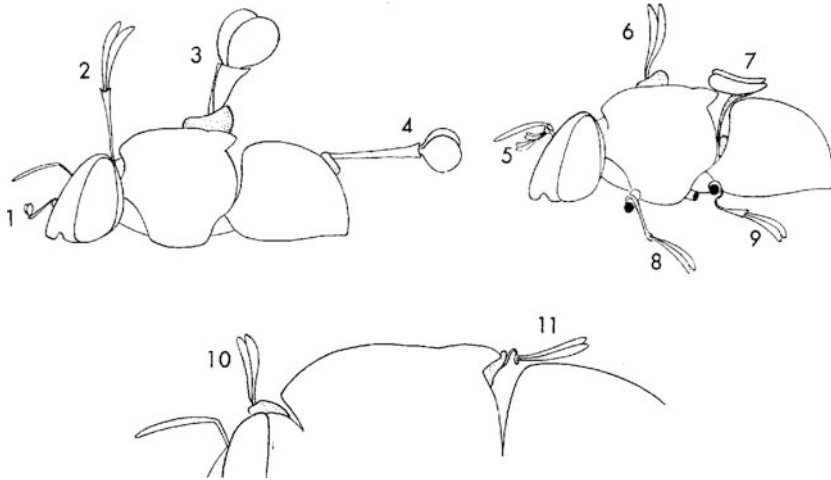
Fig. 9.6 Sticking to carriers. Outlines of Neotropical male euglossine bees showing the pollinia of 11 different species of orchid flowers, each deposited in a precise location on the bee's body. Upon entering a flower, the bee either squeezes down a narrow pathway and brushes against the sticky viscidium or triggers a mechanism that causes the pollinia to be ejected (sometimes with rather great force) onto its body. On a visit to another conspecific flower, the same sequence occurs, except that as the pollinator leaves, the attached pollinia are forced into the sticky stigmatic cavity on the flower and are removed before the insect receives its new pollinia

Charles Darwin provided an early description of this strange behavior; at the time, he believed the bees were females. However, this coevolved pollination scheme is stranger than he guessed. The pollinators, it turns out, are males in a bee tribe called the Euglossini; females never visit these flowers. These small, brilliantly metallic 'orchid bees' differ in many aspects of their behavior, but all euglossine males share two peculiar morphological traits: dense hair 'brushes' on their front feet and greatly swollen but hollow hind tibiae. They pick up floral chemicals from the orchid with special brushes on the forelegs, transferred from there by rubbing the brushes against combs on the middle legs, and finally these combs are pressed into grooves on the dorsal edge of the hind legs, squeezing the chemicals past the waxy hairs which block the opening of the groove, and into a sponge-like cavity inside the hind tibia.

The behavior of volatile collection is essentially unique in the animal kingdom, but almost 200 species of orchid bees obviously find it important. What's in it for the bees? It is clear that later, the males will release their fragrant chemicals at sites in the forest understory where matings are known to take place. However, the exact reason behind their fragrance collection continues to be elusive.

In southern Florida, USA, where perfume orchids are absent, an introduced orchid bee has become naturalized; an analysis of the contents of male tibial storage organs found 55 fragrance compounds, half of which were identical to those produced the bee's natural orchid mutualists in Mesoamerica. The fact that aromatic leaves such as basil can serve as important 'surrogate sources' of volatiles for the

bees suggests that the orchid bee/perfume orchid mutualism may be facultative for the bees, even though it is obligatory for the orchids.

As in other orchids, orchid bees collecting volatiles pick up pollinia specifically placed to ensure that cross-pollination only occurs between orchids of the same species, but for the orchid an added dimension of specificity has been obtained because each orchid species has a characteristic fragrance spectrum, and different orchid bee males are attracted to different chemicals. This can be particularly advantageous in the tropics, where plants generally do not grow in groups, and individual plants of the same species may be miles apart. Orchid bees are believed to forage on specific plants along set routes, a behavior known as trap-lining.

Over 60 distinct attractive chemicals have been isolated; one of the most common is cineole (Fig. 9.7). When tested alone under field conditions, cineole attracted 35 of 57 different species of male euglossine bees native to the area. But when one or more of the other compounds was combined with the cineole, the number of attracted species declined dramatically. Taking advantage of the specificity of this mutualism, scientists commonly use single synthetic compounds as bait to attract and collect euglossine males for study. The attractant compounds include many familiar flavorings and odors considered appealing to humans (such as methyl salicylate, eugenol, benzyl acetate, and methyl cinnamate), and others (such as skatole) that are not. The euglossine male *Eufriesea purpurata* is highly unusual in actively collecting the insecticide DDT in huge amounts from houses in Brazil, without suffering any harm from it.

Whereas perfume orchids simply offer chemical attractants, other orchids appear to offer the promise of sex—they have evolved to resemble female versions of certain insects. This sexual deception strategy is practiced by various Australian orchids and dainty Mediterranean orchids in the genus *Ophrys*. Known since the days of Pliny the Elder (23–79 A.D.), *Ophrys* flowers are commonly called bee orchids

Fig. 9.7   Smelling attractive. A male euglossine bee attracted to cineole daubed on the label of this commercial chemical

because even to human eyes the flowers of some species resemble the furry bodies of bees and other insects. Like the orchids above, these do not secrete nectar, nor is their pollen available to most insects. Female aculeate Hymenoptera are never seen visiting these flowers, but males of certain species of wasps, bees, and beetles approach the flowers, their mating instinct stimulated by chemicals exuded from the orchid's basal petals. At close range, the flower petals mimic female insects, attracting and duping the right pollinator. As they shift about, attempting to copulate (Fig. 9.8), the ardent males loosen the pollinia, which then stick to their bodies in positions specific to the orchid species involved.
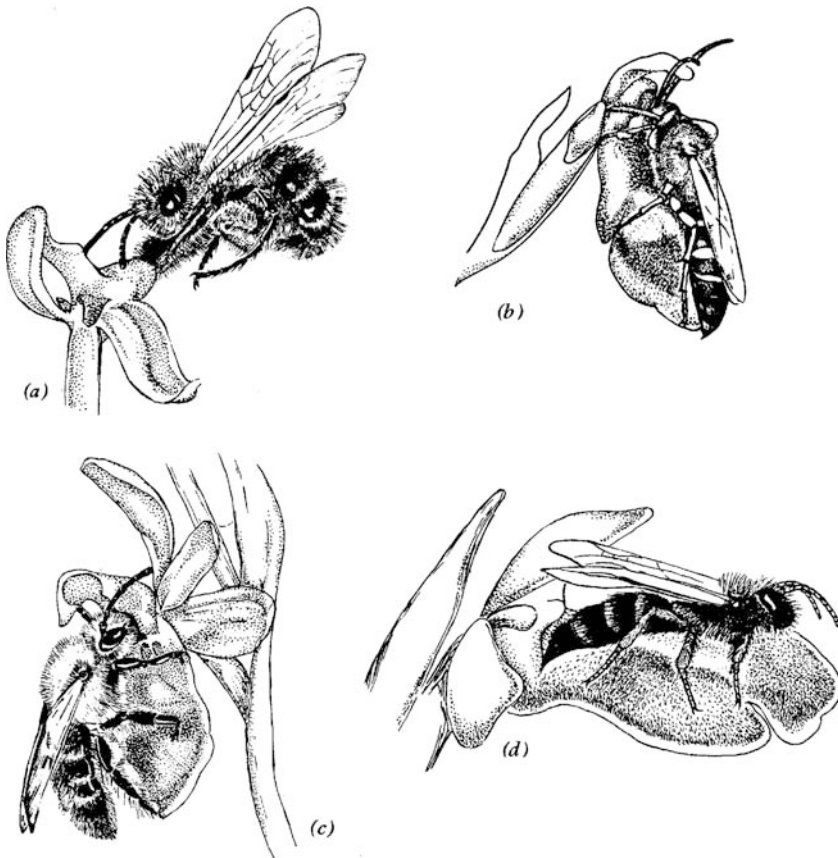
Fig. 9.8 Tricking pollinators. Flowers of the orchid, *Ophrys*, trigger copulatory behavior by males in a number of unrelated genera of aculeate wasps (**a, b**) and bees (**c, d**). After a chemically mediated attraction, vital tactile stimulation is provided by the form and construction of the orchid labellum and by characteristics of the hairs upon it, including their direction, length and grouping. Each of the approximately 30 *Ophrys* species depends upon different Hymenoptera species for pollination accomplished by entering the flower frontwards or backwards, depending on the insect species: (**a**) *Campsoscolia ciliata* on *O. speculum*, (**b**) *Argogorytes mystaceus* on *O. insectifera*, (**c**) *Colletes cunicularius* on *O.* "*arachnitiformis-sphecodes*" of *sphecodes* type, (**d**) *Andrena* sp. on *O. fusca*

Given the number of orchids in the world, more examples of pseudocopulation will probably be found. In Australia, sexually stimulated male ichneumonid or thynnid wasps assault quite unrelated orchids. In some cases the orchid's mimicry seems near-perfect. For example, the Australian hammer orchids (*Drakaea* spp.) have taken advantage of a mating ritual of a thynnid wasp species that involves a wingless female wasp waiting on top of a branch or plant for a male to spot her (see Fig. 6.7, right). The hammer orchid's flower mimics the female wasp looking upward for a male flying by, complete with a fake shiny head and furry body. The orchid even releases an enticing female wasp pheromone mimic. Place a real female wasp next to the orchid mimic, however, and the male wasp will spot the real deal. Probably because males get nothing in return for their pollination services, natural selection has favored flowers that bloom in the period when male wasps are flying but females are not yet circulating.

There is no reason to think that wasps and bees should be the only insects duped in this way. In 2005, *Bradysia* fungus gnat males were discovered to be the sole visitors and pollinators of at least four species of *Lepanthes* orchids. These orchids belong to one of the largest angiosperm genera, with over 800 species. Their tiny, colorful, structurally complex flowers offer no nectar rewards; given that most species in the genus have the same unusual flower structure, it seems likely that pseudocopulatory pollination will be found to be prevalent in this genus. The discovery that the fungus gnats ejaculate during their flower visit suggests that the term pseudocopulation might better be replaced by a term such as sexual deception.

Pollination is most often discussed as a feeding mutualism because generally we think of flowers as offering food such as nectar to the insects that pollinate them. Cases of deception in feeding evolution have produced many flower species that pretend to have food that insects want, emitting scents of coconut or even rotting meat (see Plate 9). Some evolutionary biologists have suggested that posing as a sexual suitor may not only facilitate pollination of already widely separated orchids, but may actually allow the geographic spread of plants over a wider area. After all, insect generally will travel further to find a mate than to find a meal. Testing such hypotheses will require further studies of both the mating behavior of the insect pollinators and the growth and reproduction of deceptive orchids.

9.3 Courtship and Conflict

Among some desert Orthoptera, silent satellite males become courtship parasites on calling males by intercepting females attracted to the acoustic signaling of the latter. In the parasitoid wasp *Megarhyssa*, males of three species gather and jostle one another even before a female emerges; when she does appear, conspecific males fight for access to her (Fig. 9.9). About 10 minutes before an adult female crab-hole mosquito leaves her pupa, males begin to congregate about the emergence

Fig. 9.9   Listening closely. Males of two ichneumonid wasp species, *Megarhyssa macrurus* and *M. greenei*, assemble over an emerging female. The stimuli that draw them to the site are apparently auditory but not species-specific; once the female chews out through the bark, conspecific males compete for the opportunity to mate, while males of the other species disperse
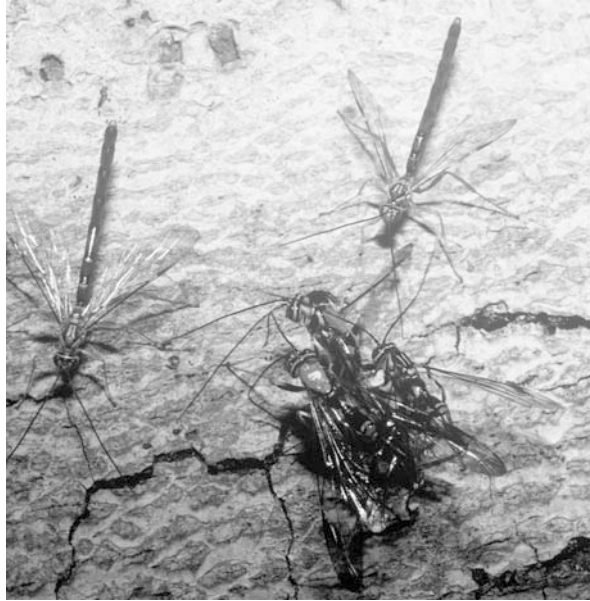
site. When the pupal cuticle begins to split, a frantic and violent scuffle breaks out between the males as each attempts to establish possession. The victor monopolizes the emerging female by standing over her and holding her in his legs; mating is established by the time she is free from the cuticle.

When the product of an interaction has the potential to yield different optima for different individuals or classes of individuals, conflict is the usual result, because each party in the interaction will be selected to manipulate the transaction in ways that move the result closer to its own optimum. Generally, these manipulations take one of three forms: persuasion, coercion, or force. In persuasion, one individual offers a fitness incentive that would increase the benefits provided to the other party. In coercion, one party (generally the one furthest from its optimum) attempts to gain control through actions that exert a cost to the other party. Force, of course, involves taking control away from the other individual by physical, behavioral or physiological means. The processes are not mutually exclusive, of course, and individuals often switch from one approach to another through time.

Sex would seem to be the ultimate social act. Yet, as Edward O. Wilson has pointed out in the context of social insects, in many ways sex can quite properly be considered an antisocial force in evolution. The 'ideal' society would lack conflict and would have a high degree of selfless behaviors and coordination, a situation most likely to evolve where all members of the group are genetically identical. Within the invertebrates, the highest forms of sociality are found in groups that create new colony members by budding—the sponges, tunicates, etc. Sexual

reproduction dilutes genetic relationships, causing a one-half reduction in genes shared among parents and offspring. Thus, a conflict of interest inevitably arises as each mate, parent, or offspring strives to increase its personal genetic fitness at the expense of others. In this view, courtship and sexual bonding are means by which organisms override the antagonism and tension that result from genetic differences induced by sexual reproduction. The complex mixtures of conflict and cooperation that result make reproductive behaviors both endlessly fascinating and challenging to study.

Darwin's theory of sexual selection remained dormant for almost a century after he proposed it. However, once resurrected, interest in the subject grew with amazing speed. For the past decade, the most active topic in behavioral ecology has been the variety of ways in which males and females pursue, persuade, manipulate, control, and aid one another so as to reach a common goal of producing offspring while still assuring parity for their own individual interests and resources.

Until the mid-1960s, researchers generally viewed mating as a sexually cooperative endeavor. Then, in an influential 1966 book, George C. Williams persuasively presented another viewpoint—an evolutionary battle of the sexes. His critical analysis suggested that because each gender essentially has its own best interests at heart, 'genic selection will foster a skilled salesmanship among the males and an equally well developed sales resistance and discrimination among females.'

One of the first predictive theories of mating behavior and sexual conflict to be based on individual selectionist thinking was the *polygyny threshold model* proposed in 1969 by Gordon Orians. Based on studies of birds and mammals, its simple premise was that females should select mates according to the quality of the male's territory and the potential for paternal care. The model (and the refinements and elaborations that arose from it) soon spawned a host of new studies on sexual selection, as researchers found that an emphasis on male behavior and the influence of ecological factors allowed them to generate a host of testable hypotheses. Developments in molecular genetics have further spurred this line of inquiry. DNA fingerprinting techniques are now routinely employed to assign paternity, allowing researchers to assess the connections between mating behavior and its genetic consequences.

9.3.1 Dimorphism, Sexual Selection, and Mate Choice

Male and female insects sometimes differ so dramatically that they look like two different species; in some aculeate wasps, in fact, matching has been possible only when males and females have been discovered *in copula*. Other males are armored (Fig. 9.10). Males of Hawaiian *Drosophila*, euglossine bees, Asian fireflies, and certain dragonflies repeatedly gather at specific sites where they display and compete for the attention of females.

Why do males and females differ in their appearance? Why are males so often the more elaborate sex? Why, for that matter, do individuals differ in appearance? And why do members of the opposite sex care? Dimorphism may be driven by

Fig. 9.10   Wearing weaponry. An 1869 illustration by Émile Blanchard, a prominent early French zoologist and entomologist, shows sexual dimorphism and the life cycle of a stag beetle *Lucanus cervus,* a well known species across much of Europe. Male stag beetles use their stout bodies and elaborate jaws to wrestle with each other for favored mating sites

food preferences, environmental factors, parasite load, or a host of other factors with no direct relationship to reproductive behavior. In some cases, each sex simply may belong to a different mimicry complex. Still, sexual dimorphism relates directly to courtship and mating in so many cases that such questions have interested biologists, psychologists, and philosophers from ancient times and are far from settled today.

The questions certainly were central in the mind of Charles Darwin as he tried to explain the evolution of what he and others called 'secondary sexual characters' (those not involving the reproductive organs), such as antlers on male deer. Natural selection alone did not seem to explain what he saw, so Darwin posed an alternative explanation—*sexual selection.* Competition for mates among the members of one sex, he reasoned, was responsible for the evolution of those traits peculiar to that sex, including all the various anatomical, physiological, and behavioral mechanisms involved in mate selection. This would include both traits useful in combat between members of the same sex and traits that increase the attractiveness of individuals to members of the opposite sex.

Sexual selection actually has a number of subcomponents (Fig. 9.11), but two major types of competition were apparent to Darwin. One depended upon choices between the sexes ('the power to charm,' in Darwin's words); this has been termed *epigamic* (or intersexual) *selection.* The other involved interactions between males (or less commonly between females); Darwin's 'power to conquer other males in battle' is now called *intrasexual selection*.

Epigamic sexual selection has been likened to a contest between salesmanship and sales resistance. As expressed by Edward O. Wilson:

The sex that courts, ordinarily the male, plans to invest less reproductive effort in the offspring. What it offers to the female is chiefly evidence that it is fully normal and physiologically fit. But this warranty consists of only a brief performance, so that strong selective pressures exist for less fit individuals to present a false image. The courted sex, usually the female, will therefore find it strongly advantageous to distinguish the really fit from the pretended fit. Consequently, there will be a strong tendency for the courted sex to develop coyness. That is, its responses will be hesitant and cautious in a way that evokes still more displays and makes correct discrimination easier.
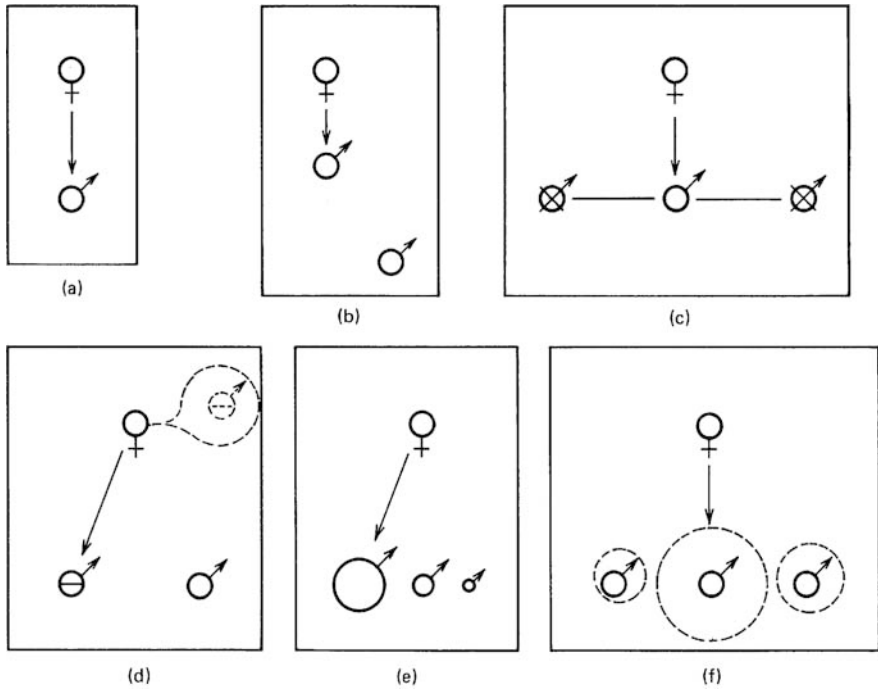
Fig. 9.11   Choosing a male. Types of mate choice open to females. (**a**) No choice, female accepts any available conspecific mate. (**b**) Female accepts most valuable mate. (**c**) Female accepts any victor of a competition among available mates. (**d**) Female chooses on basis of comparison against some absolute standard. (**e**) Female selects an extreme phenotype, simultaneously rejecting other equally available but less flamboyant males. (**f**) Female chooses among territories or position in a lek

At first glance, Darwin's sexual selection theory might seem a simple answer to a simple set of questions, but its implications are far-reaching. The subtle ways in which mate choices can influence male and female fitness are only beginning to be more fully appreciated.

Explaining how female mating preferences have evolved has been relatively straightforward in those situations in which a female's mate choice clearly influences her immediate reproductive success (fecundity). For example, in mating

aggregations based on real estate, males generally (but not always) defend territories, wait for arriving females, and perform courtship prior to mating. Many produce long-range signals to attract females. In these resource-based mating systems, *direct selection* has always been considered to have an important influence on mate preferences.

In other cases, the logic of female mate choice has been less apparent. Non-resourced based leks are a prime example. A *lek* is a gathering of males for the purposes of competitive mating display. In lek or lek-like mating systems, males' only contribution to females is their gametes; they are not involved in parenting, and if they have territories, they do not regulate a female's access to any resources that the territories may contain. Most matings occur in a mating arena, where females freely select a mate. Females have a wide choice of males with which to mate, and clearly prefer some to others. (Trivia-lovers note: A lek when females come together to compete for males is called a mung; this role reversal is rare, but occurs in the yellow-spotted millipede.)

Classical lek species were first identified in birds and mammals, and most lek research still focuses upon vertebrates. At first, it seemed that species could be strictly classified as to whether they had leks or not, but as more and more diversity has been catalogued, it has become obvious that lek-like behaviors should be considered as continuous variables that can differ independently with ecological conditions, taxonomic affiliation, and other factors. This consideration is particularly worth keeping in mind when confronted by the immense diversity in a group as large as the Insecta. In addition, some researchers consider leks to include mating swarms, whereas others see leks to include only substrate-based systems. Certainly, swarms occur in many non-mating contexts, and even mating swarms differ from substrate-based systems.

The so-called *paradox of the lek* has posed particular problems for evolutionists. Because females seem to gain no material benefits or parental care from males, it appears as though direct selection would have little relevance here. Furthermore, one would expect that persistent female choice for particular male traits such as elaborate ornamentation should erode genetic variation in them and thereby remove the benefits of choice, Paradoxically, both variation and choice persist.

A number of competing theories have been proposed to settle the paradox. Some emphasize male roles; others, female roles. The notion that females prefer clustered males because clustering facilitates mate choice is not consistently supported by field observations. In general, field and laboratory studies have failed to conclusively support one theory over another. The paradox might be somewhat alleviated by the occurrence of mutations introducing potential differences, as well as the possibility that traits of interest have more or less favorable recessive alleles. Moreover, if leks are composed of closely related males and larger leks attract more females, the paradox might be avoided because lower-ranking males could pass on their genes indirectly by helping attract mates for their brothers. Heated debate arose over two explanatory hypotheses: coevolution (and its famous extreme, runaway sexual selection) and good genes.

The first of these hypotheses rests on the understanding that lack of direct selection on a character does not exclude that character from evolving; indirect selection can occur on traits if they are correlated with traits under direct selection. In 1930, R. A. Fisher presented a brief discussion of *runaway sexual selection*, which was subsequently elaborated by others. The model postulated a sort of 'self-reinforcing choice' in which an initial assortative mating generates a statistical association between a trait and a preference that are both found in both sexes but only expressed in the appropriate one. When this genetic correlation is high relative to the heritability of the male ornamentation, as male traits evolve under the opposing forces of natural and sexual selection a correlated evolution of the female preference results. As a result, the trait and the preferences are exaggerated indefinitely as they continue to evolve. If the genetic correlation is somewhat lower relative to the heritability of the male ornamentation, the trait and preference will increase only until viability selection against further trait elaboration balances sexual selection.

Runaway sexual selection has been difficult to show empirically. Thus, it is often relegated to consideration as a null hypothesis when other explanations cannot be demonstrated. Evolutionary biologists note that the runaway process may be so rapid as to be unlikely to be observed and it can be difficult or unfeasible to conduct the experiments necessary to validate runaway. However, cases of genetic correlation between traits and preferences are beginning to accumulate, as is evidence showing that evolution of a trait can result in an evolutionary response in the preference.

A particularly clear example has been shown in studies of stalk-eyed flies (see Plate 31). When considered together, Wilkinson and Reillo's results, outlined in Case Study 9.2, provide very good support for a coevolutionary model of female choice sexual selection. Female mate preference changed as a consequence of artificial selection on male relative eye span. Because females were caged separately from males and selection was not exerted on females, the changes in female preference appeared to result from a genetic correlation between male eye span and female preference. However, Wilkinson and Reillo themselves admitted, their results did not exclude another competing model for the evolution of male ornamentation—the 'good genes' hypothesis.

Case Study 9.2: Female Choices in the Stalk-Eyed Fly, *Cyrtodiopsis*

Can female mate preference change as a consequence of selection on male traits? Little flies with huge eye spans gather in mixed-sex groups each evening, suggesting a way to test controversial mate choice theories.

Theories concerning the evolution of exaggerated male traits by female mate choice have been highly controversial. One theory maintains that male ornaments coevolve with female preferences. Another views male ornaments

as handicaps that signal increased viability. Still another holds that preexisting sensory biases for conspecific recognition lead to trait exaggeration. Gerald S. Wilkinson and Paul R. Reillo decided to test these models with a Malaysian population of a little fly that has impressive male ornamentation–stalked eyes separated by spans that often exceed a male's body length (see Plate 31).

Several aspects of the flies' life history suggested they might prove especially suitable for such study. Male eye spans are extremely variable, and such variation has been shown to be heritable. Previous field observations on Malaysian diopsids by other researchers suggested that eye span might influence mating success. During the day, the flies foraged alone, grazing on rotting vegetative matter. However, each evening, they moved to streams and formed aggregations on root hairs underneath overhanging stream banks. Each group consists of a single male and several females, with males attempting to displace one another from the root hairs as the aggregations formed. Males assess the body size of competitors by their head projection, and males of similar size engage in extended physical contests. Being the sole male in a roosting group was important, because mating occurred at dusk or dawn in the aggregations.

A few years earlier, other researchers had published studies on a related species showing that the male with the longest eye span usually won altercations between males, and that females preferred to alight on strings containing model males with the longest eye span. This seemed to be a classic lek situation—how, if at all, might a choice based on such a seemingly arbitrary choice as eye span influence female survival or fecundity?

Wilkinson and Reillo approached the question quite systematically. In January and October 1989, they counted male and female flies on root hairs along a Malaysian stream bank. To quantify sexual selection, they collected roosting flies at night, enclosing all flies on a root hair with a nylon stocking. Flies were frozen in liquid nitrogen in the field and kept frozen until they could be processed.

Analysis of their field data confirmed that females clustered, whereas males dispersed beyond random expectation. But were the females simply returning to the same microhabitats night after night, irrespective of the males that might be there? If so, the same sites should consistently contain more females. Statistical analysis said no; female aggregations did not appear to be determined by microhabitat choice alone. In the field-collected aggregations the number of females per site varied but the average number of females per male clearly increased with male eye span.

With this background, the researchers decided to observe flies more closely. They placed the insects in plastic mouse cages, fed them with ground corn twice a week, and hung strings in their cages as substitute root hairs. The flies lived well in captivity; groups of adults of both sexes could be sampled at

regular intervals up to 191 days old. Males could also be marked on the thorax with typewriter correction fluid to identify individuals.

Would the number of females per male in a caged aggregation estimate mating success? The researchers placed two males with different eye spans and body lengths into each of 24 mouse cages containing an average of five females. Then they counted and timed all the copulations for thirty minutes after dawn on two successive days. Each morning within an aggregation, most females mated repeatedly, but the larger male obtained 57% of the copulations. In the field, they speculated, the skew in his favor would be even greater because in cages females could not evade males and large males could not exclude small males.

But were females really reacting to eye span itself, or to greater body size? Wilkinson and Reillo scored frozen flies for eye span, body length, age, and if female, fecundity. They measured eye span and body length with a video digitizing system, and dissected each female to determine the number of mature oocytes within her abdomen. Following procedures established by others, they estimated fly ages from the amount of pteridine pigments in their eyes. Later, this information would allow them to examine the body size/eye span relationship and also female survival, fecundity, and other potential costs of female choices.

What would happen if they could directly compare female reactions to long and short eye-spanned males of the same body length? Measuring the ratio of eye span to body length in their population, the scientists selected ten males with the longest relative eye span and another ten with the shortest relative eye span. They mated each with 25 randomly chosen females. For thirteen generations, the scientists selected for long and short male eye span distances in this way. At the end of this time, they had two populations of males whose eye spans averaged a difference of 1.57–1.47 mm, and whose body lengths averaged from 0.05 to 0.01 mm.

To quantify mate choice in the presence and absence of male interactions, Wilkinson and Reillo decided to run four experiments. To make sure that past association with males would not influence mate preferences, the females from each selected line were caged together after eclosion without males until tested two to three months later.

For the first set, groups of five females were placed into a cage with two hanging strings and two selected line males. After two days of acclimation, the number of females with each male before daylight was counted. In 24 of 31 cages, more unselected females roosted with wide-eyed males, suggesting that male competition, female choice, or both occurred.

For the next three groups of experiments, male competition was excluded. Clear partitions set up across the cages allowed the flies to see one another

but the partitions were perforated with holes that were just large enough to allow females to move between the cage sides without allowing males through. (Food was available on both sides of the partition.) For experiment two, they used unselected females; as expected, the females preferred wide-eyed males. For experiment three, they used wide-eyed females; these also preferred wide-eyed male, but not to a statistically greater degree than in experiment two. This was surprising; if genetic correlation exists between male eye span and female preference, then selection for increased eye span should produce more choosey females. Reviewing possible explanations, the scientists decided it was quite possible that there may have been a difference that went undetected because suitable test males with extra-long eye spans were not provided. Supporting this idea were mate choice experiments with a related species in which females preferred model males with longer eye span than exist in natural populations. For experiment four, the researchers chose females with short relative eye spans; these preferred not long- but close-eyed males. In this way, they demonstrated a genetic correlation between female preference and a sexually selected male trait.

Might it be more costly for females to select large eye span males than to mate at random? If so, a negative correlation should exist between the relative eye span of the largest male in an aggregation and either female age or fecundity. In their laboratory analyses, Wilkinson and Reillo found instead that eye span of the largest male in a field aggregation correlated positively with female age, as estimated by amount of eye pigment. Thus, it appears that mate choice did not appear to impair female survival, but actually improved female survival. However, because other explanations for this correlation are possible, this conclusion must be approached with caution. One might also postulate that a longer life could be expected to yield more offspring, but the data fell short of demonstrating this advantage; the correlation between eye-span ratio of the largest male and female egg count was not statistically significant.

Fisher's theory begins at the point of rather arbitrary female preferences. As an alternative, Amotz Zahavi proposed the idea that females prefer to mate with males that have demonstrated their superior genetic quality for survivorship. He suggested that females evaluate a male's survival ability by assessing the magnitude of the handicap with which he is able to survive. Because many extreme sexually dimorphic traits increase male mortality, these handicaps to survival evolve as honest signals that allow females to assess male genetic quality. Thus, they serve as signals of 'good genes.' Several variations of Zahavi's original handicap principle (or *good genes hypothesis*) have been proposed. In one, because males without handicaps cannot be judged, females ignore them. In another, the handicap is condition dependent; a male's investment in the handicap varies with his condition such that he is optimizing the tradeoff between mate attraction and survivorship to maximize his reproductive success. The good genes hypothesis stirred up quite a bit of initial

controversy, but has come to gain much wider support since it has been shown that female preferences can indeed evolve if they are genetically correlated to the 'good gene,' which is taken to mean some heritable component for viability.

Evidence for the good genes hypothesis is lacking, but a number of studies purport links between female choices, offspring viability, and paternal genetic effects in a range of other animal species. Still it is important to recognize that costly displays by themselves cannot automatically be taken as evidence for female choice for good genes. Because mate choice involves communication, it always involves some sort of costs. The purpose of any signal is to increase the conspicuousness of the signaler against background noise; it can easily become an unintended advertisement to predators and parasites. There are physiological costs as well, either in the growth of a structure used as a signal or in the behavior of displaying the signal.

Increasingly, sexual selection studies are moving from antagonism between two competing theories to consideration of a much broader range of choices. In some cases, there is evidence that pre-existing sensory biases for conspecific recognition lead to trait exaggeration. Direct selection on preferences and pleiotropic effects can influence preference evolution. Furthermore, mate choice undoubtedly involves female attention to a whole suite of sexually dimorphic traits that are under sexual selection. Historical approaches have introduced a new dimension, as have the modern phylogenetic methods.

Direct selection, runaway selection, selection for good genes, and such are often portrayed as though they were mutually exclusive hypotheses, but in fact they may represent something more akin to the ancient tale of the blind men's encounter with an elephant, with each describing a different aspect of the same reality. Thus, former contentiousness between the holders of mutually exclusive hypotheses seems to be yielding to a new emphasis on the relative strengths and influences of these different forces when they act simultaneously.

9.3.2 Intrasexual Competition

Males of some damselflies scoop rivals' sperm from the genital tract of females they have mounted. Desert *Centris* bees gather around spots where females are emerging from the ground and jostle with one another; larger males tend to be the winners, with smaller males reduced to finding females that are missed in the first go-around. Male *Heliconius* butterflies guard females that are still within their pupal case, driving off rival males (Plate 32).

Intrasexual selection—which is almost always between males rather than between females—is based on exclusion of courting rivals. We usually think of this in terms of keeping other males from mating, often by intense fighting. Intrasexual competition is not limited to behaviors before insemination, however. Animals have developed a great number of ingenious post-copulatory devices as well. By far the greatest diversity of these occur in the insects.

Unlike vertebrates, female insects can store viable sperm from a single insemination for use during the remainder of their reproductive lives (several years in the case of some social species). At the junction where the female's pouch-like spermatheca opens to the genital tract, a sphinctor muscle parcels out sperm as eggs are laid. Scientists theorize that in cases where sperm are deposited in packets and maintain their cohesion during storage, they presumably would be used in the reverse order from which they were obtained. This 'last in, first out' principle, called *sperm precedence*, has become a widely accepted tenet of sexual selection theory, and there is evidence for it in many insect species. Its importance lies in the fact that it sets the stage for continued conflict because if the sperm of the last male to mate are the first to be used in egg fertilization, a late-arriving male would still profit by attempting to mate with an inseminated female. A second strategy is sperm removal. Odonata provide some of the best examples. The male of a pair of copulating *Calopteryx* damselflies (see Plate 33) spends most of his copulation time physically extracting sperm of other males from the female's spermatheca using his relatively elaborate penis containing recurved spines, hooks, and a scraper to accomplish this task.

Obviously, it is not to a male's advantage to have his own sperm subsequently replaced. How can he ensure that his sperm will be the most likely to fertilize the female's eggs? One way is simply to monopolize the female so that other males do not have access to her. Such a situation occurs in *Scatophaga stercoraria* dung flies. Continuing to maintain a territory has a similar effect, as does merely staying in physical contact with one's partner without actual genital contact; the tandem flight of many Odonata is a familiar example (see Fig. 9.2). So does prolonged copulation, which occurs widely among insects such as the lovebug (see Fig. 9.1), walking sticks, the queen butterfly, and the burnet moth (Fig. 9.12). Still another widespread device is the mating plug, formed by coagulation of male accessory gland secretions in the female's genital tract; such plugs prevent sperm leakage and/or physically prevent subsequent mating with other males.

Fig. 9.12   Prolonging copulation. The day flying burnet moth, *Zygaena filipendulae*, is widespread in Europe, but the majority of zygaenids are tropical. The moths have red spots on black, a warning to predators that they are distasteful; burnet moths contain hydrogen cyanide throughout all stages of their life cycle

After members of the courting sex have aggressively excluded a portion of the competition, classical intrasexual selection theory states that the more passive sex simply chooses a potential mate from among the elite group of winners or the single winner. In the process of acquiring a vigorous partner, he or she often also acquires something else of great value—a share in his or her set of resources. How members of the more actively courting sex partition these resources among themselves brings us to the twin topics of territoriality and dominance.

9.3.3 Territoriality and Dominance

Male carpenter bees vigorously chase a variety of small objects tossed near them. Male dragonflies drive off other conspecific males. Males of the ectoparasitoid wasp *Nasonia* defend host fly puparia from which females are starting to emerge. Mated females of the ectoparasitoid *Melittobia megachilis* aggressively fight other females that they encounter upon their host, ultimately partitioning the host into microterritories that are actively defended by amputating the legs and antennae of rivals.

The phenomenon of *territoriality*—broadly, any space-associated intolerance of others and, more narrowly, an intolerance based on real estate holdings—has long been well known in vertebrates, often in association with aggressive behavior. Among insects it has received less emphasis, but it is a surprisingly common and widespread occurrence.

Territoriality is almost always associated with competition for mates or food. Its function is to partition priority of access to resources that are limited and tied to a particular area. Territoriality is not always associated with overt aggression; some types of space exclusion can be settled solely through display. Nor does it even always require the owner's presence; some territorial insects such as female apple maggot flies depend upon persistent chemical marks that have a repellent effect on conspecifics.

Because territorial activities incur an expense of energy, selection for territorial behaviors tends to operate only under a limited set of conditions. One condition is that the desired but limited resource should be relatively localized in a readily defensible situation. Another is that animals should stand to obtain more of the resource by defending the area against competing individuals than by searching for new resources to exploit. For example, males of the cicada killer wasp, *Sphecious speciosus*, establish themselves on perches that overlook highly clumped nesting areas containing emerging females; investment in defense of these perches may be rewarded by extra copulation opportunities for the territory owner. Dragonflies and damselflies establish similar perches along the shores of ponds and streams (see Plate 33).

Territorial fights among vertebrate conspecifics are rarely fatal; when underlings assume various submissive postures, the combatants slow or halt their battle. In insects, in contrast, murder and even cannibalism may be routine phenomena. One of the more striking examples of aggression occurs among males in *Melittobia*, a

Fig. 9.13 Fighting spirit.
The loser never let go in this
battle between males of
Melittobia digitata; the
winner, despite his ball and
chain and the loss of the distal
portion of his right antenna,
subsequently completed
successful courtships with
several females
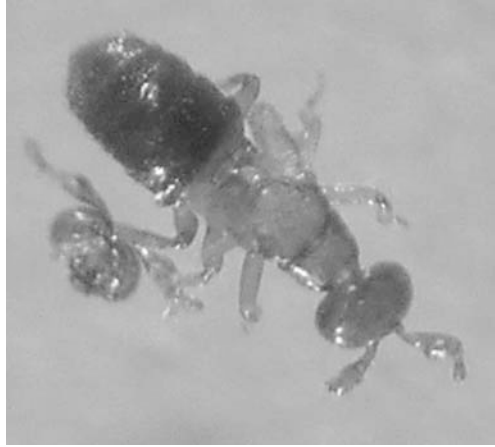
genus of tiny parasitic wasps. Predisposing their behavior in this direction is an
unusual breeding structure—males are incapable of dispersal and thus their only
mating opportunities are with sisters emerging from the same host. Upward of
150 progeny from a single mother develop gregariously and emerge from a single
host, with an overwhelming preponderance (95%) being female. Inside the host's
skin or pupal case, the few blind, flightless brothers aggressively compete among
themselves for the opportunity to copulate with their sisters, who will mate only
once. In mild forms, *Melittobia* aggression consists of intensive grappling bouts in
which contestants may lose an appendage; at its extreme, the first males to emerge
selectively decapitate their unemerged brothers (Fig. 9.13).

Particularly in species with long-lived adults, aggression may also be resolved
through the establishment of *dominance*, a ranking of individuals on the basis of
real or apparent authority, strength, or influence. The dominance concept implies an
ability to recognize individuals and remember relationships. Most examples occur
among social species, but male crickets confined to a limited space will establish
a rank order that is stable for some time (see Chapter 8). Age, size, possession of
a territory, opportunity to copulate, and the results of previous fights determine the
rank order, and the acoustic signal (rival song) of a dominant individual inhibits
the aggressive tendency of a subordinate one. If the rival male does not retreat, he
may respond with his own rival song. Until the hierarchy is established, aggression
includes not only singing but jumping at one another, biting, and lashing with
antennae.

9.3.4 Nuptial Gifts

A male of a non-predatory bug, *Stilbocoris natalensis*, collects a seed, injects it
with saliva that apparently partially predigests it, then offers it to a female; a male
without a seed may court, but he cannot persuade the female to copulate. In the
katydid species *Isophya krausii*, a male's spermatophores include sufficient directly

absorbed nutritive material to meet a mate's caloric needs for a full two days. Males of the beetle *Neopyrochroa flabellataduce* ingest toxic cantharadin while feeding; cantharadin transfer during mating has been shown to enable a female to use the chemical to protect her eggs from predation.

As examples like this make apparent, during courtship the 'salesmanship' of many male insects includes significant gift-giving, and their potential mates seem quite open to such bribery. *Nuptial gifts*—male material donations transferred to a conspecific female during mating—are delivered by two basic routes. One route includes oral gifts that are donated by a male and ingested by the female during mating (Fig. 9.14; see also Fig. 6.9 and Plate 29). The other type comprises seminal gifts that are ejaculated into the female reproductive tract and absorbed from there. Either way, the gifts may include nutrients and/or defensive chemicals. These gifts are obtained from sources as diverse as leftover prey, carrion, purposively collected foodstuffs, and secretions from male salivary or reproductive glands.

The published literature holds many examples of nuptial gifts. When the immatures of many insects feed, they accumulate various toxins, particularly alkaloids, in their tissues that subsequently carry on to adulthood; in other cases, males garner the toxins as adults. In various species it has been shown that males that offer toxin-bearing secretions either strengthen the female's toxic protection to her eggs, replace toxins she may have depleted during previous oviposition, or protect the female herself.

The moth family Arctiidae seems particularly prone to host-derived chemical defenses. The bella moth, *Utetheisa ornatrix*, is the most thoroughly studied in this regard (Fig. 9.15), thanks to perceptive studies by Thomas and Maria Eisner and

Fig. 9.14   Courting with an oral gift. Nuptial feeding in a scorpionfly, *Bittacus apicalis*. Through this habit, widespread in the Bittacidae, females gain increased reproductive success as measured by increased oviposition
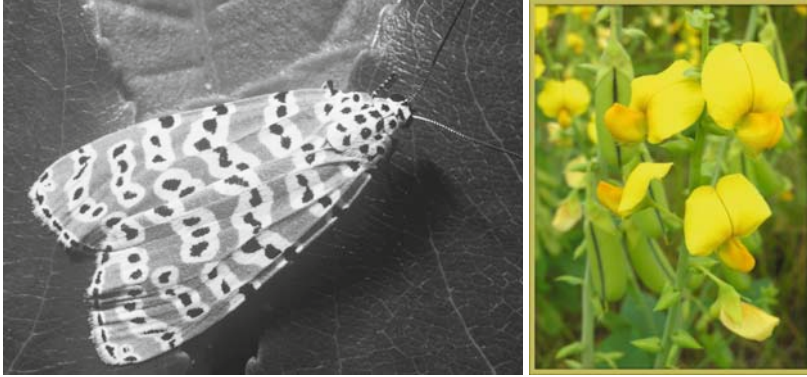
Fig. 9.15 Passing along alkaloids. The rattlebox moth, *Utetheisa ornatrix*, (*left*) feeds on the toxic legume *Crotalaria spectabilis* (right) as a larva. Unaffected by the plant's pyrrolizidine alkaloids, the larva stores these toxic chemicals and carries them along into adulthood. Thus, females are able to pass the alkaloids to their eggs; they also obtain an additional dose of the alkaloids from males as a seminal gift during each copulation

their associates. This day-flying moth gains its alkaloid from its specialized larval diet of rattlebox, *Crotalaria,* a legume that contains toxic pyrrolidizine alkaloids (PA). The chemicals are stored systemically, retained into adulthood, and passed on to eggs, thus providing all life stages of this moth with protection against spiders, beetles and wasps. Moths of both sexes actively transmit PA to the next generation. Females do it directly, in the process of laying hundreds of eggs. As a result, their PA levels can drop over time. However, they can obtain more PA by mating, because males gift them with a sizeable sperm package. Sometimes amounting to over 10% of the male's body mass, it contains both PA and nutrients.

Another example is the arctiid moth *Cosmosoma myrodora* (Case Study 9.3). Males in this species produce fine cuticular filaments in abdominal pouches, and discharge them in bursts during courtship (see Plate 34). If males feed upon plants that produce PA, the filaments are laden with these alkaloids; a female laden with these toxic filaments is protected against predators such as *Nephila clavipes*, a common spider, and she passes some of this protection on to her eggs. Males deprived of alkaloids produce filaments that confer no such protection.

Case Study 9.3: Nuptial Gifting in the Arctiid Moth, *Cosmosoma*

During courtship, a male of the scarlet-bodied wasp moth envelops its future mate in a cloud of gauzy filaments that cling around her body. What is the value of such a strange behavior?

Small *Cosmosoma* moths (see Plate 34) are not particularly abundant in Florida, but their aposematic coloration and strange habits caught the attention of William E. Conner, Ruth Boada and their associates. For her master's thesis, Boada studied the courtship of these moths. Like many other moths, a male *C. myrodoa* is attracted to a pheromone emitted by the female. However, once he nears the female, he does not alight. Instead he flutters nearby, then suddenly discharges bursts of fine filaments that swirl in the air around the female like an explosively delivered net. These filaments cling all over her body as the pair copulate, a lengthy process can take up to nine hours in this species.

Unlike most adult Lepidoptera that are only known to feed on nectar, *Cosmosoma* moths are attracted to juices from plants such as dogfennel (*Eupatorium capillifolium*), a common roadside weed throughout the southern and eastern United States; as its name suggests, the leaves and flowers of this plant smell unpleasant when crushed. It also belongs to a plant group with members known to produce strong pyrrolizidine alkaloids (PA). Watching the moths closely, one might see them probing the plant's surface with their proboscis, feeding or attempting to feed from excrescent material. Because the larvae of these moths feed upon climbing hempvine (*Mikania scandens*), a relatively common and fast-growing southern weed that appears to have no alkaloidal defenses, the researchers wondered if the males might be obtaining PA as they probed about. If this were so, did the filaments they released during courtship also contain pyrrolizidine alkaloids? Might the filaments offer any protection against predators?

For answers, Conner would need many individuals of these relatively rare moths. Happily, he was aware of a collecting technique that many old-time naturalists had used to collect rare butterflies and moths. In nature, a number of Lepidoptera visit flowers, stems, and leaves to obtain alkaloid-rich juices, but roots of the plants contain the highest concentrations, and thus can be used as a lure. Collecting roots of *E. capillifolium,* Conner hung them in moistened clusters about 1.5 m above the ground. That night, *Cosmosoma* moths began arriving; all but one was a male. Using mercury vapor light traps, he collected female moths as well.

In the laboratory, the researchers raised the offspring of these field-collected individuals on their natural larval food plant, climbing hempvine. While they grew, he ran chemical analyses of both *M. scandens* and *E. capillifolium*, and confirmed that the larvae's natural food was PA-free, but the *Eupatorium* roots were loaded with alkaloids, mostly intermedine and lycopsamine but also four other PA, two of which apparently have not been described from elsewhere in nature.

When adult males eclosed in his laboratory cultures, Conner presented one batch with a crystalline offering of PA mixed with sugar, upon which the males fed readily for an hour each day over the next five days. Then he killed some, extracted flocculent out of their abdominal pouches with forceps, and ran chemical analyses of their bodies and floss. Both contained PA, but it was about 20 times more concentrated in the flocculent than in the moth's body.

What protection, if any, did males gain from being PA-laden? As a test predator, Conner decided to use *Nephila clavipes,* a common spider that coexisted with *Cosmosoma,* particularly along the edges of lakes and streams. The researcher flipped a half dozen PA-fed males individually into the spider's web. Then he did the same with males that had no access to alkaloids. As each became entangled, he watched the spider to see whether it ate the moth or cut it free from the web. Every one of the PA-fed males were cut free, live and uninjured. In contrast, five of seven PA-free males were eaten.

Would flocculent alone protect females that received it, or were PA necessary as well? Conner placed conservative amounts of flocculent (about half that present in a male's pouches) in plastic containers with young virgin females. As the confined females fluttered about, they stirred up flocculent and coated themselves with it. Some females received flocculent from a male that fed on the alkaloid/sugar mix; others received flocculent from a male that had no access to alkaloids. Then Conner flipped each one individually into the web of a *N. clavipes* spider. As they became entangled, he watched the spider once again. All eight females coated with PA-free flocculent were eaten. In contrast, the spider rejected and cut free over half the females whose flocculent came from PA-fed males.

Wondering whether females might also gain PA during the lengthy copulation process, Conner confined various combinations of males and females overnight in cages; copulation typically began at dusk and lasted most of the night. When he analyzed their bodies afterward, he found that all of the females that mated with PA-fed males now contained alkaloids as well, but in amounts that differed depending on whether they had laid eggs. This seemed to indicate that the females not only received PA, but passed some of it onto their eggs. Chemical analysis confirmed that the eggs did, in fact, contain PA.

Was enough PA passed to a female and her eggs in this way to be protective? Strikingly so. While five of seven virgin females and five of six females mated with alkaloid-free males were eaten, all seven virgin females mated to alkaloid-fed males were cut from the web by the spiders, without sustaining injury. Furthermore, the amount of alkaloid in these protected females' eggs (on the order of 1 μg per egg) was shown in a study with another arctiid moth (*Utetheisa ornatrix*) to be effective in egg defense against ants, coccinellid beetles, and chrysopid larvae.

Oral gifts are particularly evident in different predatory taxa, where they appear to have evolved independently. Thus, they were initially viewed wholly as a mechanism for appeasement, that is, inhibition of the normal predatory instincts of the participants, especially the female. However, other explanations for this behavior have also been put forth. One is that males with prey are more conspicuous to females. Females probably also enjoy a selective advantage by consuming prey at a point where they need extra protein and calories to convert into eggs; male fitness is also increased by providing such prey because the success of his genetic contribution to the next generation is intimately tied to the survival and reproductive success of each of his mates. In addition, the very act of feeding upon a gift tends to keep a female occupied, making it likely that a male would benefit from longer copulation that results in transferring more sperm.

Sexual cannibalism would seem like the ultimate oral gift, but this has been a matter of some debate. Mantises generally begin feeding upon a prey insect by biting off its head, and females sometimes do the same with males (Fig. 9.16), at least under laboratory conditions. If mating has begun, the male's copulation motions may become even more vigorous.

Early researchers noted that ganglia in the abdomen, not the head, control the male's movements, and proposed that sexual cannibalism was a strategy that females had developed to enhance fertilization while simultaneously obtaining sustenance. Others have proposed that submissive males should be evolutionarily

Fig. 9.16   Living dangerously. With good reason, mantis courtship has sometimes been described as a 'sneak attack'. In this pair of copulating mantises, photographed in the field in Costa Rica, the female has eaten the head, prothorax, and prothoracic legs of the male while their genitalia remain coupled. Scientists are still debating whether males passively submit to such sexual cannibalism because a well-fed female would optimize the number and condition of their jointly-produced offspring, or whether males actively try to stay alive to mate again

favored because they achieve a selective advantage in their offspring when a female copulates longer and is better fed; this theory is supported by the observation that both copulation duration and chances of fertilization are as much as doubled when a male is cannibalized. However, still other research with well-fed *Tenodera sinensis* mantises indicates that the behavior of these extremely visually sensitive insects is very open to human disturbance; when the mantises were given the opportunity to copulate in a vacant room, with only a running video recorder to witness the event, instead of sexual cannibalism they displayed elaborate courtship behaviors that changed a female's interest from feeding to mating. Other studies similarly suggest that males mate repeatedly and do not merely submit to cannibalism; rather, they appear able to assess a female's hunger level and adjust their behavior accordingly.

Seminal gifts often appear to provide similar caloric or nutrient benefits to oral gifts but simply delivered by a different system. However, evolutionary biologists have been intrigued by an additional possibility. If mating is as much conflict as cooperation, gifts that are directly produced by the male might contain manipulative substances that enhance his potential at the expense of hers. For example, a seminal gift might contain a hormone that induced female refractoriness (resistance to further mating), thus reducing the chances that a later rival would overtop his own sperm with theirs; in some cases, this has been demonstrated. However, it is important to remember that there is no compelling reason to believe that all nuptial gifts must function in the same way, nor is it necessary that the costs and benefits to each sex play out in the same way for every species. Clearly, in many species the females gain significant benefits from their gifts, and prefer males that bear larger gifts. Likewise, in cases where gift-bearing males directly increase the number and fitness of offspring as a result, they are making a contribution similar to those in species that practice parental care (see Chapter 10).

To date, the concept of nuptial gifts as manipulation has been supported more by theory than by empirical evidence. However, it has given rise to a number of predictions that are potentially testable in various gift-giving species. The best known of all gift-givers undoubtedly are the dance flies. This group of small Diptera received its name from the flies' habit of circling about in complex patterns as they search for prey on the bark of trees. Dance flies present an enormous diversity in nuptial gifts ranging from clearly useful items such as bits of prey to more puzzling tokens such as elaborate silk balloons to inedible twig fragments. Why should females require what appears to be a worthless gift as a condition of mating?

In many textbooks, dance flies are used as a model system to support an evolutionary progression toward ritualization in courtship; a proposed sequence outlines a decline in male investment in the mating effort from prey to a silk-wrapped dried insect fragment to an empty silk balloon. Sexual conflict theory suggests a second, simpler model in which token-giving arose in species that once gave nutritional gifts, and males exploited female preferences by substituting more easily obtainable but worthless items. Both models rely on male cheating and female inability to distinguish between worthwhile and worthless gifts, suggesting an evolutionary race analogous to those that occur with other systems such as insect-plant coevolution and predator-prey relationships.

Fig. 9.17   Cheating pays. Dance flies with oral gifts. (**A**) *Rhamphomyia longicauda,* male above, mating with female while she feeds upon the gift of a small tipulid crane fly (**B**) Females of *Rhamphomyia sulcata* usually accept a nutritious gift, but researchers substituted a cotton ball, males presenting the token were rewarded with a copulation equivalent in duration to what they would have received bearing a small genuine gift

An interesting experimental study questioned how easily cheating could invade a species in which males normally provide valuable nuptial gifts. Males of the dance fly *Rhamphomyia* normally provide an actual prey item, and dance fly pairs mate on vegetation while the female eats the gift (Fig. 9.17a). Natasha LeBas and Leon Hockman removed the gifts from mating pairs, replacing them with either a large or small genuine gift or a large or small worthless cotton ball; then they timed the copulation that followed. In this species, larger males usually carry larger gifts, so by using this design, the researchers uncoupled the influence of the nuptial gift from the influence of the male that produced, caught, or collected it. Their data showed that females treated cotton ball tokens as equivalent to small prey gifts (Fig. 9.17b). The researchers suggest that sexual selection in this species is acting to decrease gift size because males are more maneuverable and flight-efficient in the lek with a small gift; thus large and highly visible gifts, even if worthless, allow males to provide a large visual target to females while minimizing carrying costs. Presumably, even though larger gifts increased duration of copulation, these shorter copulations, whether natural or token-induced, are still long enough to result in adequate sperm transfer. Selection would be expected to act strongly against males that fed females for no reproductive return.

Three observations suggested that males were exploiting female sensory biases with their cheating behavior. First, LeBas and Hockman observed that males given cotton balls sometimes flew off with them after copulation, then returned to use them again to pair up with new females. Second, the female reactions were similar to responses to a supernormal stimulus. Cotton fibers are whiter than, but otherwise quite similar to, the fibers of seed tufts that some dance fly males carry, and not too different from the silk balloons and swollen foreleg projections that mimic a carried

gift in other species. Third, during copulation the females tried to feed upon the cotton ball as though it were a genuine prey. (Similar behavior has been observed in other species where males regularly present inedible tokens, suggesting that in those species as well, males previously gave nutritious gifts.) However, copulation duration was not significantly different for large versus small tokens, suggesting that females take a set time to determine a gift's edibility.

9.4 Mating Systems and Parental Investment

During her nuptial flight, a honey bee queen mates with several males in succession, each of which dies after copulation. Sand fly males defend small arenas where they emit pheromones; females choose freely, and a single male sometimes obtains all the matings. A female of the hippoboscid fly *Lynchia* nurtures her single egg inside her body until it has passed entirely through the larval stage and is about to pupate; if a male encounters a female in this condition, he will dig his hook-like tarsal claws into her back and ride about like this for hours before finally copulating with her after she deposits her prepuparium.

In sociobiology and behavioral ecology, a mating system is any of the ways in which animal societies are structured in relation to sexual behavior. These mating relationships also may or may not be associated with social relationships, in which the sexual partners stay together to become parenting partners. Thus, there has been some debate as to whether mating systems should be classified in a way that reflects pair bonds and the rearing of offspring. The most straightforward classification simply considers the number of copulatory partners. The mating systems most commonly recognized in animals are monogamy, polygamy, and promiscuity. In monogamy, a male and female mate only with each other either during a particular breeding cycle or throughout their lives. Often called 'pair bonding,' monogamy is rare among insects. Where it occurs, it is generally an evolutionarily derived condition. Fidelity tends to evolve only under certain ecological circumstances, usually when the advantages of cooperation in rearing offspring outweigh the personal advantages to both partners of seeking extra mates.

Polygamy is the state in which an individual has two or more mates, none of which mates with other individuals. It has two forms. One is polygyny, where a single male mates with several females; this is the most common system in insects. The reverse case, polyandry, which occurs when a single female mates with several males, as happens in honey bees, is relatively rare in insects, as in animals generally. Thus, the terms polygamy and polygyny are sometimes used synonymously.

Promiscuity also takes two forms. In simple promiscuity, both males and females mate repeatedly, but no pair bonds are formed. In polygynandry, two or more males have an exclusive relationship with two or more females; this has been best described among bird species in which males jointly help rear and/or protect nestlings. The numbers of males and females need not be equal in a polygynandrous system; in vertebrate species studied so far, the number of males is usually less than

the number of females, suggesting that polygynandry could be considered a variant of polygyny.

It is interesting to note that virtually all the terms used to describe animal mating systems were taken over from social anthropology, and were originally devised to describe systems of human marriage. Any analogies should not be pressed too far; in human societies, marriages typically have to be recognized by the entire social group in some way, and there is no equivalent process in animal societies. Furthermore, although mating systems can provide a convenient way to characterize a species, variation can occur at the individual level. For example, DNA fingerprinting studies in birds and mammals have shown that even in pair-bonding monogamy, mating outside the pair (extra-pair copulations) occurs with fair frequency, and a significant minority of offspring result from them. In addition, some species show different mating systems in different circumstances, as for example in different parts of their geographical range, or under different conditions of food availability, and, mixtures of the categories may sometimes occur.

As in so many other areas of behavioral study, research on mating systems has steadily been shifting from description toward prediction. After the question 'what sort of mating system does this insect have?' has been answered, the second question is 'why?' On a broader scale, how and why have particular mating systems evolved? What factors might explain the variety that is observed? Do they have predictive power?

One set of potential answers centers upon *parental investment*—contributions of time and/or energy that increase the probability of some offspring surviving to reproduce but occur at the cost of the parent's ability to generate additional offspring. Different strategies of parental investment exist. For example, one species may invest highly in a few offspring, while another may produce many but invest very little in any one of its young.

Within a given species, the sexes generally differ in their degree of parental investment (Fig. 9.18), beginning with the fact that males and females make unequal physiological investments in the production of gametes. The clutch of eggs a female lays may more than equal her total body weight, whereas even over an entire season, sperm production usually represents a mere fraction of this. Moreover, the commitment of time and energy required in such aspects as egg maturation, oviposition, or birth are borne solely by the female, but in most insects a male's only reproductive role is to provide a set of genes.

Because of this general imbalance, a reproductive mistake has much greater consequences for a female. 'Coyness' during courtship is one strategic result. Another is that in almost every species, the female chooses a mate, not the reverse. Females are under selective pressure to pick a male with a superior set of genetic instructions; and to the extent that such discrimination is possible, the outcome tends to be that a select group of males with superior traits mates with a large proportion of the female population. It should be to a female's advantage to mate with a male that signals genetic quality, no matter how many times he may have already mated. Therefore, one should expect insect species, like most other animals, to be fundamentally polygamous (or more properly, polygynous).
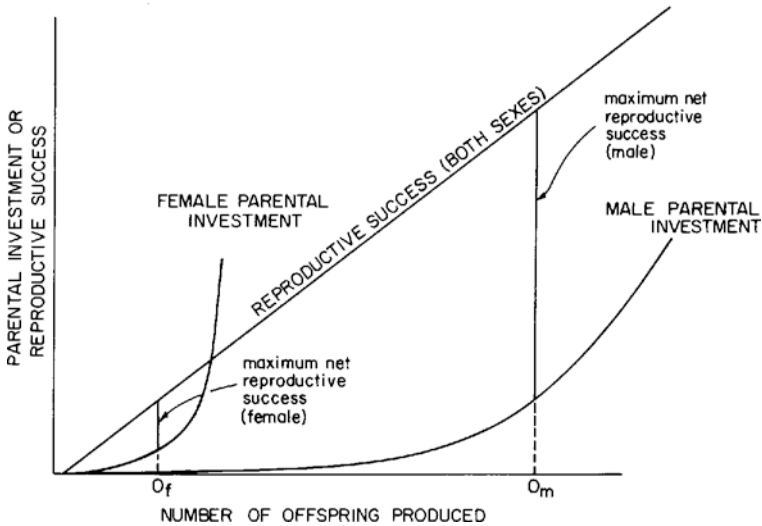
Fig. 9.18   Differing viewpoints. The central principle of sexual selection reformulated in terms of parental investment. In the common situation illustrated here, the optimum number of offspring (O_f for the female, O_m for the male) differs for mothers and fathers. Because the female must expend a greater effort to create offspring, her greatest net production comes at a lower number than in the case of the male. This sets the stage for a conflict between the sexes

9.5   Oviposition Behavior

A female locust or grasshopper begins tapping the soil with the tip of her abdomen and probing with her ovipositor. Rejecting surfaces where the ground is hard, she comes to a soft and sandy place where she begins to dig. Raising her body on her first two pairs of legs, she arches the tip of her abdomen downward and scrapes particles of soil sideways and upward with valves at its tip. As a hole forms and deepens, her abdomen lengthens considerably. (If she is a migratory locust, *Schistocerca*, she may dig to a depth of 14 cm.) To maintain necessary body pressure, she expands her airsacs and swallows air into her crop and midgut caecae. Once the hole is dug, if the soil is saline or dry, she rejects it. If the soil is moist, however, she begins to lay groups of eggs (Fig. 9.19). To maintain hemolymph pressure, she continues to pump air into her tracheal system by vigorous ventilatory movements of her head. About 20 minutes later, her airsacs occupy the whole cavity of the first five abdominal segments, and the volume of her tracheal system has more than doubled from the start of oviposition. Finally, when all her eggs have been laid, she forms a frothy plug in the mouth of the hole, then withdraws her abdomen completely and scrapes dirt over the top of the hole with her hind tibiae. All together, the process has taken her about 2 hours.

Insects deposit their eggs in an almost infinite number of ways. Sometimes both parents participate, but more commonly gravid females have sole responsibility for the fate of their eggs. As the above example illustrates, the oviposition process can
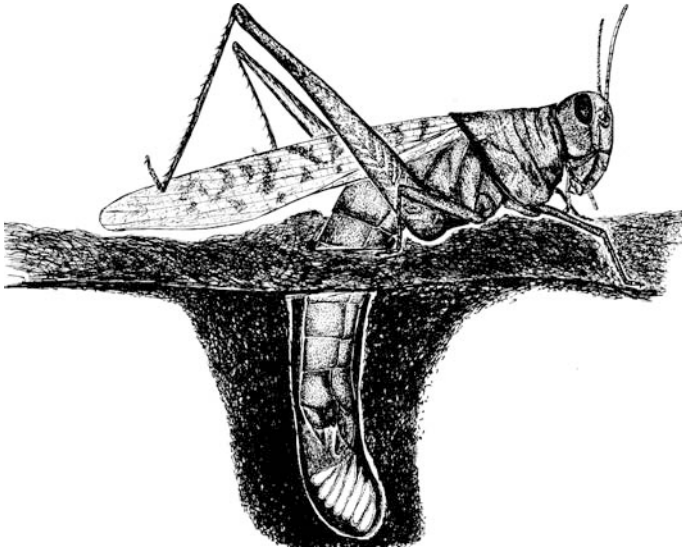
Fig. 9.19 Ovipositing underground. The migratory locust, *Schistocerca,* (see Plate 4) digs a shaft by opening and closing her dorsal and ventral ovipositor valves like a clam-shell posthole digger, then lays a pod of eggs. After deposition, the eggs absorb water via a special pore in one end and swell to twice their initial size. Successful breeding depends on rainfall patterns, and final choice of site is positively influenced by the presence of other ovipositing locusts

be longer and more difficult than is generally assumed. Laying eggs is a significant expenditure of body energy reserves, as well. Because oviposition mistakes may severely lower reproductive success and hence individual fitness, the stimulus–response sequences tend to be quite complex, minimizing chances for error. In general, the behavioral chain of events leading to oviposition closely parallels that used in food location (see Chapter 4).

9.5.1 Selecting a Site or Host

Adult female mosquitoes are attracted to water, influenced by the presence of vegetation and amount of light reflected from the surface, but do not automatically oviposit once they have reached it; when they land upon the water's surface, some first judge salt content and others assess the pH of the water through their tarsal sensilla. Buprestid beetles of the genus *Melanophila* are attracted to burnt trees over distances of several kilometers through an oriented response to infrared radiation emanating from forest fires (see Fig. 3.7).

Site selection generally has two or more phases that vary in their sensory involvement. First, there is a general reaction to the environment; this is followed by much more specific final selection stages. For example, site selection by the tobacco hornworm moth includes both approach and landing. Approach is largely mediated by

Fig. 9.20 Tasting by foot-touch. Butterflies in the genus *Pieris* sense mustard oils in cruciferous plants with their tarsi. Thus, in the laboratory they can be induced to lay their eggs on other surfaces as long as their feet contact the proper foliar cue

visual cues and is not particularly discriminating. The decision to land, on the other hand, involves subtle olfactory responses to smells emanating from host plants. After landing, contact chemical stimulation elicits egg deposition. Similarly, female cabbage butterflies are attracted to blue or yellow when searching for nectar, but not when ready to lay eggs; an oviposition-ready female lands upon a plant and drums upon it with her forelegs, sensing through her tarsal receptors whether the plant contains mustard oil before she hangs upside down and oviposits her eggs on the underside of its leaves (Fig. 9.20).

Among species that do not practice any form of parental care following egg deposition—a situation that describes the vast majority of insects—proper egg placement is particularly crucial. Considerable time and energy may be spent on fine discriminations during site selection. Some stimuli that influence the behavior of egg-laden female insects are negative, course. For example, certain plant-derived chemical factors inhibit boll weevil oviposition (in one cotton species, by 40%). In other cases, the stimuli for oviposition may be only indirectly related to actual larval feeding preferences, a situation that may have unusual consequences (Fig. 9.21).

Many species have evolved a fine-tuned ability to assess host suitability factors such as the egg or larval load already upon a host. Female bean weevils, *Callosobruchus maculatus,* do not deposit their eggs in mung beans at random but compare the present bean with those previously encountered; a bean that is larger or bears fewer eggs than the last one they came across is more likely to receive an egg. The resultant nonrandom pattern of oviposition increases larval survival by 70%
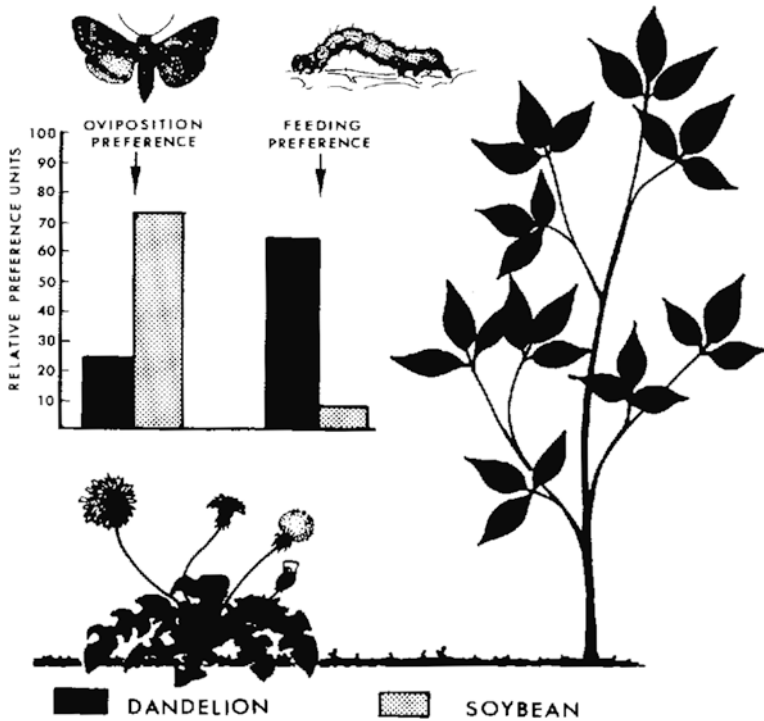
Fig. 9.21   Differing cues. Although the larvae have a marked feeding preference for dandelion, adult females of the noctuid moth *Autographa precationis* clearly prefer soybeans over dandelions for oviposition, apparently because the shape of the dandelion leaves is a less effective oviposition stimulus

over what would occur if eggs were laid randomly. Likewise, some species of hover flies (Syrphidae) whose larvae feed on aphids are sensitive to aphid density and lay their eggs in numbers proportional to the abundance of the aphid population. In a similar vein, females of the parasitic wasp *Tiphia popilliavora* control the sex of eggs they lay according to the size of their beetle host, *Popillia*; in third instar larval hosts, the parasites lay fertilized female eggs, but in smaller second instar hosts they lay smaller unfertilized male eggs.

At the same time, there is strong selective pressure for discrimination of potential danger from parasites and/or predators. Among cannibalistic species such as preying mantises, even one's own young may be a threat to siblings. For example, the caterpillars of female heliconiine butterflies in the Neotropics will eat eggs and one another. Ovipositing females often spend considerable time inspecting the host plant prior to oviposition; it has been suggested that this is a visual search for other *Heliconius* eggs or larvae. Probably the search is for other egg predators and parasites as well; one study estimated that over 90% of these butterflies' eggs were killed by parasites. Such pressures may have led to uniformity in egg

dispersion becoming a widespread trait among many parasitic and phytophagous insects.

Some parasitic wasps have eggs that keep on dividing, resulting in as may as 1,500–2,500 young from a single egg. Some termite queens can lay 6,000–7,000 eggs a day and the queen can live more than 15 years; one colony of the South American *Nasutitermes surinamensis* had three million termites. Upon a small host, a *Melittobia* parasitoid wasp may lay 150 eggs during her one-month life span; on a larger one, up to 800.

At first glance, the reproductive capacity of a given species would seem to be easily determined. In truth, however, records of egg laying or total egg output rarely give a true picture of the reproductive potential of any species. A variety of factors, both internal and external, influence total egg production. Nutrition is probably the single most important factor. Many insect species, particularly those having a short adult life span, can lay eggs without having ingested any proteinaceous food. The short-lived mayflies (Ephemeroptera) are a prime example of this phenomenon, which is termed *autogeny*. Some autogenous insects never eat at all as adults; others ingest only water or carbohydrates such as nectar. Most autogenous species, however, lay relatively few eggs under such conditions; given the opportunity to ingest proteinaceous foods, they will produce additional egg batches (which brings us back to the potential value of nuptial gifts, see Section 9.3.4). In at least some cases there appears to be a correlation between autogeny and larval nutrition, those individuals with adequate nutritional reserves as larvae being more likely to be autogenous. In many other cases autogeny also appears as a consequence of adverse climatic conditions. For example, autogeny in mosquitoes is common in temperate and cold regions, where hosts and adult food sources are sometimes scarce. High arctic mosquitoes are voracious biters, but there are few mammals available upon which to feed. Confined to feeding on nectar, they can still lay a few eggs to assure propagation of the species until an appropriate host appears (also see Fig. 4.1).

Environmental factors such as light, temperature, and humidity wield an influence not only by their direct effects but also indirectly through effects upon feeding and mating activities. Day length, for example, has such a dual effect. Reproductive diapause (see Chapter 3) is common, as is hibernation, which may be thought of as a type of reproductive winter diapause. Both appear to be induced by photoperiod.

Finally, any attempt to ascertain an insect's reproductive capacity must take note of the fact that mature eggs may simply not be deposited. For example, some unmated females may mature a full complement of eggs but retain some or all of them until after mating. In other cases, where the proper substrate or host is not available, even fertile eggs may be retained and later reabsorbed.

In summary, it is doubtful whether data from laboratory colonies can ever realistically be equated with egg-laying in natural environments. Insects reared in the laboratory generally live under better conditions, especially with respect to temperature and the availability of food, but natural ecological relationships are difficult to sustain under artificial conditions.

9.5.2 Reproductive Rates and Energy Allocation

Certain earwig and dipluran females brood their egg clutches prior to hatching (see Plate 43). Females of the weevil *Byctiscus populi* construct rolls from young poplar leaves, within which eggs are deposited and larvae develop (Fig. 9.22). Walking sticks continuously drop single eggs apparently at random as they move through the forest foliage. Parasitic wasps of the family Trigonalidae leave thousands of eggs on foliage likely to be consumed by the caterpillars that serve as intermediate hosts. What adaptive bases might there be for such diverse patterns?

To answer this question, we must consider an insect's *reproductive effort*, a term that includes not only the caloric content of eggs and sperm but the whole variety of phenomena involved in the production of reproductively successful offspring: the energies expended in seeking mates, searching for appropriate oviposition sites, building nests, guarding eggs or young, feeding young, etc., and the risks resulting from the performance of these behaviors. For any given species, the question becomes this: How much effort and/or exposure to danger will be optimal for maximizing the number of viable offspring, and how should this be apportioned among those offspring that are produced? Phylogeny offers little help in answering this, because birth rates often vary enormously from one species to another, even between
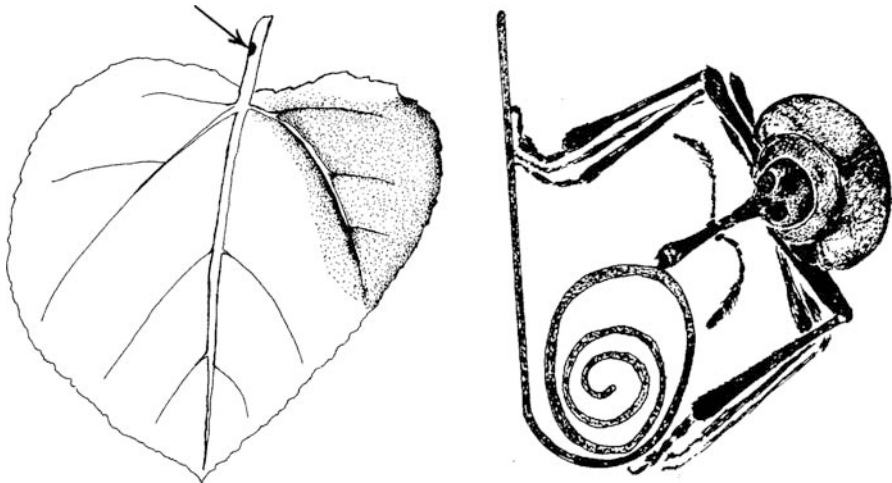
Fig. 9.22   Rolling one's own. Construction of a leaf roll from a single aspen leaf by a female weevil, *Byctiscus populi.* After notching the leaf petiole (*arrow*), the beetle walks around on part of the leaf blade (*stippled area*), perforating the epidermis with its tarsal claws and sometimes its jaws. Then *Byctiscus* positions itself parallel to the leaf edge, sinks in its claws, and draws its legs up toward each other, using the snout to help guide the developing roll. Creeping inside the roll, the weevil chews a longitudinal slit through one layer before reversing position to deposit a single egg. Only then does she complete the roll and glue the last edge in place with anal secretions

closely related species. Instead, one must turn to ecological factors and consider theories with an applicability that ranges beyond insects.

In an ideal environment, one with no predators and no intraspecific competition for resources, a population would increase at its maximum rate, r, a value simply obtained by subtracting the population's death rate due to old age from its birth rate. The whole reproductive thrust of every species is directed toward maintaining r as close to maximum as possible. In the non-ideal real world, two very different strategies for doing this are possible, depending on the amount of competition and rigor of the environment. One may increase birth rate or decrease death rate. Uncrowded and nearly ideal environments tend to favor increases in birth rate, raising r in the process. For this reason, selection that acts to raise the maximum rate of population increase has been called 'r-selection' (more properly, 'r_{max} selection'). Species that are r-selected are opportunists, able to quickly discover new habitats. However, they are rarely able to persist successfully for long in such habitats, since they tend to be poor competitors. They often have what may be termed 'big bang' reproduction, good colonizing ability, and short adult life spans. They can be termed 'r-strategists'.

Other species live in approximate equilibrium with each other; their densities do not fluctuate much. Their population levels persist at just about carrying capacity, K, the number of individuals that the environment can support. There are no uncrowded habitats to find and exploit; however, being able to survive where one is, particularly for a long period, takes on new importance. There is little advantage to producing large numbers of young, but behaviors that increase the survival of one's young become important. These species can be termed 'K-strategists'.

It must be appreciated that r and K are theoretical constructs that represent the endpoints of a continuum, and that a given organism may display some traits typical of one strategy and other traits more representative of the other. Related to all of this is the matter of energy allocation. Any organism has only a limited lifetime with a limited amount of time and energy to partition among the various activities of its life. Each animal must divide its time and energy among three major requirements, which are (in their usual order of descending importance) food, defense against predators, and reproduction. For each species this total time and energy will be divided in a different manner depending upon environmental and evolutionary constraints. However, just as in any other budget, to the extent that one priority is easily satisfied, more expenditure can be devoted to activities of the other priorities.

Chapter 10
Parental Behaviors and Social Life

10.1 Introduction

Webspinners (Embioptera) of all life stages live gregariously in a series of chambers constructed from silk spun from glands in the forelegs of adults. Male and female *Geotrupes* dung beetles dig a burrow in the soil together and store dung for their larva, which is tended for most of its life by the female. Certain earwig females (Dermaptera) lay their eggs in burrows and guard them until they hatch.

Since almost all insects are selective to one degree or another in their choice of oviposition sites, one might say that the most fundamental rudiments of parental care are nearly universal, namely, the laying of eggs in the correct place at the correct time for proper development of young. Likewise, one might view internal incubation and the birth of live young as elementary forms of parental care. However, after a parent insect has fulfilled its responsibility for placing the egg (or larva in some instances) in an appropriate environmental situation, most insects simply leave it.

Many insects go far beyond these basics, however, and tailor the environment to the needs of their young through various behaviors collectively called parental care. In most cases, a group of young are born and reared as a batch, or *brood*. Thus, when behavioral involvement of the adults in feeding and protection of a batch of young extends past the time of oviposition or birth, it has been called *brood care*. 'Sociality' is a more complex concept, and various scientists use the term itself in different ways. Thus we will defer discussion of a more precise definition until later (Section 10.3), here noting only that among the most highly developed social insects, the brood has become the core around which all activity is centered, and adults rear the brood all the way from egg to adulthood.

Parental care and social life in insects have been subjects of fascination and speculation for millennia. Philosophers as diverse as Aristotle and Aesop found inspiration and instruction for humankind reflected in these remarkable little societies that seemed so like ours (see Fig. 1.11). Natural histories of the most obvious and extreme examples, particularly honey bees and ants, seemed only to underscore the moral lessons to be learned. During the scientific and technological revolution that coincided with the later part of the Middle Ages and through the Renaissance, scientific ideas in physics, astronomy, and biology evolved rapidly. New organizations and institutions were established for the study of the natural world. Knowledge

of proximate causes of insect behaviors and information about the mechanisms underlying certain behaviors advanced with surprising speed. However, ultimate causes seldom entered people's minds; insects were what they were, and always would be.

Then, just under two hundred years ago, Charles Darwin placed biology, and with it, insect parental care and sociality, in an entirely new context: that of evolutionary history, adaptations, sexual selection and a host of other ultimate-causation questions. In this expanded context, insect parental care and social behavior has become a major area of inquiry, not only in entomology but also in the biological sciences as a whole.

10.2 Social Organization

Bumblebees are attracted to those flowers where other bumblebees are already foraging. Given a choice, male swallowtail butterflies prefer to land at artificial puddles with a butterfly decoy. Female Mediterranean fruit flies reared in groups visit and oviposit in more host fruits than solitary raised females do.

Most insects come together at least temporarily for mating; many also come together for other reasons, forming temporary to relatively permanent groups. Some of these are based on relatedness such as parent-offspring groups; others are not. Some groups undoubtedly result simply from a common response to some particular environmental factor, such as presumably occurs when aggregations of bush flies cluster on any available space (Fig. 10.1). At other times, mutual attraction is clearly involved; some of the communicative devices involved have already been mentioned in Chapters 6, 7, and 8 .

Might these be called 'social responses'? The answer depends upon whom you ask. Biologists use the term 'social' in a wide variety of ways. Some might speak of the social relations between sexes during courtship and mating; others speak of social interactions among animals in a herd, birds in a flock, or fish in a school. Ecologists sometimes refer to all of the organisms in a habitat or community as a society. However, a single thread is common to all these varied uses—the indication of adaptively significant (often cooperative, but sometimes exploitative) interactions between two or more individuals. Such interactions, mediated by reciprocal communication, produce effects that are qualitatively different from the mere summation of the independent activities of the individuals.

Rather than getting mired in a bog of definitions, let us recognize that we are dealing with a continuum of relationships. Attempts to classify the various kinds of animal associations and interactions have been based on their form, basis for association, degree of interactions of members, and the nature and duration of association. One useful simple system is that represented in Table 10.1.

10.2.1 Aggregations and Simple Groups

By flashlight, one can sometimes find clusters of bees or wasps assembled together to pass the night (Fig. 10.2). Up to 200 or 300 individuals may be involved, usually,

Fig. 10.1 Feeling crawly?. An aggregation of Australian bush flies, *Musca vestustissima*, clustered on a man's back. The harmless flies thrive in the vast semi-desert Outback, constituting a continual annoyance by their sheer numbers and tenacity

but not always, of one species. Often they will return night after night to the same location, but they do not cohabit a nest or rear young together, and the basis of their individual attraction to the sleeping roost is unknown.

When an assemblage is composed of conspecific individuals including more than just a mated pair or family, all gathering temporarily in the same place but not internally organized or engaged in cooperative behavior, it is termed an *aggregation*. Many kinds of these 'uncoordinated' groups are common among various insects (see Plate 5).

The causal factors behind aggregations are often unknown. Some result only from limitations of suitable habitat. In other cases, aggregations grade into slightly

Table 10.1 A simple classification of insect associations, excluding those involving sexual activities[a]

Association	Basis	Interaction among members	Duration	Nature of association	Selected examples
Aggregations	Facultative 'mutual attraction,' mediated by intrinsic or environmental factors	Uncoordinated	Temporary (often seasonal)	Open; members of other populations uncritically accepted	Butterfly communal roosts; bee sleeping clusters; beetle hibernation clusters
Simple groups	As above	Coordinated movement	Temporary, facultative	Open	Locust and butterfly migrations
Primitive societies	Siblings groups; parental care	Reciprocal communication; may cooperate in nesting	May persist over a life stage; centers on nest	Open; members often ± related	Passalid beetles; tent caterpillars; embiid webspinners
Advanced societies	Obligatory interdependence of all developmental stages	Highly integrated, cooperative; division of labor	More or less permanent	Closed; members closely related; all others excluded	Ants, termites, all other so-called 'eusocial' insects

[a] Overlaps are common.

more sophisticated associations in which members exhibit at least some coordination in their movements. Such simple groups, again comprised of conspecific individuals remaining together for a period of time, are made up of group members that interact with one another to a distinctly greater degree than they do with other conspecific individuals. Swarms of midges, parasitic wasps, chorusing cicadas, and migratory swarms of locusts (see Plate 4) or butterflies (see Plate 3) all provide good examples of simple coordinated groups.

Every behavior has costs and benefits, and is expected to have evolved only if the latter exceed the former. How might individuals benefit from associating with conspecifics? In mating swarms, for example, individuals might benefit from increased reproductive opportunities. Opposing this is the potential cost of increased interference and competition for mates; there also may be an increased risk of being deceived or manipulated, as occurs with *femme fatale* fireflies (see Chapter 7).

Similar cost/benefit analyses apply to feeding assemblages. Food detection and/or utilization may be more efficient in a group. When food supplies are patchy and transient but rich, a group may locate and be able to defend such food supplies more efficiently than isolated individuals, particularly if some sort of communication between the individuals has developed. (Fully social insects excel at recruitment

Fig. 10.2   Sleeping aggregations. (*left*) A cluster of males of the solitary bee, *Chalicodoma*, from Australia 'sleeping' on a clothespin. These males returned every evening to the same site for about three weeks. (*right*) A group of male *Actinote surima surima* butterflies roost at night in Brazil. Similar sleeping aggregations of various butterflies and solitary bees and wasps occur commonly worldwide

of large numbers of workers to exploit food resources.) Costs include heightened competition for the food and the necessity to share.

Enhanced defense can be another benefit of groups. First, any assemblage of individuals is likely to improve the chances of detecting potential predators, the so-called *group vigilance effect* (see Plate 17). Additionally, gregariousness may enhance predator confusion, reducing a predator's hunting success, as well spreading the risk that any particular individual in the group becomes a predator's meal. Massive periodical cicada aggregations are a striking example of a situation where potential predators are simply overwhelmed.

Mollification of the environment through such effects as reduced convective heat loss or evaporative water loss benefits individuals in a cluster. A possible disadvantage is that individuals in such groups may be more vulnerable to pathogens and disease outbreaks.

More subtle influences sometimes are also at work. *Blattella germanica* cockroach females apparently feed more and reproduce more quickly in the presence of conspecifics than if kept alone. When confined in groups, *Pogonomyrmex* ants show more intense digging behavior than isolated individuals given the same conditions. Human beings show analogous behavior. For example, it takes a great deal of resolution to avoid joining in when faced with a yawning or laughing person.

Social facilitation may be defined as an increase in the pace or frequency of a given behavior due to the presence or activities of another conspecific individual. An example of its workings may be seen in the Australian spitfire sawfly, *Perga affinis*,
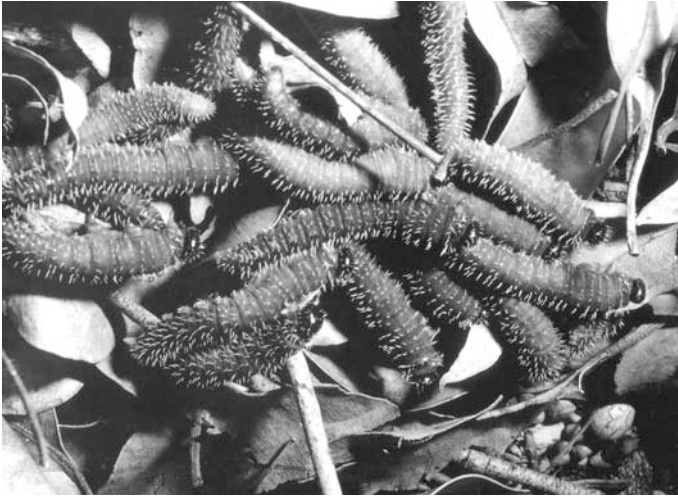
Fig. 10.3 Burrowing battalion. Australian sawfly larvae of the genus *Perga* crawling on the forest floor prior to cocooning. In order to successfully construct cocoons and pupate they must first penetrate the crusty soil. Although individuals are poorly adapted for such burrowing, in larger aggregations at least one larva usually succeeds in breaking through and the others are then able to follow. If disturbed, the writhing mass of larvae rear up and regurgitate sequestered droplets of liquid rich in the essential oils of their eucalyptus host plants, a behavior that gave rise to their common name, spitfires

where an individual's very survival depends upon it. Females lay their eggs in pods within the tissue of eucalyptus leaves; after hatching the young must first gnaw an exit hole before they can begin feeding. This is a difficult task, but if one succeeds, the others follow. There is a strong correlation between pod size and larval mortality. In one study, pods with fewer than ten eggs suffered 66% mortality, but among those containing more than 30 eggs, mortality was only 43%. Social facilitation is also involved when mature *Perga* larvae leave the tree to pupate (Fig. 10.3).

10.2.2 Parent-Offspring Interactions

Certain female sawflies guard their eggs and young (Fig. 10.4). Young *Gargaphia solani* bugs orient to their mother and follow her from place to place. Scarab beetle pairs cut out a chunk of freshly deposited manure, roll it off, and place it in an elaborate underground burial vault where eggs are eventually deposited. The parents of Brazilian *Phloeophana longirostris* pentatomids apparently provide nourishment for their nymphs in addition to protecting them.

   More than a dozen orders of insects include at least some species that care for their young. Parent-offspring groups are the most common form of social assemblage in the insects and most often parental care equates to maternal care. Next most common is biparental care, followed by exclusive paternal care, and finally

Fig. 10.4 Guarding young. Maternal care in the Brazilian sawfly, *Themos olfersii*. Throughout the approximately 20 days required for incubation, the conspicuous orange and black female straddles her eggs. If disturbed, she displays one of a series of at least ten different types of defensive or threatening reactions. Later, even when the fully sclerotized gregarious larvae migrate together to the basal portion of their host leaf and begin feeding, their mother continues to guard them, sometimes accompanied by other females that happen to be nearby. Apparently because of their distastefulness and warning coloration, the adults are only rarely subject to predation, and eggs and young also benefit from this protection

by a taxonomically small group of truly miscellaneous assemblages that were once lumped together under the term 'communal insects.'

The roots of maternal care and biparental care are fairly easy to envision. Female insects in any population probably vary in the alacrity with which they abandon their eggs. For females in ecological situations where a tendency to stay around might repeatedly result in greater offspring survival, such persistence would be evolutionarily favored. However, in other cases, leaving immediately might be a better female strategy because it would allow more opportunity for the additional feeding necessary to mature further clutches of eggs. Biparental care probably had its roots in an extended association of the sexes after mating; for a male, remaining with one's mate until eggs are laid has the result of increasing a male's certainty regarding parentage (see Chapter 9).

As one looks at cases where parental involvement stretches ever further into the life of the offspring, various incipient social behaviors begin to appear. Among scarabaeid beetles, for example, one finds a spectrum of behavior from species in which the adults simply amass manure provisions upon which eggs are laid to species such as *Copris* where the mother stays with her young until they reach adulthood. In conceptualizing the development of sociality, it is tempting—but misleading—to see such variation as proof of a linear, unidirectional evolutionary

march toward some sort of 'perfection' represented by 'true' sociality. Models of insect sociality that arose in the early twentieth century relied heavily on such ideas; one of the best known was that of William Morton Wheeler, in which social evolution progressed through seven steps of increasing parental care to an apex presided over by his own favorite social insects, the ants. The caution here is that one must remember to recognize these correlations as useful organizational devices, rather than reflections of an evolutionary progression.

Parental investment theory predicts that because parental care adds to the inequality of male and female investment, under most conditions it will merely reinforce a polygynous mating system (see Chapter 9). In highly polygynous systems and in promiscuous systems, paternal care of young will be rare or there may be no parental care at all.

As parental investment theory predicts, when parental care exists, females almost always are the sole providers. Unassisted male parenting has been estimated to occur in fewer than 150 of the nearly one million insect species that have been described. However, it has been documented in diverse species, including the Hymenoptera, Coleoptera, Hemiptera, and Thysanoptera, and in a few species the male's contribution to the fitness of his mate and offspring is extensive.

Almost all cases of unilateral paternal care occur in one bug family, the Belostomatidae, or giant water bugs. Water bugs in the genus *Abedus* are a striking example. These moderate-sized to large aquatic hemipterans are predators, some of the few insects that prey directly on small vertebrates such as tadpoles and fish fry. Two aspects of their reproductive behavior are unusual. One is that females invariably attach their eggs to the backs of males, where the eggs remain until they hatch (Fig. 10.5). The other is that the females go their own way shortly after mating and oviposition rather than sharing in parental care as some other insect pairs do.

Reflecting a prevailing chauvinistic attitude as to the 'proper' sex roles, early observers generally believed that the egg-bearing water bugs were females carrying their own eggs. Some authors even described the oviposition process, attributing the feat to a long protrusile ovipositor that could be extended over the female's body. In 1899, F. W. Slater (a woman) set the record straight in a delightful account not totally emancipated from chauvinistic overtones:

> That the male chafes under the burden is unmistakable; in fact, my suspicions as to the sex of the egg-carrier were first aroused by watching one in an aquarium which was trying to free itself from its load of eggs, an exhibition of a lack of maternal interest not expected in a female carrying her own eggs.

A few years later another entomologist, while mentioning the 'indignity' of such male servitude, noted the 'peculiar fact' that copulation took place in connection with oviposition in the species he observed. However it took almost 75 years before Robert Smith's pioneering study (Case Study 10.1) began to make the situation understandable, and even today studies of male parental care in these bugs continue to yield new insights.
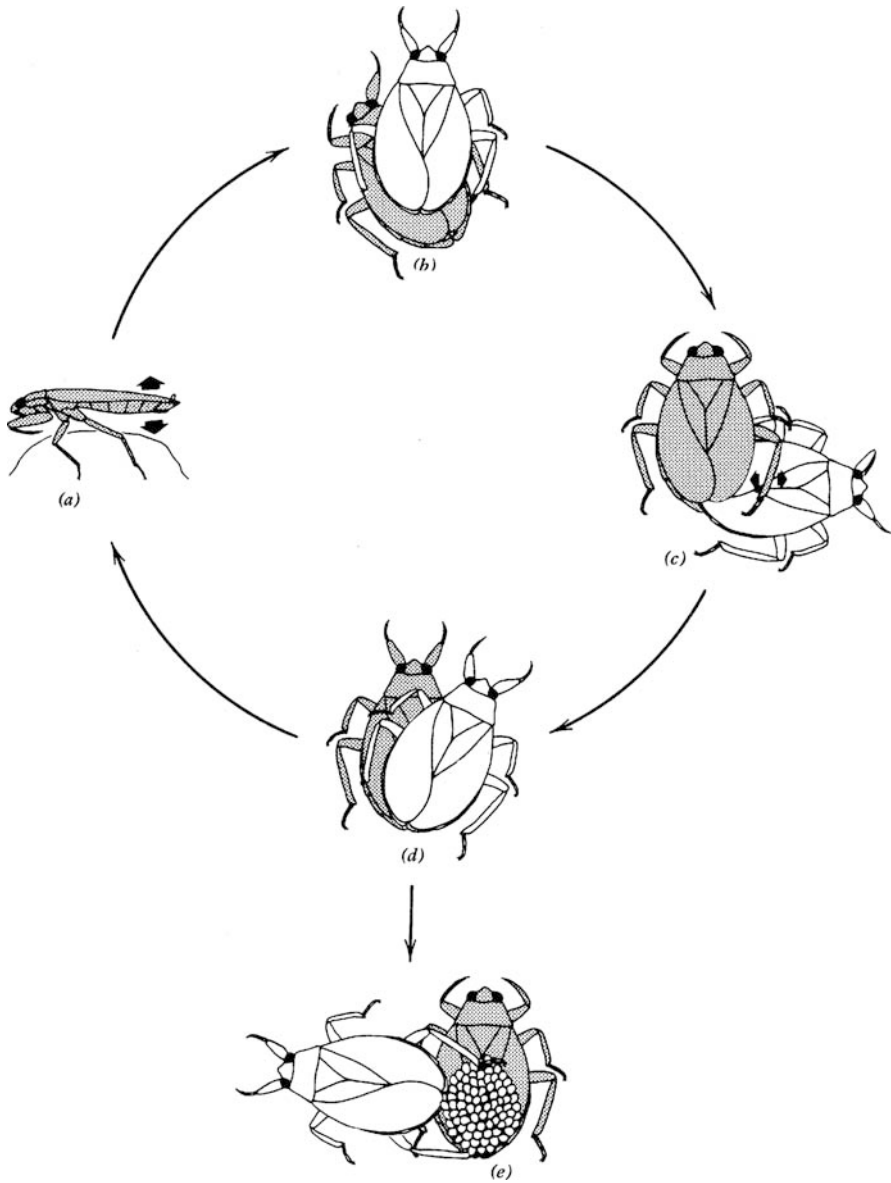
Fig. 10.5 Reversing roles. The copulation-oviposition cycle of the giant water bug, *Abedus herberti*. After preliminary sparring between the sexes, receptive males perform vigorous pumping (*a*). Females respond by climbing on the male's back (*b*) as if to oviposit. With one hind leg, the male manipulates the female off into a copulatory position (*c*). About one minute after intromission, the male abruptly 'scrubs' one hind leg on the female's hemelytra. Immediately the female repositions herself (*d*) and begins to lay eggs, starting at the apex of the male's hemelytra. After about five minutes, although the female has laid fewer than four eggs, the male's temporary quiescence ends. Forcing the female out of position with his hind leg, the male begins a new bout of vigorous pumping. This cycle continues until the female's total egg clutch is deposited on the male's back (*e*)

Case Study 10.1: Reversed Sex Roles in the Giant Water Bug, *Abedus*

Female water bugs abandon their eggs to males that proceed to care for them. What has caused such an unusual behavior?

Among the giant water bugs, *Abedus herberti*, females oviposit on the backs of males, and the latter carry them about until the first instar nymphs emerge and swim away. An egg-encumbered male of the common giant water bug, *Abedus herberti,* can be placed in an aquarium with a bit of water and a spot to perch, and an unusually high number—about 97%—of the eggs will usually hatch. In the mid-1970s, Robert Smith began with some simple questions. Does this high egg survival rate depend upon eggs being carried about upon the back of a live male water bug? If so, why?

Removing egg pads from the backs of six males, Smith placed each egg pad in a separate fingerbowl in the laboratory; three were covered with water and three were allowed to dry. None of the eggs survived; those kept in water developed a fungus after about four days, and those allowed to dry became desiccated. Repeating the experiment but first washing the eggs with distilled water, he got the same result. Was something about the male exoskeleton necessary to their development? Smith killed egg-bearing males and left them with eggs intact in their containers, but these eggs also failed to hatch. Attachment to a healthy male appeared essential for eggs to develop normally and hatch. Why?

Brooding males, Smith noticed, tended to prefer shallow water and seemed to continually be adjusting their position to keep their egg pad at or above the water's surface. Perhaps regular exposure to atmospheric air was a requisite for normal development. To test this, he placed an egg pad in a finger bowl and added water to a depth of less than 3 mm. Evaporative losses tended to expose the unattached ends of the eggs in the center of the pad, so he added water each day. After two weeks, he was excited to find that some of the centermost eggs began hatching. And although only 14 of the 72 eggs in the pad finally hatched, the success was a notable improvement over previous results. Nevertheless, it still appeared that the live brooding male was providing services beyond simply exposing the eggs regularly to atmospheric air.

Observing brooding males of a related species of belostomatid bug in the field, Smith noticed that submerged egg-bearing males frequently pulled their hind legs vigorously and repeatedly over their egg pad from front to rear, whereas unencumbered males only rarely stroked their backs, and then apparently only as part of normal grooming behavior. Perhaps such stroking also was necessary. Watching *A. herberti* males, he saw what seemed to be analogous behavior of a slightly different form. Egg-carrying males spent nearly one third of their submerged time in 'brood pumping'; resting on submerged

vegetation or the stream bottom, they rocked their bodies repeatedly forward and backward, pivoting on their middle legs while remaining in a fixed position. He also noted that before they began to rock or pump, males of both species patted or touched the eggs with their hind legs.

Was patting an essential precursor to pumping or stroking? Smith quickly peeled off egg pads after a pumping bout had been initiated but while the bug was still under water. The males all continued to pump. Later, when they felt about for the eggs and found them gone, they no longer would pump. Thus, Smith concluded that male water bugs used patting and stroking to inform themselves of the status of their egg pad.

Why should males take on such a task? It seemed evident that a brooding male is exposed to extra risks. The additional weight of developing eggs would impair his swimming and perhaps reduce his ability to escape predators. Smith measured swimming speeds of egg-carrying and unencumbered males and found that the latter could swim considerably faster. The behaviors involved in the father's parental care undoubtedly also increase risk of predation. Because water bugs normally rest motionless, protected by their cryptic coloration, pumping or stroking behaviors probably make them more vulnerable by betraying their location.

Perhaps males were merely being tricked into doing this work. If so, it seemed likely that they could be tricked into carrying any female's eggs with equal likelihood. Were male *A. herberti* carrying eggs that they had not fertilized themselves? Through detailed observations of *Abedus* mating behavior, Smith showed that courtship and oviposition were under overwhelming male domination. The male waterbug commanded the female to copulate, guided her into the copulatory position, signaled his desire to uncouple, and determined the length of time she was given to oviposit. He allowed no oviposition to take place at all until after the female had mated with him at least once and usually several times. Then, as the female began laying her eggs, he interrupted her frequently to insist upon additional copulations. As predicted by sperm precedence, by insisting on copulation prior to oviposition, the male water bug ensures that the eggs he receives will have been those that he has fertilized. By limiting the period of oviposition he also minimizes the chance that he will mistakenly accept eggs fertilized by another male. Does this mean that belostomatids are monogamous? Apparently not. Smith was able to show that males are able to simultaneously brood and fertilize multiple clutches of eggs from different females; bug's strict control over the situation would assure that these offspring were his own, as well.

Thus, Smith established that male giant water bugs have developed a whole set of courtship and mating behaviors that maximize individual male fitness by ensuring paternity and maximize female fitness by placing brooding behavior under male care and thus freeing themselves to capture the prey necessary to make additional clutches of eggs.

Smith proposed that male brooding in water bugs arose by *ancillary selection*, a form of natural selection that produces characters supported by primary traits. In this case, the primary trait was selection for large body size that occurred more than 150 million years ago. Larger bugs were able to take advantage of vertebrate prey, but larger size also meant larger eggs. Because of the way that insect eggs develop, those beyond a certain size cannot develop unattended under water, and thus the stage was set for parental care in these species.

Why should it not be the female water bugs, rather than males, that brood the young? An *enhanced fecundity hypothesis* that was originally proposed for birds may provide an answer. Basically, this model suggests that if one of the costs that a female incurs by brooding is a reduced ability to obtain nutrients needed to produce eggs, selection will favor male traits that reduce this cost and improve the number of offspring the pair can produce. Because males require only enough nutrition to maintain their body, rather than to maintain it and produce energetically costly eggs, they can invest in parenting behaviors at a lower cost than females can.

Research suggests that this theory applies very well to giant water bugs. In several feeding studies in which adults have been given generous prey opportunities immediately after mating, female water bugs have consumed many more prey than males have eaten. (In one case with goldfish, females killed five to nine times as many fish as males did over a seven to nine day period.) Males seldom feed while brooding, and also appear to be inhibited from feeding on prey in the size class of first-instar nymphs, an adaptation that may minimize the risk of males consuming their own hatchlings. Even stronger evidence was provided by a study that compared the effects of food limitation on fitness of males and females. One group was fed every day; the other received one prey every ten days. The results were dramatic. Both well-fed and poorly fed males sired statistically similar numbers of offspring. However, well-fed females laid 3.5 times as many viable eggs as poorly fed females did. Thus, as a result of freeing females to pursue prey while males assume the task of parental care, both sexes benefit through an increase in offspring numbers.

Because *Abedus* males insist on a copulatory bout after every few eggs, it can take hours before a female finishes depositing her full complement of eggs. Is the threat from other water bug males really so great as to require going to such lengths for paternity assurance? Smith mated a female to a male that was homozygous for a dominant genetic marker. Then he paired that female to another male that he had 'ductectomized' so that it was unable to fertilize eggs. When this sterile male's brood hatched, all bore the genetic label from the female's previous mate (Fig. 10.6), demonstrating both sperm precedence and a very real threat of cuckoldry in this species.

10.2.3 Solitary and Communal Nesters

All stages of the house cricket, *Acheta domestica,* spend the day concealed in nooks and crannies. As soon as they hatch, the larvae of bagworm moths (Psychidae) begin

Fig. 10.6   Brooding about baby. This male giant water bug has been made an experimental cuckold; the stripe on the first hatched nymph's back identifies its father as a genetically marked male that copulated with his mate before she was placed with him

making a mobile case of silk and environmental materials; extending the front as they grow, and excreting waste out the back, they move about, consuming vegetation. Adult males leave to mate, but females remain in the bag; birds that eat them pass the hard-shelled eggs unharmed, spreading the population. Across much of Australia, homeowners are familiar with the massive nests constructed in unusual locations by the continent's largest mud dauber wasps, *Abispa* (see Plate 35).

Many larvae take advantage of refuges, from naturally occurring crevices to cavities formed as a side effect of their own feeding. Others construct their own shelters as feeding contrivances, such as the funnels made by the ant lions and worm lions (see Fig. 4.6) and the cases constructed by caddisflies. Only the broadest definitions consider these to be nests, however. A *nest* is more often defined to be a structure that an adult animal builds to shelter its young, using available natural materials that it modifies in some way. When adults build nests for their offspring, the behavior is considered to be a hallmark of a high level of parental care. A *colony*, on the other hand, is the social unit that occupies the nest, consisting of brood as well as adults. (This distinction will become quite useful in discussing fully social insects later in this chapter.)

Leaving aside the complex nesting behaviors outlined in the 'social register' later in this chapter, let us consider here the solitary nesters, in which one adult or at most a pair of adults build the nest and in some species, defend it. These are not numerically common behaviors, but they have appeared in a taxonomically diverse array of insects, often occurring in those groups closely associated with the soil. For example, nesting is found in certain earwigs, burrowing crickets (Fig. 10.7), some cockroaches, various solitary bees and wasps, and a variety of beetles, including the dung beetles.

As an example, let us consider the latter. The term 'dung beetle' has commonly been applied to three subfamilies of the large beetle family Scarabaeidae. Only
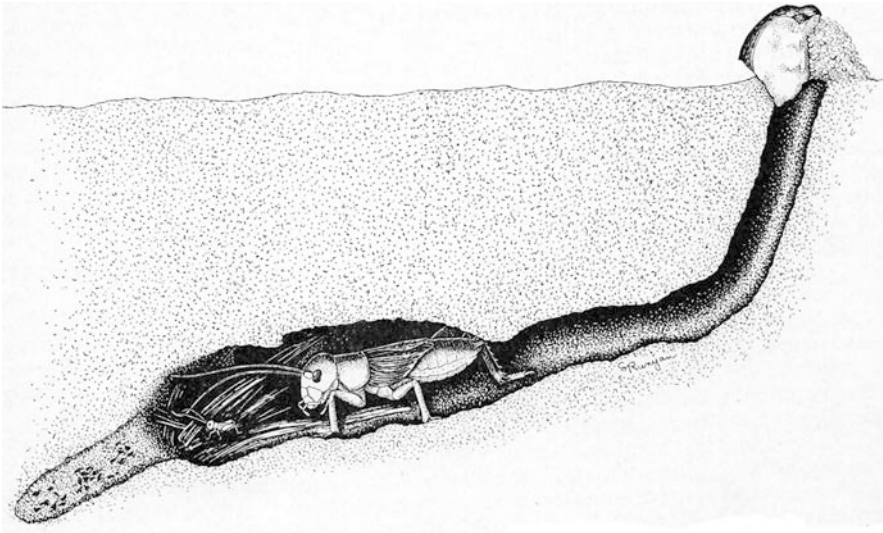
Fig. 10.7   Burrowing crickets. A female of *Anurogryllus arboreus* in her brood chamber. To the right is the exit burrow; to the left, a filled defecation midden. A single newly hatched nymph may be seen touching antennae with the mother, while an egg pile lies beneath her abdomen partly covered by soil. The chamber floor has bits of grass she has gathered, upon which nymphs feed. In this species, special miniature trophic eggs laid by the mother also serve as baby food, an unusual trait; these nonviable eggs are very attractive to the offspring, which crowd around them and fight for their possession

in the Scarabaeinae, however, are the vast majority of the roughly 4,500 species coprophagous, most feeding on the excrement of large mammals. No known adult Scarabaeinae have mouthparts capable of chewing or cutting solid food, hence when dung begins to desiccate it becomes unusable to them. This, plus the clumped discontinuous distribution of dung pats of many grazing animals, creates a fierce competition. Food relocation to constructed nests is a key behavioral feature of this subfamily and is thought to have evolved to reduce predation, parasitism, and competition, especially from coprophagous flies. Nest construction in this subfamily is nearly always the cooperative endeavor of a male–female pair. The association is a close one, and once a pair bond is formed, it endures, at least until after the dung has been lodged in its final resting place.

Gonzalo Halffter and his colleagues, the team responsible for the most comprehensive studies available on the natural history of dung beetles, recognize two major behavioral groups, burrowers (Fig. 10.8) and rollers. (A third small group are the dwellers.)

Burrowers, which include the well-known genera *Copris* and *Synapsis*, compact a piece of dung, cut it into spheres and place them in a nest they have excavated below or adjacent to the dung pat. The female beetle attends the offspring until they pupate, cleaning mold growth from the surface of the spheres and applying antimicrobial chemicals derived from her sternal glands. Males help dig the nest,
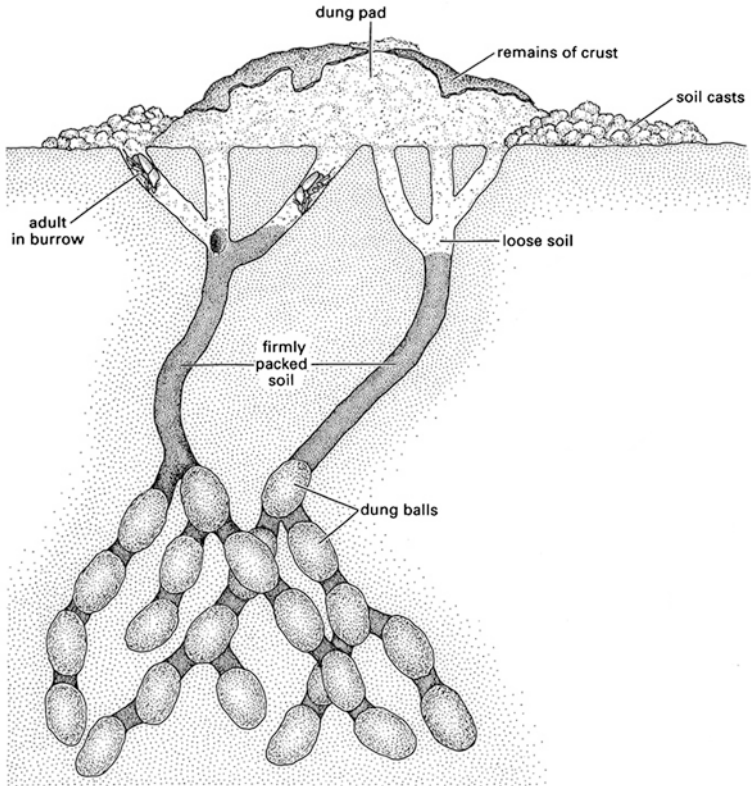
Fig. 10.8 Burrowing dung beetles. In burrowers such as *Onthophagus gazella,* couples excavate burrows below a dung source, then make a series of brood balls that the beetle's larvae consume as they complete their development

provision it, and compact the dung. During this period of participation, they also actively defend the nest using (in many species) the prominent horns on their head or prothorax.

Rollers (also called tumblebugs) (see Plate 36) are the second major group; they include most of the tribe Scarabaeini. The sacred scarab of ancient Egypt belonged to this group. The ability to roll a ball of dung overland (sometimes up to 40 m from the source) sharply distinguishes this group and results in a quite homogeneous group behaviorally. Generally the male pushes and the female pulls or rides on top, walking in place like a hamster on a treadmill. Because morphological adaptations to dung rolling (especially longer and more slender legs) often mean a partial or complete loss of digging ability, there are no elaborate nests or impressive excavations in this tribe, and some do not bury the brood ball at all.

The Australian continent lacks native large mammalian herbivores. Consequently, native dung beetles have evolved as specialists on the small bits of excrement characteristic of marsupials such as wallabies and kangaroos. With the advent of sprawling cattle ranches in northern Australia, cattle dung became an

unanticipated blight on the countryside as large amounts accumulated in the pastures. To restore the 'balance of nature,' Australian entomologists have imported several species of dung beetles from Africa. There is, however, one 'odd-ball' native Australian dung beetle that perhaps more properly should be called a 'compost' beetle. This beetle (*Cephalodesmius armiger*) is quite common in parts of northern Queensland where bisexual pairs dig elaborate burrows that they stock with dead leaves and other plant debris gathered from the forest floor. This plant matter is then prepared into small food balls to which the beetles add their own excrement and possibly a particular type of fungus, and eggs are laid individually in each ball. As a larva grows, biparental care continues; the male brings additional leaves that the female prepares and progressively adds to the food ball as the larva consumes it from within. When the larva pupates the female covers the exterior of the brood ball with a mix of excrement and remains in the nest until she dies. This species displays the most complex social behavior in its subfamily.

Extensive biparental care also is the hallmark of burying or carrion beetles of the family Silphidae, another group that has convergently evolved behaviors similar to dung beetles. They face a problem similar to that of the dung beetles, in that the cadavers that serve as their food are valuable, spatially unpredictable resources, for which competition is keen. To secure a small carcass prize such as a mouse against competing flesh flies and other carrion-feeding insects, *Nicrophorus* beetle pairs transport the carrion away from the discovery site, then bury it. Working below ground, they proceed to extensively process the carcass, removing its fur and adding embalming antibiotic secretions. They then cooperatively raise a brood of young, feeding them partially predigested meat, for which the larvae even appear to beg in a manner analogous to hungry fledglings in a nest. The parents also defend their offspring from predators such as staphylinid beetles and conspecific nest usurpers. One curious aspect of carrion beetle behavior is the propensity of females to lay more eggs than the carcass resource can support, only to later cull out some of the brood.

In their nest-building activities, wasps, ants, and bees exhibit some of the most complex behaviors known in invertebrates. We have discussed some of these before: the 'fixity of instinct' shown in the nesting activities of *Ammophila pubescens*, the interaction between predator and prey in the cricket-hunting *Liris nigra*, and the remarkable ability of the bee wolf, *Philanthus triangulum,* to learn the locality of her nest and the stereotyped sequence of behaviors involved in prey capture. All of these predatory wasps are in the family Crabronidae (formerly called Sphecidae), a large and diverse group.

Consider another example. In early summer, sand dunes throughout the world are alive with large yellow and black wasps flying briskly about low over the dune surface. Later, these flying wasps seem to dwindle in number, but closer inspection will usually reveal wasps quietly at work, each digging, filling with prey, then closing nest burrows in the sand. Each female does everything alone, without assistance from the others. A patient observer may be rewarded by the sight of a wasp suddenly appearing with a large, brown fly under her body held by her middle legs. The wasp alights, makes a few digging movements synchronously with her front legs, then quickly disappears through this previously invisible door. At the burrow's

end, several inches below the surface, one finds a chamber with a legless, helpless yellow-white grub feeding on the flies brought in by its mother. After eating about two dozen, the grub will spin a cigar-shaped cocoon inside which it will eventually metamorphose into an adult.

Like these sand wasps, the vast majority of wasps live solitary lives. Their nests belong to three broad types: those dug in a substrate such as soil, rotten wood, or plant pith; those constructed in preexisting cavities such as hollow twigs; and those constructed wholly of foreign materials such as plant pulp, mud (see Plate 35), or resin. Many of the details of solitary wasp nesting behavior appear to have been molded by biotic factors, notably various natural enemies and nest associates. For example, among ground-nesting crabronid wasps several species construct accessory burrows, blind-end false tunnels close beside the true nest burrow. In every case the accessory burrows are left open and the true nest entrance closed off. There is evidence that such accessory burrows divert the attention of parasites; bombyliid flies may lay their eggs in them (Fig. 10.9), and velvet ants often spend time investigating and digging in the bottom of such holes.

Species nesting in the soil have another problem relative to pests, namely, soil removal. A mound of dirt at the nest entry can be a dead giveaway of the presence of that nest. So while some species simply let the displaced soil accumulate outside the nest entrance, others carry out the soil a bit at a time in their jaws, flying off a short distance before dropping it to the ground. Still others push or rake the dirt backward out of the nest and then by a variety of behaviors remove or at least disperse
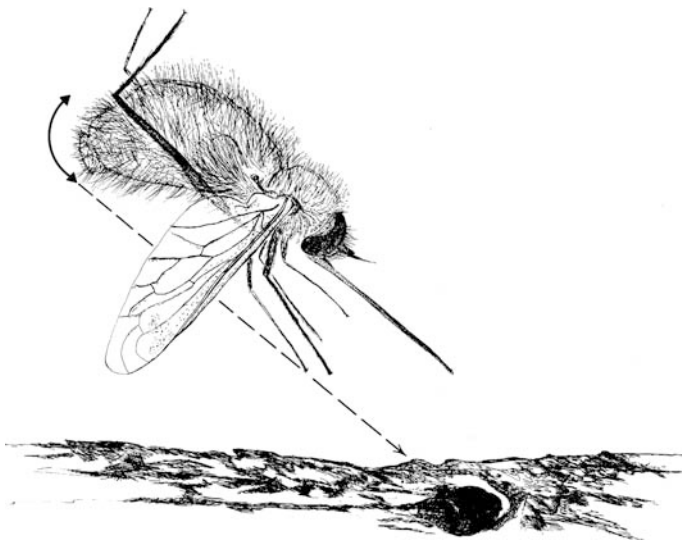
Fig. 10.9   Deceiving enemies. A bombyliid bee fly hovers over an accessory burrow of a solitary wasp. With repeated flicks of her abdomen she flings several eggs into the hole, which is actually a fake nest entrance made by the wasp
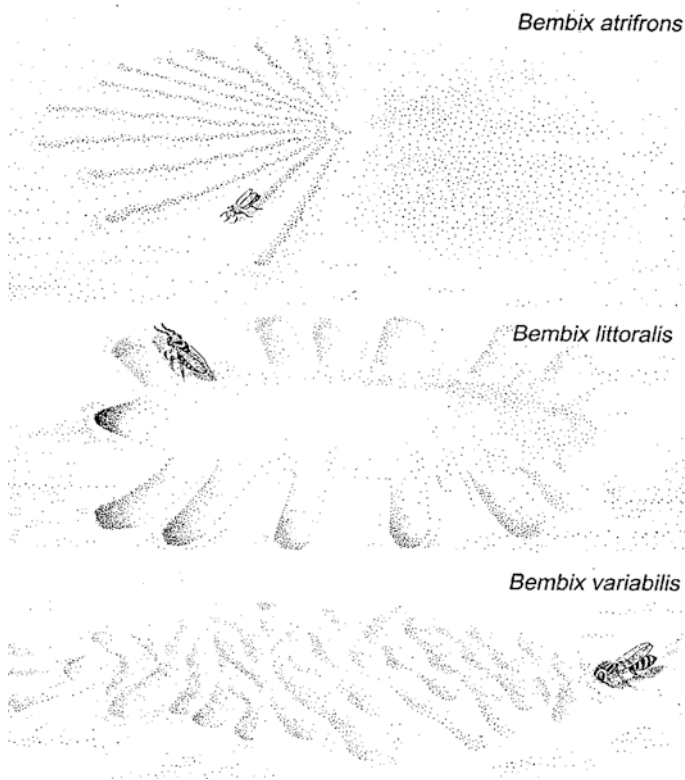
Fig. 10.10 Hiding the evidence. Patterns created by mound-leveling behavior of three Australian *Bembix* sand wasps during nest construction. Throughout both digging and leveling, synchronous motions of the long-spined front tarsi rake the sand, producing a species-characteristic pattern

the conspicuous mound. These leveling behaviors, which are a species characteristic, typically consist of repeated passages over the mound while scraping with the front legs and turning slightly from side to side (Fig. 10.10). The enigmatic resultant patterns, highly diagnostic of the species that made them, are often elaborate but ephemeral due to the homogenizing action of wind and weather. In addition to dispersing the mound, it has also been postulated that leveling may serve to disperse or cover any wasp scent that might be detected by foraging ants or other predators, parasites, or scavengers.

Solitary nesting species sometimes clump their nests into aggregations with conspecifics, in this way gaining some measure of support in defense, but many solitary bee and wasp species have evolved another strategy. Each female provides the food for her own offspring, but several females occupy a *communal* nest together. Such nest sharing takes various forms that differ in duration of association and degree of cooperation between females. In some species, females co-occupy nests soon after emergence and simultaneously provision different cells for several days, but

finally all but one of the females is forced out. In other species, females stay together apparently amicably for prolonged periods.

Several advantages for this communal behavior have been proposed, including increased efficiency at nest building, reduced parasitism, and improved nest defense. However, because communal nesting is uncommon, there must be substantial, if as yet largely unidentified, costs to this system as well. One almost certainly is the ever-present temptation for kleptoparasitism (see Section 4.2.5) and prey theft.

10.3 The Insect Social Register

Asked to name an example of a social insect society most of us would quickly come up with at least ants or honey bees, if not also paper wasps or yellowjackets. Awe-inspiring due to their complex division of labor, fierce defense of their nest, and sheer numbers, they fascinate scientists and nonscientists alike (Fig. 10.11). Yet these highly social species are in many respects only the tip of the iceberg. Diverse social arrangements have evolved in many other insect groups from bugs to beetles, and even caterpillars and cockroaches; insights gained from such diversity can help us to better understand and appreciate the highly social forms.
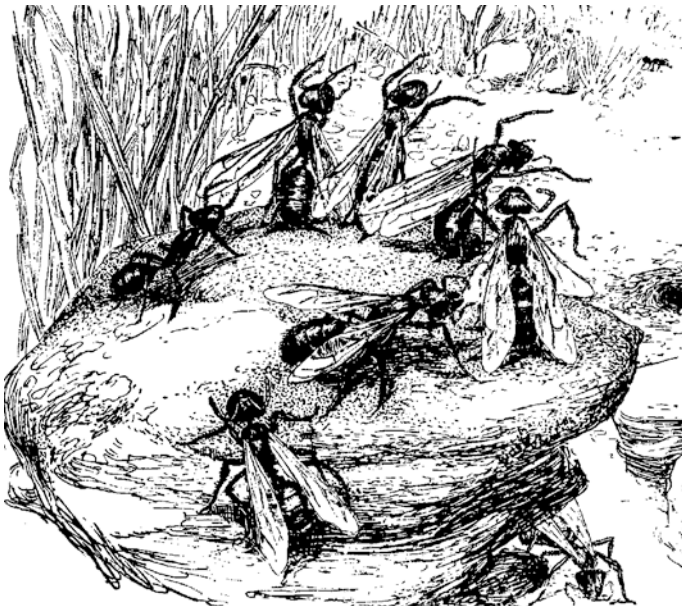
Fig. 10.11 Going places. The Rev. H. C. McCook, an early American myrmecologist, wrote this illustration's original caption, 'Winged female ants at play on the plaza.' Actually, these are virgin females preparing to leave on their mating flight

The name of this section is drawn from an old custom apparently specific to the United States; the Social Register is a directory of names and addresses of prominent American families who form the social elite in a number of major cities. These traditionally were the 'members of polite society' (i.e., those with 'old money'); recent editions now also include those with 'newer' wealth, the political or corporate elite.

Like that human social register, the insect social register includes the well-established examples, with a nod to newcomers. The level of social organization recognized as a society includes most instances of parental care discussed in the first part of this chapter. It also embraces some groups of developing individuals of the same generation (see Plate 37). Certain tent caterpillars, for example, spin a home web at which they gather gregariously to sleep and a feeding net which also serves as a protective community shelter; successful foragers deposit chemical trails that elicit preferential following by unfed individuals (see Fig. 6.13). In most insect species parents die before progeny mature, or else offspring disperse and do not remain associated with the parent. In some, however, at least some young persist with their parent(s) for one or more generations as an extended family living in some type of domicile (Fig. 10.12).

As in so many areas of biology, many of the first serious scientific efforts to understand social behaviors involved attempting to classify them. However, trying to cram the ever-expanding number of examples of insect social groups into existing

Fig. 10.12 Living in a log. Horned passalid beetles, *Odontotaenius disjunctus*, sharing a common tunnel system in a decaying oak log during the fall. During this nonreproductive season, both adult sexes are present but young are absent. In the following breeding season, pairs cooperate to rear a brood of larvae, sometimes with the help of other adults. Both adults and larvae produce a diversity of audible sounds in one of the richest auditory repertoires known for any insect, but their functions remain poorly understood

classification frameworks that date back to the early 1900s has led to such confusion as to call into question the value of such an activity. Even the widely cited traditional lexicon from the 1960s (pre-, sub-, quasi-, semi-, para-social) is cumbersome, somewhat teleological, and has difficulty accommodating the range and complexity of cooperative interactions of insects. Beginning in the mid-1990s a number of alternative classifications were proposed that ranged from conceptual expansion, to narrowing or redefining, to total abandonment.

Today there is a growing consensus in favor of a return to a broader, more inclusive interpretation of social behavior, with a shift in focus to the case-by-case examination of natural histories and a focus upon particular ecological constraints that promote group behavior. Thus, we retain only the term applied to the most advanced societies: *eusocial*.

While it seems that all levels of intraspecific interaction from completely solitary behavior to highly complex coordinated societies are found in insects, comparatively few species are eusocial. They number a few thousand species and are included in five orders, Hemiptera (bamboo and gall-forming aphids), Thysanoptera (gall thrips), Coleoptera (a bark beetle), Hymenoptera (ants, bees, and wasps), and Isoptera (termites). Molecular phylogenetic study suggests that the termites should properly be considered as a family of cockroaches (Blattodea), an idea that has a long and often contentious history (see Chapter 1). To minimize confusion we will mostly avoid using either ordinal name and simply refer to this group as the termites.

Eusocial insect species are traditionally considered to include only those whose societies meet three criteria: they live as groups of adults of different generations, with cooperative activity, and with different individuals obligatorily performing different roles essential for the success of the group. The last of these three is the essential defining criterion that sets the bar relatively high for admission to this exclusive club. As originally applied, it refers to the presence of a *reproductive division of labor*, in which there are sterile workers and one or more fertile queens. A broader but still succinct definition of eusociality has been offered by Edward O. Wilson, 'care across generations of the offspring of a reproductive caste by a non-reproductive or less reproductive worker caste'.

Castes are defined as a subset of the colony or group that is both morphologically distinct and behaviorally specialized. The physiology of caste determination is beyond the scope of this book, but appears to involve changes in regulation of highly conserved molecular pathways interacting with life history attributes in the different social lineages.

Division of labor is a prominent feature across all the eusocial insects, and worker and queen castes are the most common job descriptions. Among eusocial bees, wasps and ants, workers are female adults and usually sterile, although some may occasionally produce eggs. Among honey bees, highly developed task-related specialization has evolved; despite both being genetically female, the worker caste and the queen caste differ in at least 53 quantitatively distinct morphological features in addition to their obvious physiological and behavioral differences.

Caste polymorphism reaches its most spectacular development in termites, the other large eusocial group. Workers are of either sex and include immature stages as

well as adults. Queens of some species develop huge abdomens so distended with developing eggs as to resemble a small sausage (Fig. 10.13), and soldiers specialized for defense may exhibit either enlarged heads with powerful jaws or conical nozzle-like heads that eject a sticky substance (see Fig. 5.10).

In addition to caste polymorphism, as colony complexity increases and the range of duties surrounding the care of the young becomes correspondingly greater, in some cases an age-related division of labor also develops. For example, in the ant *Myrmica scabrinodis*, worker individuals that have emerged during the present season function as nurses; those that became adults during the previous season are builders, and even older individuals act as foragers. Such temporal *polyethism* reaches its greatest development among the honey bees. On emergence, a young bee works as a cleaner for about three days. After this, coincidental with labial gland development, she becomes a nurse, producing secretions with which she feeds larvae. About the tenth day of her life her abdominal glands begin to produce wax and her labial glands atrophy; she becomes a builder. At about the sixteenth day she begins to receive nectar and pollen loads from foragers and stores them in the comb. On about the twentieth day, she fills the post of guard. Finally, she becomes a forager, working at this for the rest of her life. Age polyethism, though well developed, is not inflexible. If a hive is divided so that one half contains only young bees and the other only older foraging bees, after a few days of adjustment, workers in each half carry out all normal hive tasks (see Case Study 1.1).

10.3.1 The Ants

Of all eusocial groups, ants are the most widespread and numerically abundant and contain more known genera and species (approximately 12,000) than all other eusocial groups combined. In variety of ecological and social adaptations they are unparalleled.

Like the termites, early ants nested in soil and leafy compost, putting themselves in position to exploit an extremely rich microhabitat and to build and maintain long-term nests in a protected location. However, because they began as predators upon other arthropods (see Plate 38), primitive ants were not bound like termites by a cellulose diet dependent on intestinal symbionts. The development of a wingless worker caste, an innovation already present as far back as the mid-Cretaceous period, increased ants' ease of access into soil and plant crevices. Acids secreted from the metapleural glands, an anatomical development possessed by all ants but by no other Hymenoptera (see Fig. 6.1), inhibit the growth of microorganisms in their moist nest chambers.

Most ants live in soil still, either excavating chambers or constructing elaborate mound structures. Many others, however, have adopted an arboreal existence with tough carton-covered nests or homes in hollow twigs or specialized plant parts such as hollow thorns (see Plate 8). Others like the leaf-cutter ants (see Chapter 4) cultivate gardens of fungi. Weaver ants (see Plate 19) are unique in their use of larval silk to fasten leaves together to form large baglike nests. Members of the largest ant

Fig. 10.13 Social insect castes. (*above*) Two castes of the African termite *Macrotermes*. The soldier's huge head serves in colony defense, but soldiers must depend upon the smaller workers to feed them. (*below*) The extreme physogastry of this termite queen dominates the picture; her sausage-like abdomen greatly overshadows her tiny head and thorax. Her abdominal tergites have become pulled widely apart by the stretching of the intersegmental membranes and appear as crescent-shaped islands on a sea of whitish membrane. Attending the queen are numerous workers
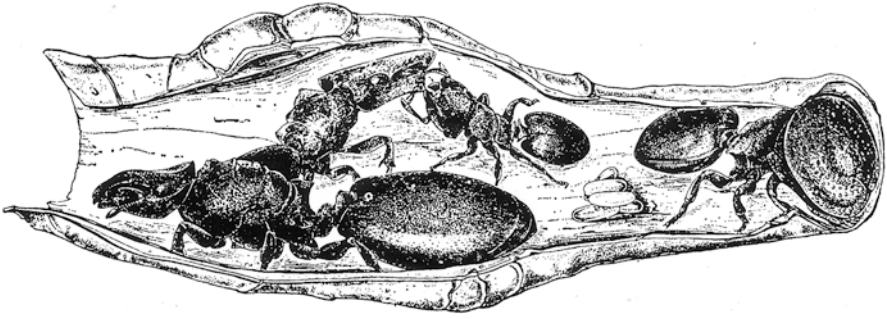
Fig. 10.14   Blocking entry. A colony fragment of the myrmecine ant *Zacryptocerus varians* in a hollowed-out stem of red mangrove. Three female castes are shown: the queen rests on the floor of the nest to the left, while on the right a large major worker blocks the nest entrance with its saucer-shaped head. Behind the queen another major worker receives regurgitated liquid from a minor worker

genus—the carpenter ants (*Camponotus*), with about 1,500 species—excavate nests in wood. In a number of wood nesters, larger workers possess distinctive disc-shaped heads used to form living plugs at nest entrances (Fig. 10.14).

Some ants make no permanent nest. The term 'army ant' popularly includes any of the 200 or more carnivorous ant species that live as nomads and send out sorties of great numbers of workers. In a stricter sense, 'army ant' applies just to members of the ant subfamily Dorylinae, awesome predators that pioneer myrmecologist William Morton Wheeler called the 'Huns and Tartars of the insect world.' Nearly blind, these predominantly tropical ants feed almost entirely upon live arthropods captured during mass expeditions or raids. Moving like great armies across the land, overcoming every obstacle in their path, even bridging small streams with living suspensions of workers, they seem to have military precision. Columns of ants maintain infantry formation while, like a real army, being accompanied by both scouts and fighting soldiers.

The first investigator to study army ant behavior objectively in detail was Theodore Schneirla, who spent over 35 years studying *Eciton* in both laboratory and field. Case Study 10.2 presents some of his work, in which he demonstrated that the interrelationships among colony members provide the driving force for the cyclical behavior of army ants (Fig. 10.15). Over time, it has become increasingly clear that pheromonal mediation takes place in the army ants and that the ultimate adaptive significance of the alternation of quiescent and nomadic phases is to protect not only the helpless young but the queen as well through a time when both are most vulnerable. While little mention of the queen's role in the two phases has been made, early in his studies Schneirla observed that queens captured during the nomadic phase had considerably less swollen abdomens than those captured during the statary phase. The queen lays her clutch of thousands of eggs all during just a few days in the mid-statary phase. As the colony enters the nomadic phase, her ovaries cease activity.

Case Study 10.2: Cyclical Foraging in Army Ants, *Eciton*

Any first-time visitor to lowland rainforests of the New World tropics will quickly note the ubiquity of ants patrolling nearly every surface. Periodically, conspicuous hordes of army ants ominously swarm over every piece of vegetation driving hapless arthropods before their onslaught. How is this system maintained?

Each day within the tropical forest, *Eciton* workers stream out at dawn to begin their raids anew, their branching columns quickly overrunning areas up to 100 m from their nest. At the front line, biting, stinging ants attack insects and other arthropods, tearing their prey apart and carrying the softer pieces back to the nest so that the forest floor soon has a series of two-lane highways traveled by steady streams of advancing raiders and returning victors. So efficiently does the massive raiding progress that one colony may haul in more than 100,000 other arthropods in a single day. Then, as night begins to fall, the whole colony begins to emigrate along one of the day's principal raiding trails. Moving in solemn procession, sometimes through most of the night, the colony finally settles in a new *bivouac*, or temporary camp, often under a low-hanging branch or vine. After about two weeks, however, the colony's behavior abruptly changes. It appears to quiet down and enter a *statary* phase. Few workers go out on raids; when they do, the forays are much smaller. No longer do nightly migrations occur. Remaining at the same site for about three weeks, the colony acts as though it had gone partially dormant. Then, just as abruptly, a new *nomadic* phase of intense foraging activity begins.

What factors underly such spectacular phasic behavior? Walter Schneirla decided to investigate. At the time, most scientists accepted a straightforward and seemingly logical explanation: depletion of food supply. The army ants, they argued, simply stay in one place until the food supply is exhausted and then move on to new hunting grounds. However, an alternative explanation also had some appeal. Perhaps the cycles were cued to some environmental phenomenon, such as phases of the moon, or perhaps changes in temperature, humidity, or air pressure.

Detailed observational data on colonies in the field were sorely needed. Schneirla began following a single colony, then another and another, through one or more complete cycles. Painstakingly, he logged a dozen armies through whole cycles and more than a 100 more through partial cycles, taking down data in the field and repeatedly sampling the internal colony composition at various stages of the behavioral cycle. One thing quickly became clear. Within a single environment, several colonies were often present; of this number, some were generally in the nomadic phase, others in the statary phase. This seemed to rule out major environmental factors as the determinant of the
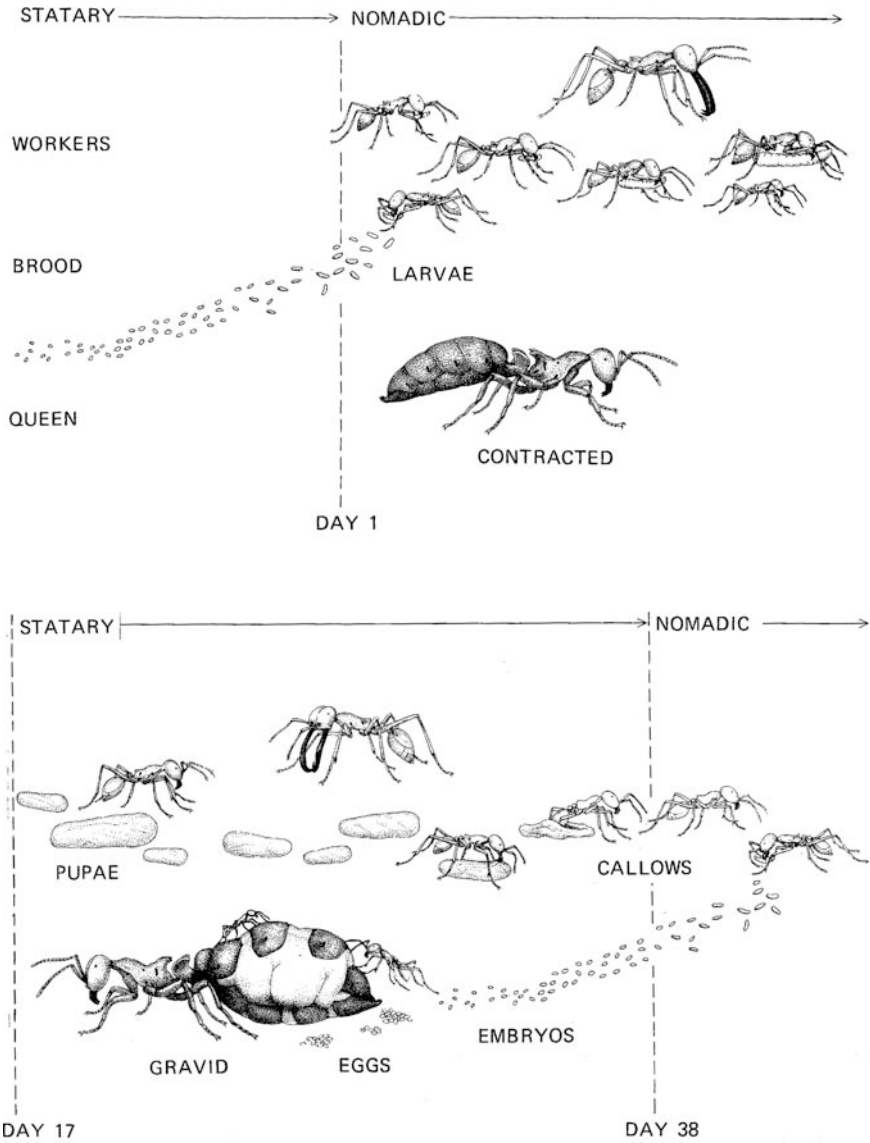
Fig. 10.15 Raiding ant cycles. The alternation of statary and nomadic phases in the colony cycle of the army ant, *Eciton burchelli*. Nomadic phases are triggered by worker–callow interactions and maintained by worker–larval interactions. As cocooning of mature larvae begins, intensity of mutual stimulation between adults and brood declines temporarily and the colony lapses back into the statary condition until the pupal brood emerges

nomadic cycle. The second hypothesis was more difficult to substantiate or reject, but persistent observation eventually provided a clue. Schneirla was able to confirm that a nesting site vacated by one colony would sometimes be moved into by a second colony the following night; in some cases the newcomers would remain for the whole three-week statary period. These observations seemed clear evidence that the food supply around the bivouac had not been depleted.

This, of course, left Schneirla without an established hypothesis for the colony cycle. As he began to analyze brood samples from different stages in the behavioral cycle, however, a new picture began to take shape, implicating the breeding cycle within a particular colony as the determinant of its cyclical behavior. The nomadic phase, it appeared, always coincided with the period when a larval brood was developing in the colony. The statary phase, on the other hand, always seemed to begin at the point when mature larvae started to spin their cocoons. In fact, the statary phase coincided with a point in which only pupae or newly laid eggs were present, neither of which required daily feeding by the workers.

A sentimental explanation was this: while helpless young exist, the workers protect them with a fixed bivouac, but once eggs hatch and pupae eclose, the workers must suddenly feed this massive number of new mouths, so they become nomadic. Although this might explain the adaptive significance of such behavioral cycles, it does little to elucidate proximate mechanisms. Impressed by the role of trophallactic interactions among all social insects, Schneirla turned to that phenomenon for his answer. Although by the end of his first trip to the tropics he could only phrase it loosely, Schneirla was able to theorize that the regular fluctuations in *Eciton* colony activity were regulated by some sort of stimulative interactions between the colony's large developing broods and the adult workers. What might these 'stimulative interactions' be?

In the field and in the laboratory, Schneirla watched as workers cared for pupae of different ages. During maturation in their cocoons, pupae appeared to become progressively more attractive to the workers; these handled them more frequently, even partially tearing the cocoons open. Upon emergence, the new adults (callows) became the objects of much licking, stroking, and handling by the older adults; in turn, the callows themselves became quite hyperactive. This reciprocal stimulation resulted in a rising crescendo of excitement that soon seized the whole community and led invariably to colony emigration initiating the nomadic phase.

Although he had no evidence of pheromone involvement at this time, Schneirla had no trouble calling this a trophallactic interaction because he interpreted trophallaxis broadly to include not only the actual exchange of food but the mutual exchange of all 'equivalent' stimuli, including touch. Whatever the mode, some sort of bond among colony members was obviously

being forged. Colonies from which he removed all callow brood appeared lethargic in contrast and invariably failed to initiate nomadic behavior at the expected time.

But while trophallaxis between workers and callows was appealing enough in theory, Schneirla's observations at this point did not rule out a second possibility, namely, that the necessity to feed developing larvae and new adults was causative. In fact, during later stages of the nomadic phase when the larvae had grown and developed voracious appetites, they seemed to become the source of the colony 'drive.' To test the role of larval brood in stimulating the workers' activity, Schneirla split a colony into two parts of comparable size. In one group he left the larvae intact; in the other he removed them. The workers in contact with larvae continued to show considerable activity, but those in the broodless portion were much less active. In another experiment, Schneirla removed the entire larval brood from a colony that was in the nomadic phase. True to expectations, the colony stopped emigrating, and the intensity of its daily raids diminished.

Army ants display a remarkable syndrome of traits—nomadism, obligate collective foraging, and permanently wingless queens whose abdomens alternately swell to enormous proportions and then shrink. What controls the queen's reproductive cycle? Schneirla postulated that the queen was stimulated to feed in excess because of the intense worker activity that occurred when mature larvae began to reduce feeding demands prior to spinning cocoons, thus freeing an abundance of food. The brood cycle may well serve as an endogenous pattern generator that triggers a cyclical cascade of physiological changes in the queen.

10.3.2 The Eusocial Wasps

Eusociality in wasps is almost wholly restricted to some members of a single family, the Vespidae. The paper wasps (Polistinae) and the yellow jackets and hornets (Vespinae) are entirely eusocial; eusociality is facultative in the hover wasps (Stenogastrinae) of the Old World Tropics. All of the most commonly encountered eusocial vespids construct nests of paper made from plant fibers chewed off weathered wood and/or dead plants, but hover wasp nests are often constructed of mud.

The nests of eusocial wasps are begun by mated females called *foundresses*. Life on a social wasp nest is a matter of uneasy and shifting alliances, so no consideration of social wasp behavior is complete without a discussion of *dominance*, a ranking of individuals on the basis of real or apparent authority, strength, or influence. The dominance concept implies an ability to recognize individuals and remember relationships, and results in a ranking called a dominance hierarchy. Particularly evident in species with long-lived adults, dominancy hierarchies can be found not only

among social wasps, but among dragonflies, crickets (see Fig. 8.10), and passalid beetles, among others.

In the life of a social wasp nest, a *colony cycle* is the period of development that lasts from the end of one reproductive episode to the end of the next. In temperate species nests are normally annual; one foundress or a group of them starts a nest, which grows and expands until late summer or autumn, when a reproductive phase culminates in mated females overwintering to start the cycle anew the next spring. *Polistes* paper wasps provide a good example. Sometimes, a single queen must find a new nest location on her own, and bear the risk of nest building and foraging for herself and her first batch of young. In other cases, groups of females join together in the spring to begin their nests, but each fertile potential queen then competes in laying eggs, and soon relatively rigid hierarchies are established. Dominant *Polistes* maintain their reproductive superiority by three means: laying the greatest number of eggs, physically removing and eating the eggs of any subordinates that may have succeeded in ovipositing, and demanding and receiving the greatest share of food. Interactions between dominant and subordinate individuals are often matters of posture; the dominant individual rises on her legs above the subordinate, which crouches and lowers its antennae (Fig. 10.16). The dominant female also performs a conspicuous side-to-side vibration of the abdomen (tail wagging) more frequently than other individuals do. *Polistes* castes are difficult to distinguish morphologically but they are behaviorally clear. During the first half of the summer, only workers are produced. In late summer and early fall, sexual forms (males and reproductively competent females called gynes) start to appear; concurrently, the colony slowly declines, finally abandoning the nest entirely.

Fig. 10.16   Bullying nestmates. Dominance and subordinance behavior in the paper wasp *Polistes fuscatus*. The female on the left shows the relatively elevated posture characteristic of a dominant individual. The subordinate (*right*) has been seized at the hind leg and crouches with antennae lowered

For tropical social wasps, on the other hand, seasonal constraints may be less rigorous, and in many species the components of the colony cycle seem to have become dissociated. Several cycles of brood may be produced before a reproductive brood is produced, a nest may be used for variable lengths of time of up to several years before it is abandoned, or a colony may routinely occupy two nests successively before producing any reproductives. Many of these tropical species start their colony cycle with swarm-founding. A *swarm* can be thought of as a reproductive unit that is essentially a colony without a nest or brood. In honey bees, it consists of a hive's old queen and about half of the workers; the remainder stay behind with a new queen and the brood that are already in the hive. In swarm-founding wasps, it consists of a group of reproductives that disperse, leaving a fraction of the population back at the nest to repeat the colony cycle.

There are many advantages to swarm-founding, including reduced risk for the queens. Rather than scouting for a new nest site, they remain in the security of the natal nest while workers take on this job, and are exposed only while flying to the site. In addition, they never have a period where they must take on the risks of foraging. Finally, having a large worker force from the start provides the strong defense that is needed against predators, in particular ants, a formidable enemy force in tropical regions (Fig. 10.17).

Nests covered by envelopes are universal to the second group of eusocial wasps, the vespines, a predominantly temperate group that includes the hornets and yellowjackets. Their annual nest cycles (Fig. 10.18) are basically similar to that of *Polistes*, except that the queen and worker castes are morphologically distinct. Most species of yellowjackets construct subterranean nests; hornet nests are typically aerial or built within hollow trees. Most wasps feed upon a variety of arthropods
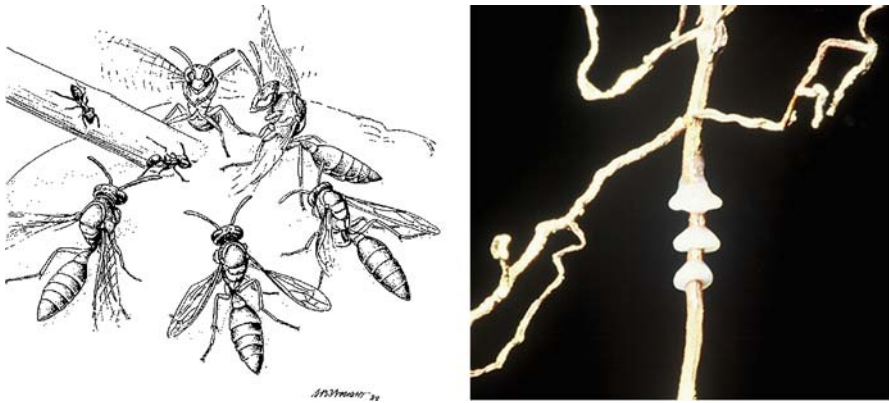
Fig. 10.17 Defending the fort. (*left*) *Polybia occidentalis* workers rear back and buzz their wings in short bursts, directing intermittent blasts of air at two fire ant (*Solenopsis*) foragers that are attempting to climb on the nest. Ants that face this windstorm usually retreat, If an ant does pass the defenders, a wasp will grasp the ant in her mandibles, carry it away from the nest, and drop it. (*right*) 'Ant guards' made by the hover wasp *Parischnogaster* on a rootlet above the nest attachment. The substance is secreted by the Dufour's gland and applied to the substrate
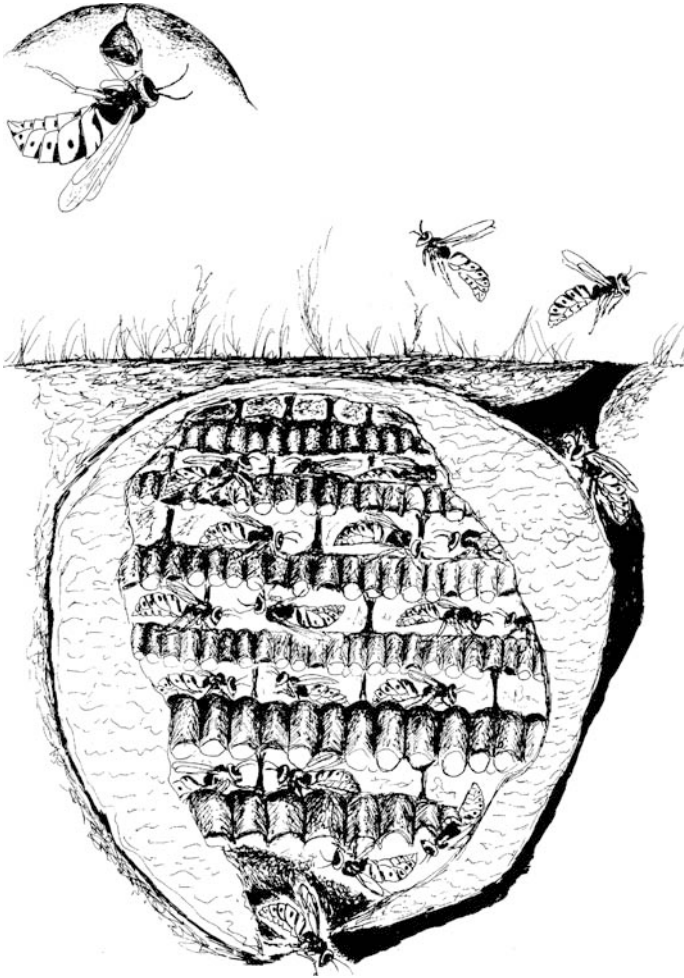
Fig. 10.18 Seasonally changing. The annual colony cycle of a yellowjacket wasp (*Vespula*) includes solitary and colonial phases. In early spring fertile queens awaken from hibernation and alone initiate nests by constructing a few paper cells hung from the top of a preexisting soil cavity such as an abandoned rodent burrow (*upper left*). After the first workers emerge the colony grows rapidly through the summer, with the nest ultimately reaching the size of a basketball. By late summer, cells of the bottom combs (here two) are distinctly larger than those in the uppermost combs. These bottom cells give rise to males and virgin queens, while the cells in the upper combs produce only workers. From this point the nest declines. Almost always, only the newly produced queens overwinter to repeat the cycle the following year

caught alive and carried back to the nest piecemeal in their jaws, but some yellowjacket species become nuisance pests, scavenging around picnic and recreation areas, especially in late summer.

The Stenogastrinae, the third social vespid group, are delicate slender wasps with hovering flight that are denizens of rainforests of the Indo-Pacific region. The

approximately 60 species are poorly known, and their colonies never become very populous.

Outside the Vespidae, almost no other wasps are eusocial. However, a group of four genera in the family Crabronidae are apparently unique in producing silk from abdominal glands that have not been found elsewhere in this wasp family. The silk is used in nest construction, and more than one adult is commonly found in these nests, suggesting the possibility of social behavior. The most completely studied species, a tiny Central and South American wasp called *Microstigmus comes*, preys exclusively upon Collembola. Inside its pendent bag-like nests (Fig. 10.19) as many as 11 females cooperate in nest defense and cell provisioning; genetic evidence indicates that colonies include a mother and her daughters, with one female having well developed ovaries.

10.3.3 The Bees

Few insects are more familiar than the ubiquitous honey bee. Elsewhere, we have discussed its unique dance language, its ability to sense the earth's magnetic field and other sensory capabilities, and the multiple roles of the queen substance pheromone in colony life. At this point it is appropriate to put the honey bee into perspective as but one of several hundred species of eusocial bees, surrounded by many times that number of relatives showing all manner of social behaviors, because the bees, more than any other insect group, display the full spectrum of social evolution.

Bees have arisen from a different part of the Hymenoptera phylogenetic tree than ants and vespid wasps, but are so like crabronid wasps that they can be regarded as being simply a sort of wasp that has specialized on collecting pollen instead of insect prey as larval food. For over 50 million years bees have evolved in close contact with the angiosperm plants upon whose flowers they depend. Social behaviors of various kinds crop up repeatedly, but eusociality appears independently in two of the nine families of bees recognized today—the Halictidae and the Apidae.

The Halictidae are a behaviorally diverse family of over 5,000 species of mostly small insects that are often called 'sweat bees' because of their often-annoying habit of lapping up perspiration from people's skin during hot weather. In many areas of the world, they are more important elements of the bee fauna than most people recognize; for example, in one study, halictid bees accounted for up to half of all the individual bees collected on flowers at one site. Most halictid bees nest in soil; a few nest in rotting wood. Many halictid bees nest in aggregations that can be dense (150–200 nests per square meter have been reported) and sometimes long-lasting (35 years in one report). Because aggregations are easier to find than individual nests, they are better studied. They also are easier for predators to locate; in a study of *Halictus rubicundus*, cell mortality was twice as high for aggregated nests as for isolated nests.

Social behavior is extremely variable in sweat bees. Solitary, variously social, and parasitic behaviors occur not only among lineages but sometimes among and within populations. Three independent clades in the family show eusocial behavior.
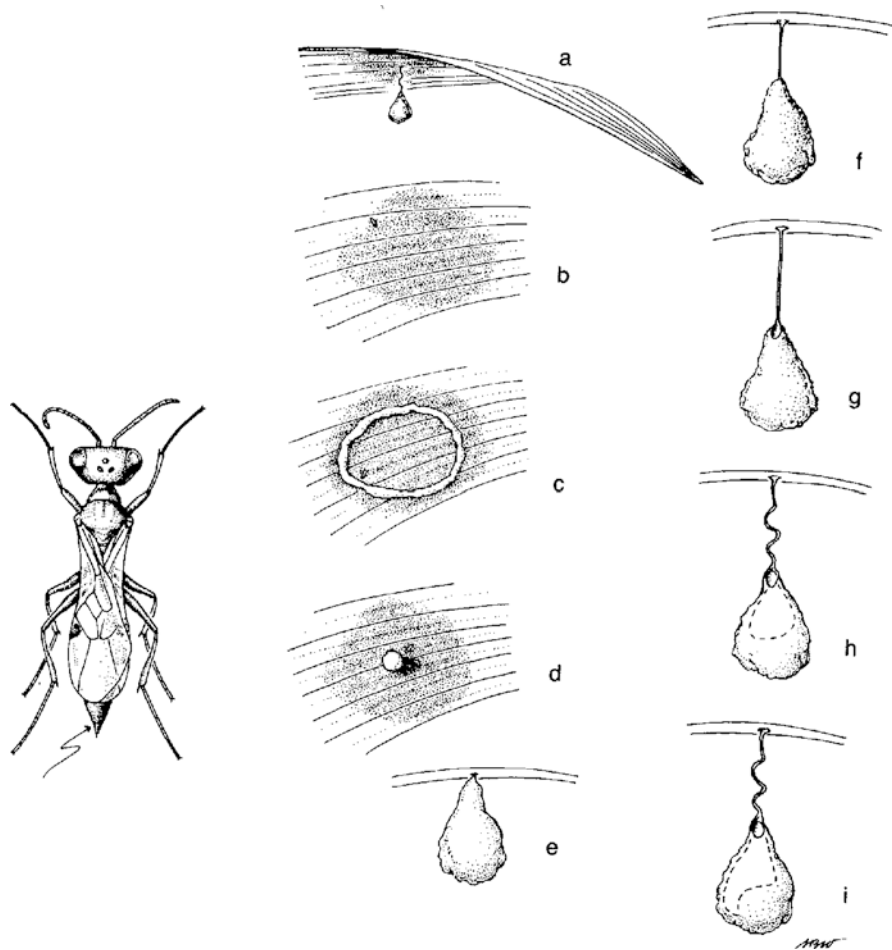
Fig. 10.19 Crafting with silk. Thumb-sized nest constructed by the eusocial crabronid wasp, *Microstigmus comes*. The nest is formed of plant fibers bound together by silk thread produced by unique glands found in the tip of the adult female's abdomen (*arrow*). The plant fibers are first loosened and scraped from an area on the underside of a palm leaf (**a, b**), then gathered together to form an undifferentiated mass which is bound with the silk (**c–e**) and then slowly lowered on a silken thread pedicel (**f**). The pedicel coil and entrance hole at the base of the pedicel are then added and the upper portion of the interior hollowed and prepared with the first cell (**g–i**)

Within certain sweat bee colonies, even if there are only two individuals, one is a female that has mated, has developed ovaries, lays eggs, eats others' eggs, dominates others, rarely forages for pollen and nectar, and is the oldest or largest; the other has not mated, has underdeveloped ovaries, lays few eggs and has these eaten, is dominated, frequently forages or guards the nest, and is younger and/or smaller than others.

Whether halictid bees were once fully social and are evolving toward solitary behavior or vice versa continues to be a matter of academic debate. As might be expected with such a large group, the majority of sweat bees are still unknown behaviorally, and information is limited for many others. Furthermore, most of the species that have been studied are from the temperate zone, where environmental correlates such as flowering synchrony may influence social biology.

The family Apidae includes many eusocial members. The true honey bees in the genus *Apis* are the best known, but another group shares many behavioral similarities with them. The Meliponini, or stingless bees are among the most conspicuous and numerous bees in these tropical regions. Like honey bees, these bees live in perennial colonies that produce new colonies by swarming; individual queens or workers cannot survive alone for long. Furthermore, both have queen and worker castes that differ, behaviorally, physiologically, and morphologically. They both develop large populations, up to 180,000 workers in some stingless bee species. Colony integration and communication are necessarily complex, and both of these bee groups have evolved elaborate means of communicating the location of food sources (see Chapter 8). Both honey bees and stingless bees also build nests with wax secreted from abdominal glands. Larvae of both are reared in individual cells arranged in combs within the nest, while separate cells are used to store honey and pollen (Fig. 10.20). However, honey bees and stingless bees belong to different clades, and do show other differences. One major difference is that meliponine larvae are mass provisioned; those of *Apis* are fed progressively. Another is that honey bees defend their nest by stinging; meliponines defend theirs by aggressively biting intruders.

Another social group familiar to almost everyone is the genus *Bombus*, which includes the robust hairy bees commonly called bumblebees. Bumblebees are characteristic of cool north temperate climates around the world; with few exceptions, they have not succeeded in invading the tropics, except at high elevations where they may become very abundant locally. A behaviorally cohesive group, all of the more than 250 *Bombus* species have relatively small annual colonies (Fig. 10.21) founded by a single overwintered queen. Abandoned rodent burrows are preferred nest sites; inside, a queen fashions her nest from wax secreted by abdominal glands. Rather than directly feeding her brood as do other eusocial groups, the bumblebee queen characteristically stocks pollen and honey separately from the brood cells in special wax storage pots. She then lays several eggs together in a single distensible wax brood cell; thus, the bumblebee larvae are reared in groups but since they are contained in a capped cell with their entire food supply, there is no trophallaxis contact between parent and offspring.

Finally, some unusual eusocial behaviors are found among the so-called allodapine bees. Unlike the nests of all other known bees, those of allodapines have no cells. Larvae are kept together on the nest floor like ant larvae, and like the young of ants they are moved about the nest by the mother and arranged in groups according to age (Fig. 10.22). Allodapine larvae are fed progressively, being given more frequent pollen meals as they grow, a behavior that promotes mother–offspring contact. In most species, the mother dies before her young emerge, but in some species
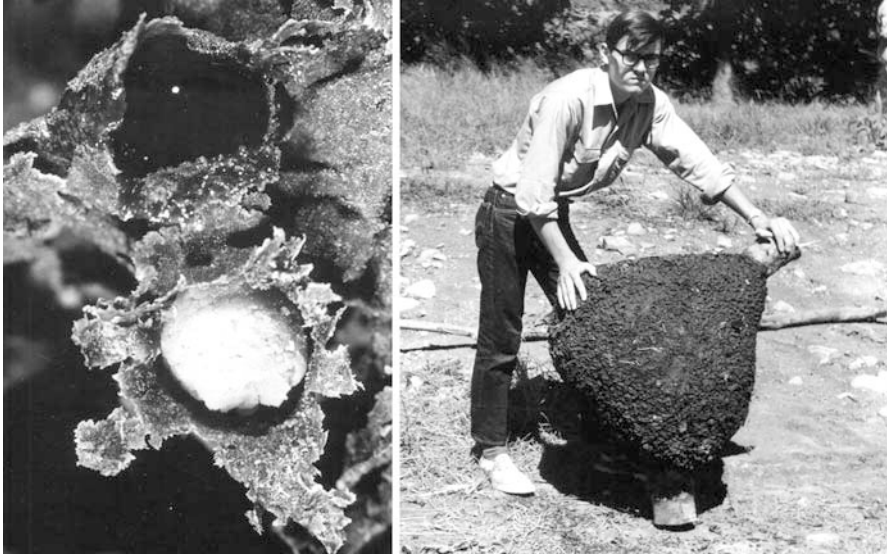
Fig. 10.20 'Beeing' stingless. One of the species of stingless honey bees of the genus *Trigona* from Costa Rica builds large aerial nests (*right*) of secreted wax mixed with large amounts of resin to form a tough material called cerumen. Inside the nest, pollen and honey pots (*left, below and above* respectively) fill the brood chamber. While *Trigona* cannot sting, they actively defend their nests by vigorously biting intruders

the mother's life overlaps the adulthood of her offspring, who often remain in the parental nest and help rear a second generation.

10.3.4 The Termites

A cosmopolitan but predominantly tropical group, termites include more than 2,600 species. All of them are eusocial. Termitidae is by far the largest family, and contains the most advanced species. Because termites mostly feed on dead plant material, they are of considerable ecological significance, particularly in subtropical and tropic regions; a significant number also are economically significant as pests that can cause serious structural damage to buildings, crops or plantation forests. Often the first external evidence of infestation may be when they swarm (Plate 45).

Along with the closely related *Cryptocercus* cockroaches (see Plate 39), termites are the only wood-eating insects that depend on symbiotic intestinal protozoans and bacteria to break down energy-rich but nitrogen-poor cellulose into usable sugars (see Chapter 4). It appears that termite societies began as feeding communities and only later evolved social brood care, in a sequence that is the reverse of social evolution in the Hymenoptera.

Termite nests are essential to termite life, because termite workers have a soft cuticle and are easily desiccated if exposed directly to the outside environment. A

Fig. 10.21 Living in a mouse nest. A colony of the European bumblebee, *Bombus lapidarius*. The larger individual at the *lower center* is the queen, resting on a cluster of pupae-containing cocoons. At the *upper left* are several communal larval cells. Open cells contain pollen or honey
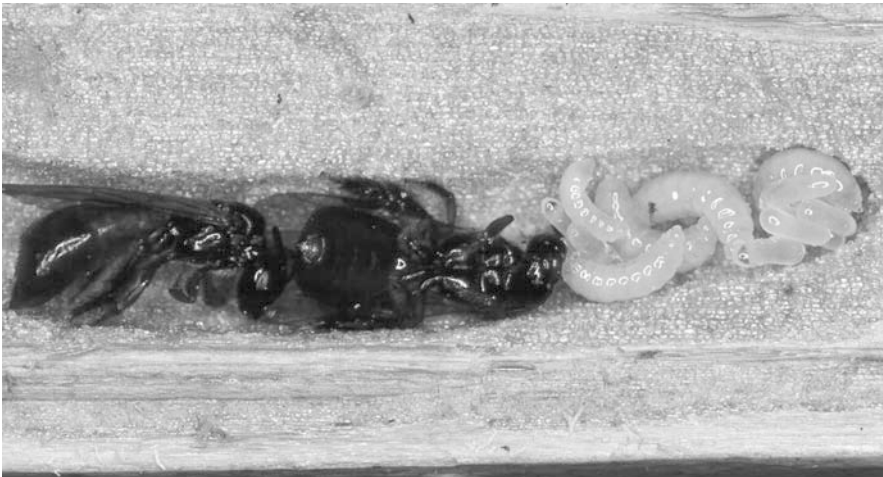
Fig. 10.22 Developing progressively. A nest of an allodapine bee, *Exoneura*, showing eggs and developing brood grouped together in an opened pithy plant stem. Larvae are fed progressively on small pollen balls brought in by cooperating female bees
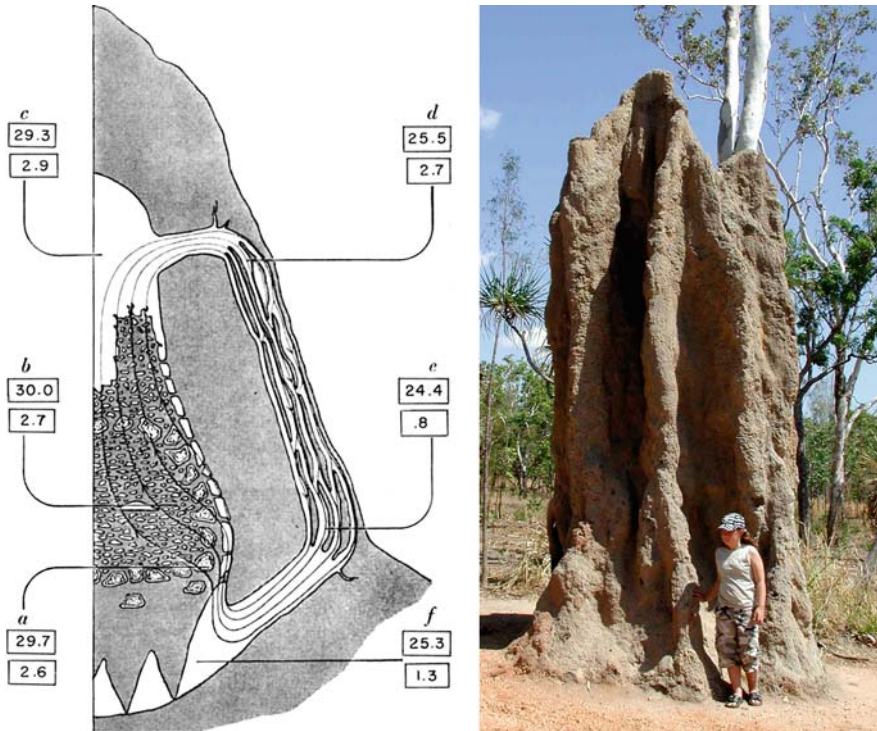
Fig. 10.23 Ventilating the fort. (*left*) Environmental control in a termite nest is evident in this cutaway view of the interior of the nest of *Macrotermes bellicosus*, an African fungus-growing termite, that shows the temperature and percentage carbon dioxide concentration at different positions. Metabolic heat from the huge biomass of colony members is concentrated in the central core of the nest, rises by convection to the large upper hollow cavity, then diffuses toward the sides where it flow into a network of narrow channels close to the surface; here the air is cooled, and gaseous exchange occurs by diffusion through the thin dry walls. Refreshed air then sinks to the lower passages of the nest and eventually recycles. (*right*) Cathedral mound of *Nasutitermes triodiae* from northern Australia

typical colony contains eggs, nymphs, workers, soldiers, and reproductive individuals of both genders, plus one to several egg-laying queens. Nests are punctuated by a maze of tunnel-like galleries that effectively ameliorate air temperatures (Fig. 10.23) and control carbon dioxide/oxygen balance, as well as allowing the termites to move through the nest; foraging is typically done along radiating covered tunnels built out from the nest. Constructed of soil, excrement, and saliva, nests vary in location from completely subterranean, to inside wood, to entirely arboreal. The most conspicuous nests are begun underground and as they grow begin to protrude progressively, eventually assuming impressive species-characteristic shapes.

Although termites are sometimes called 'white ants' they are not at all related to ants. In a very literal sense, termites are 'social cockroaches' that have attained their eusociality from a base extremely remote in evolution from the Hymenoptera, yet surprisingly the differences between these eusocial groups are not as great as one

Table 10.2 Major distinctions between termites and eusocial Hymenoptera

Termites	Eusocial Hymenoptera
Similarities	
1. Caste number and kind are analogous, especially between termites and ants.	
2. Trophallaxis occurs, and is an important mechanism in social regulation	
3. Chemical trails are used in recruitment; comparable trail laying and following behaviors	
4. Inhibitory caste pheromones exist, and act in similar ways	
5. Frequent grooming between individuals transmits pheromones	
6. Nest odor and territoriality are of general occurrence	
7. Comparably complex nest structures have precise temperature and humidity regulation	
8. Cannibalism is widespread, but not universal	
Differences	
1. Castes in 'lower' termites are determined chiefly by pheromones; sex and other factors are involved in some 'higher' termites	1. Castes are determined chiefly by nutrition; pheromones sometimes play a role
2. Worker castes consist of both sexes	2. Worker castes consist of females only
3. Larvae and nymphs contribute to colony labor, at least in later instars	3. Larvae and pupae are helpless and almost never contribute to colony labor
4. No dominance hierarchies occur among individuals in the same colonies	4. Dominance hierarchies are commonplace but not universal
5. Social parasitism between species is almost wholly absent	5. Social parasitism between species is common and widespread
6. Anal trophallaxis occurs in all 'lower' termites, but trophic eggs are unknown	6. Anal trophallaxis is rare, but trophic eggs are exchanged in many bees and ants
7. Primary reproductive male stays with queen after nuptial flight, helps construct first nest. No mating during nuptial flight; mating occurs periodically as colony develops.	7. One or more males mate with the queen during the nuptial flight and die soon afterward; female stores gametes in spermatheca for up to several years
8. Diploid sex determination	8. Haplodiploid sex determination

might expect (Table 10.2). The most striking differences in the two groups concern the nature and care of their young. The Hymenoptera are holometabolous, and because the larvae of eusocial Hymenoptera are helpless grubs that must be nursed continuously, their care requires a great deal of adult labor. Termites are hemimetabolous, so the young stages of termites, on the other hand, are active creatures quite similar to the adults and quite able to fend for themselves, particularly among the so-called 'lower' termites. Many termite workers are nymphs that may eventually develop into winged adults. Others, termed *pseudergates*, are workers that for chemical reasons will probably never grow up, although they retain the

potential for developing into any of the castes. Thus, up to a point it may be said that termites rely upon 'child labor' for the maintenance of their societies. Another difference is that the male sex in termites participates in colony labor, which is never true for male hymenopterans.

10.3.5 Lesser Known Candidates

Though ants, wasps, bees, and termites are the best known members of the insect social register, new members continue to seek admission as studies turn up eusocial behaviors in diverse groups. A small number of thrips and aphids—two unrelated groups of small insects that suck plant juices—plead a specially convincing case for inclusion.

Thrips (the name is both singular and plural) are small hemimetabolous insects in the order Thysanoptera; many are serious pests upon hundreds of different crops. In about 300 species in the suborder Tubulifera, a single female (or sometimes a male and female together) alter plant growth to form galls, in which they live and feed; another dozen species do not actually form galls, but have other ways of making closed spaces in which to feed on plant tissues. Females in some of these species develop extreme physogastry and lay hundreds of eggs. In many species the life span of gall foundresses overlaps with that of their adult offspring. Interestingly, all bisexual thrips species are apparently haplodiploid, like Hymenoptera.

The dwellings that thrips produce on Australian acacias are often contested by other thrips species that do not build domiciles of their own. Some of these species simply take over abandoned galls, but at least one species fights and sometimes kills the domicile owner. As though in response to such threats, some gall-forming thrips have what amounts to a soldier caste; some adult males and females have enlarged, heavily sclerotized forelegs (see Plate 40) that are lacking in other group members. These soldiers are often (but not always) sterile, and have smaller wings than the other thrips.

Aphid societies consist of clones established parthenogenetically from a single foundress, and the soldier caste appears early in development in the larval rather than the adult stage. Unlike the haplodiploid thrips, aphids are colonial diploids. Given their clonal condition one might expect most aphids to be eusocial, but in fact eusociality is mostly restricted to some members of just two closely related families, which also happen to be the two groups capable of inducing galls on their host plants. Thus whereas not all gall-making aphids are social, all (known to be) social aphids are gall-makers. Some 40–50 aphid species have a life history that roughly parallels the gall-making thrips, including development of a soldier caste.

One's mental picture of aphids as docile 'plant lice' or tiny cow-equivalents tended by ants (see Plate 10) needs some readjustment in the face of these aphid soldiers—fierce defenders that patrol the colony, grappling with intruders and stabbing with their short thick beaks. Recall that even non-soldier aphids are not defenseless; many secrete chemicals from their cornicles that incite clone mates to quickly scatter (see Fig. 6.14). In some social forms, the cornicle secretions

recruit soldiers to confront a threat. Galls clearly are resources that are generally worth defending; in some cases, tending ants are also part of the ecological mix; one study showed that excluding ants dramatically increased the aphids' soldier to non-soldier ratio.

One more unusual social insect that deserves mention is the Australian beetle *Platypus (=Austroplatypus) incompertus.* Unlike most bark beetles that attack dead or dying hosts, this ambrosia beetle attacks the heartwood of living *Eucalyptus* trees, forming galleries that sometimes persist for several years. Each gallery houses a cooperative family group composed of a single fertilized female, accompanied by several unfertilized females that maintain and patrol the galleries and process the mycelia of ambrosia fungi, ensuring a rich food supply.

10.4 Implications and Correlates of Social Life

Evolutionary biologists look for finely tuned adaptive behavior in the animals they study, and are happy when they find it. Insects have a long evolutionary history, and most of their behavior patterns apparently do, as well. However, sometimes a seemingly imperfect system can be even more interesting and in puzzling about it scientists can be led to insights that might never have arisen otherwise.

Such is the case with golden egg bugs (see Plate 41), a group that has captured the attention of a number of biologists, including Arja Kaitala and his students and the same Robert Smith who studied *Abedus* water bugs (see Case Study 10.1). Most Hemiptera oviposit on foliage or other environmental objects, and very few tend their eggs in any way. Golden egg bugs and giant water bugs are only distantly related, but their convergence in a behavior as unusual as egg-carrying fairly begged for comparative study (Case Study 10.3).

Case Study 10.3: Egg-Carrying in the Golden Egg Bug, *Phyllomorpha*

If both sexes of an insect carry eggs, and the eggs are almost never their own, can it be parental care?

Phyllomorpha laciniata are plant-sucking insects with a bizarre appearance (see Plate 41) and equally strange behaviors. In most Mediterranean countries, a careful observer who managed to spot these little coreid bugs (which are actually camouflaged by their elaborate leafy spines) would find both sexes to be wandering around on vegetation, many with variable numbers of small, golden eggs fastened to their backs.

Do the bugs deliberately attach their eggs to other bugs? Is such behavior obligatory? Is either sex more likely to carry eggs? What is the carrier's genetic relationship to its eggs? Do carriers even know the eggs are there? Do carriers show any other behaviors indicative of care toward their eggs?

Field observations and collections by members of Arja Kaitala's research team established the basics. The bugs they caught each held about five eggs, but numbers varied from one to 30; most of the eggs were glued on the bugs' backs, but sometimes the researchers found them on undersides, legs, heads, and even antennae. Males carried only slightly more than two-thirds of the eggs; females carried the rest. Laboratory observations and experiments revealed a portrait of female golden egg bugs eager to lay eggs on any conspecific, regardless of its sex. In most situations, female potential recipients could resist by simply avoiding other females. Males were in a more difficult bind. They persistently courted females, but were often unsuccessful in procuring copulation; instead, they ended up with the female's egg attached somewhere on their body. When they did successfully mate, the pair remained coupled for long periods, often from several hours to an entire day. Other mated females sought out such pairs, and took advantage of the situation by laying eggs on both participants.

Knowing that close relatives of the golden egg bug lay their eggs exclusively on their host plant, Smith and Kaitala compared the reproductive condition of field-captured and laboratory-held female *P. laciniata*. Those taken directly from the field had several eggs in their oviducts; those that spent time in the laboratory enclosure had few to none. Apparently the crowded conditions of the enclosure allowed females to quickly unload their eggs. In the natural setting, they could have simply dumped their eggs on vegetation but instead they were retaining mature eggs until they could locate conspecific carriers.

Why should carrying be so important? Another member of their team, Xavier Espadaler, provided the answer. Seven ant species with a shared taste for golden eggs were frequent visitors to the host plant. When the researchers removed eggs from bugs and placed them on host plant flowers, ants discovered and ate the eggs within minutes or hours.

Having identified a major benefit, the researchers began looking for the costs of egg-carrying, and soon found them, but not quite where they expected. Reasoning that the added weight of the eggs might slow bugs down, they conducted bug-race experiments; bugs bearing eggs were statistically just as likely to win as unencumbered bugs were. Instead, the major cost seems to be that bugs with golden eggs are more conspicuous to predators, and probably to parasitoids as well. Gangs of one particularly aggressive ant species attacked egg-laden bugs, and often killed them.

Might egg-carrying in *P. laciniata* be a case of parental care, perhaps analogous to that in giant water bugs? For several reasons, Smith and Kaitala thought it was not. By definition, parental care requires parents and their offspring, a bond that was strangely lacking in golden egg bugs. Females, of course, cannot be the mothers of the eggs they carry; they do not lay

eggs on themselves. Furthermore, there is little reason for golden egg bug females to show preferences in terms of the sex of the carrier or the degree of relatedness between egg and carrier simply because any conspecific carrier probably increases the chances that eggs will survive by about the same amount. However, unlike the situation in water bugs, golden egg bug males did not appear to be carrying their own offspring either. Samples sent to Stockholm University for molecular genetic studies showed that egg-laden males had fathered only a very small percentage of the eggs they carried. Furthermore, hundreds of hours of observation did not reveal any type of parental nurturing analogous to the behaviors of male water bugs.

Thus, Smith and Kaitala concluded, although it has obvious benefits, egg-carrying in *Phyllomorpha laciniata* appears to be a purely passive behavior, rather than parental care, at least at this point in time. Perhaps, however, its imperfection is a clue that we are being given a rare glimpse at something we almost never see—an evolutionary work in progress.

Three aspects of *Phyllomorpha laciniata* biology—flexibility of oviposition behavior, the fact that males carry most of the eggs, and the demonstration that males carry both genetic offspring and unrelated eggs—have made this system the subject of continuing controversy. However, García-González and colleagues make a strong case that *sperm mixing* is the key to explaining golden egg bug behavior. In most insects, 'sperm precedence' is presumed to occur, so that the most recent male to mate with a female fertilizes most of her eggs, but in *P. laciniata*, their studies show that the last male to copulate with a female sires only about 43% of her eggs, and this percentage does not change significantly over a period of several days. Because females lay single eggs at intervals for four to five months rather than producing clutches, they could be expected to benefit by promoting a sperm competition mechanism that would maximize the number of males accepting eggs, and the context in which they are likely to accept them. Sperm mixing ensures that each male that has copulated with a female has some chance of fathering her offspring, but he also has no clue as to when his own offspring will be produced. Despite this lack of confidence in paternity, male egg-carrying is favored because males do not suffer mating costs when they carry eggs, and the survival of eggs (including perhaps their own) is so much higher when eggs are carried rather than being left on plants.

10.4.1 The Ecology of Parental Care

Over the past seventy years, it has become increasingly apparent that the evolution of parental care—an important behavior both in and of itself, and as a key component of more comprehensive social life—correlates with many aspects of an organism's ecological milieu. A number of general aspects of the physical and biological

environment have been identified as being particularly important, not only among insects but also among a wide variety of vertebrates that practice parental care. It has been suggested that two extremes are likely to push animals toward parental care: a very stable environment and an unusually harsh one; let us follow the reasoning behind this idea.

The first of these, a stable, predictable environment, favors the evolution of parental behaviors because the *K*-selection (see Chapter 9) that tends to prevail in these conditions has certain demographic consequences: the animal tends to live longer, to grow larger, and to reproduce at intervals. As an example, consider rotting logs on a forest floor; these would seem to fit the stable, relatively constant environment criterion. Two lineages of cockroaches have evolved extended bi-parental care of slow-growing, highly dependent offspring in such an environment; the most thoroughly studied exemplars are members of the genera *Panesthia* and *Cryptocercus* (see Plate 39).

Extended bi-parental care has also evolved independently in *Odontotaenius* (=*Popilius*) *disjunctus*, a large, glossy black beetle in the family Passalidae (see Fig. 10.12). The young of most cockroaches and beetles can forage independently from an early age; they are analogous to many types of precocial birds that begin to peck and feed themselves soon after hatching. The young of these three wood-feeding groups of insects are more like the altricial young of robins and wrens—reared in small slow developing clutches, highly dependent on their parents to provide food and protection, and unable to forage for themselves. Both of the wood-feeding cockroaches require the help of bacterial symbionts to digest their cellulose diet; the parents produce bacteria-rich soups to inoculate the digestive systems of nymphs that line up like pigs at the food trough to imbibe the hindgut fluids. In contrast, unlike most other wood-consuming species, bess beetles apparently lack digestive symbionts. Instead, an important part of their diet is fecal frass, which acts as a substrate for bacterial and fungal development and is reingested. Adult bess beetles live two or more years; between rearing their yearly generations of young, they are somewhat gregarious, many adults being found in the same tunnel system. However, during the reproductive season, each pair of beetles maintains its own tunnel system in which 20–60 eggs are laid. The developing young feed on material prepared by their parents, and when ready to pupate they cooperate with the adults in construction of pupal chambers.

A second circumstance that may propel an animal toward parental care is penetration of a physically stressful environment where offspring would require some sort of protection, at least during the most vulnerable period of their development. In extremely harsh environments, many insect species guard their offspring. For example, the staphylinid beetle, *Bledius spectabilis*, occupies intertidal mud; the female of this beetle constructs a bottle-shaped burrow in which eggs are laid. She remains with her eggs and young, twice each day plugging the burrow entrance to prevent the tide from entering, then reopening it to prevent the young from suffocating; this care continues until the larvae complete their first instar and disperse to establish their own individual burrows. Eggs in burrows from which the mother was removed all perished, either to mold or to predation by other beetles.

Many ecological factors are probably involved in every insect's life, and there is often considerable challenge in finding what factors actually lie behind an observed case of parental care. For example, adults of the tropical stink bug *Antiteuchus tripterus* possess potent chemical defenses and are aposematically colored. They generally live relatively long and are able to produce young two or three times during their life. However, their offspring start life quite vulnerable to predation and parasitism because their stink glands do not become functional until they reach their second instar. William Eberhardt's studies of maternal care in this species (Case Study 10.4) showed how parental behavior and ecology are well correlated, as predicted, with risks of predation and parasitism acting as important selective factors.

Case Study 10.4: Parental Care in the Stink Bug, *Antiteuchus tripterus*

Stink bugs are aptly named. Their distinctive odor, derived from abdominal stink glands, is familiar to most everyone. Less well known is the extent to which some mother stink bugs care for their young.

Antiteuchus tripterus is a tropical pentatomid bug common on a variety of landscape trees and shrubs in urban areas of Cali, Columbia. It lays its barrel-shaped, unusually thin-shelled eggs, in compact masses almost always numbering 28, on the undersurface of leaves. For 15–16 days following oviposition, females remain with their clutch without feeding while the eggs develop and hatch and the nymphs grow to reach the second instar. Such parental behavior is not uncommon in the Pentatomidae, and representatives of several genera have been reported to have similar behavior. Why? William (Bill) Eberhard reasoned that the parent bug was defending her eggs against predators. His first experiment was simple. He removed brooding females from some batches of eggs while leaving others nearby untouched to serve as controls. Not one bug survived from 48 unguarded egg masses, most of which vanished, whereas 50% of the protected eggs produced bugs! Later observations revealed that several species of insects, especially foraging ants, fed on undefended eggs. Thus, the females' defense of their eggs against such 'generalized' predators appeared to be highly effective, and necessary.

Nevertheless, a 50% mortality of the guarded eggs seemed surprisingly high, considering the time investment of the mothers. Eberhard presented artificial insect-sized models to brooding females. These elicited a repertoire of defensive behaviors, including waving antennae in the direction of the stimulus, tilting the body to form a shield between the threat and the nymphs, general body 'shuddering,' scraping of the front legs along the periphery of the egg mass, and kicking backward with the middle and hind legs. Although like all other stink bugs *Antiteuchus* possessed glands which could spray a highly repellent chemical, this defense was never employed against the insect-sized stimulus. Eberhard assumed that such chemical defense was reserved

for larger potential predators, for when the body was tilted for spraying, the bugs also vividly displayed aposematic orange bands along the sides of their abdomens.

Attempting to rear the eggs, Eberhard discovered that a number of them yielded, instead of bugs, tiny scelionid parasitoid wasps of two different species. Why were they so successful despite constant maternal vigilance? Stereotypy in maternal orientation provided a clue. *Antiteuchus* females consistently aligned their bodies parallel with the axis of the leaf upon which their eggs were laid, generally facing toward the leaf tip. Observing them carefully when their overt behavior (kicking, scraping, etc.) indicated they were aware of the presence of a wasp attacking their eggs, Eberhard was unable to document a single instance when a mother bug turned and assumed a new orientation over its eggs. The consequence of this constant maternal orientation behavior (Fig. 10.24) was that, while females' defenses did effectively deter many wasp oviposition attempts in eggs situated on the front and sides of the egg mass, eggs to her rear were not effectively guarded. Analysis of the distribution of parasitized eggs within the mass confirmed this.
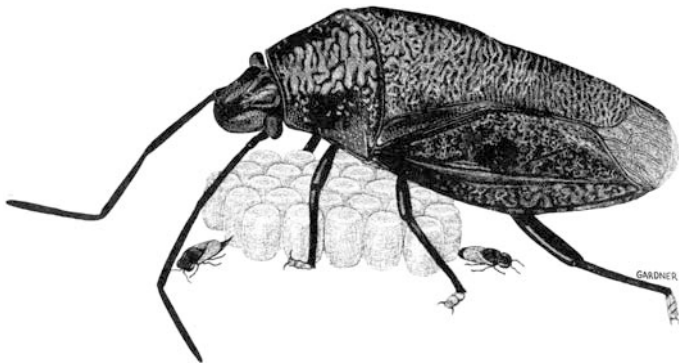
Fig. 10.24 Defending against attack. A female *Antiteuchus tripterus* in characteristic guarding position over her eggs. As the bug lowers her antennae and scrapes with her front foot along the egg mass in an attempt to drive off *Phanuropsis*, a parasitic wasp which attacks from the front, a *Trissolcus* wasp oviposits in an egg at the poorly guarded rear edge

Would wasps attack more if eggs were not guarded at all? To exclude the foraging ants and other walking predators that had decimated unguarded eggs in his previous experiment, Eberhard ringed the trunk and branches of the host tree with a sticky barrier. One of the scelionid wasps, *Trissolcus*, attacked the eggs at the same rate in the mother's absence. However, removing the mother

caused significantly *reduced* parasitism levels for the other, *Phanuropsis*. In fact, parasitism was lessened by over half, from 64% on controls to 29% on unguarded eggs!

These unexpected results led Eberhard to conclude that perhaps the presence of egg-guarding females served more or less as a visual 'beacon' to this parasite, serving to identify location of potential hosts. Several observations seemed to support this idea. For one, *Phanuropsis* often approached or rested near quiescent individual bugs of both sexes. When a guarding female was removed several centimeters to one side of her eggs, female *Phanuropsis* waiting nearby typically ignored the undefended eggs and moved instead to realign themselves with the bug's new position. That this response was visually mediated was supported by the additional observation that the wasps' searching activity was limited to daylight hours, peaking about midday.

Thus, even though the parental behavior of *Antiteuchus* seems well suited to combat activities of parasites and predators in general, she still suffers a net loss of eggs to at least one parasite species that has turned her defensive habit to its own advantage for finding hosts.

10.4.2 Paradoxes of Insect Sociality

Because all living members of both the termites and the ants are totally eusocial, they can tell us little about the *origins* of social behavior. Attention has therefore centered about the bees and wasps, since both of these major groups exhibit a range of stages that suggest a 'progression' to eusociality. The other orders with eusocial species also display a range of solitary to cooperative behaviors, making them a rich resource for comparative study as well. All of these suggest that social groups can form either by cooperation among adults of the same generation or via parent-offspring (family group) associations (Fig. 10.25). The latter is thought to be the most common pathway, and formed the cornerstone of William Morton Wheeler's treatises on social insects in the 1920s.

Regardless of which evolutionary route has been taken, however, the resultant society seems to present an evolutionary paradox in the existence of *altruism*, or self-sacrificial behaviors. One example is the awesome willingness of many bees to throw themselves into suicidal battle (Fig. 10.26). Charles Darwin wrestled with another aspect of the paradox: if natural selection favors the individual able to produce the greatest number of viable offspring that live to reproduce, then how can one explain worker sterility? Social insects must represent a special case, he reasoned, an example where natural selection was operating on the level of the colony, or family group, rather than on the single organism.

Group selection is defined as the differential survival and reproduction of entire cooperative groups. Perhaps the foremost later proponent of group selection was a Scottish scientist, Vera C. Wynne-Edwards. In an influential 1962 book,
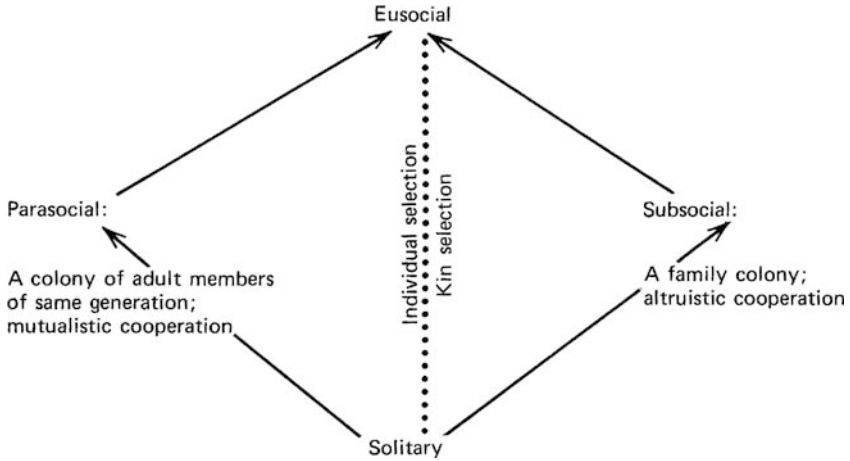
Fig. 10.25 Evolving eusociality. Postulated pathways to complex social behavior in Hymenoptera. Examples of each stage can be found in extant species of bees and wasps. However, one should not consider that that all species are inexorably progressing toward eusociality. Rather each type of group association is presumed optimally adaptive given the particular set of environmental conditions

Fig. 10.26 Injecting venom. The ultimate self-sacrifice is to be sterile and die defending one's home. Honey bees have evolved a barbed sting; upon delivery, it remains in the victim and disembowels the bee, resulting in the bee's death

he interpreted a vast array of animal social behaviors as adaptations to prevent overexploitation of shared resources, a sort of density-dependent population control. He asserted that such adaptations would evolve over time, because groups

of self-sacrificing restrained individuals would out-compete groups that contained selfish individuals.

Wynne-Edwards' version of group selection reflected ideas that were generally accepted by biologists at the time. For example, social insect colonies were regarded as *superorganisms*, a term coined by Wheeler in 1911, in reference to the fact that individuals acted in ways that benefited the good of the group or colony, even if and when their behavior was individually disadvantageous. However, ideas began to change after a seminal 1966 book by George C. Williams persuasively renewed emphasis on individual selection, and the latter became the dominant paradigm into the twenty-first century. When scientists observed behavior apparently beneficial to groups but disadvantageous to the individual donor it was almost mandatory that they explain it in terms of individual selection, most often by invoking pedigree.

Although some of the basic aspects of *kin selection theory* had been advanced by others, it was William D. Hamilton who formalized the concept in the mid-1960s, John Maynard Smith who gave it a name, and Edward O. Wilson who promoted it in broader and more generally understandable form. In essence, kin selection refers to changes in gene frequency across generations that are driven at least in part by behavioral interactions between related individuals; in theory, the enhanced fitness of relatives sometimes can more than compensate for fitness losses that an individual incurs.

The combined sum of an individual's direct fitness (via personal reproduction) and indirect fitness (genes contributed through help to non-descendent kin to produce relatives) is termed *inclusive fitness*. Inclusive fitness is not the simple sum of an individual's own offspring plus offspring produced by relatives, however; rather, each must be adjusted by a coefficient of relationship *(r)*. In essence, this is the probability that a random gene of the recipient of an altruistic act has an identical copy in the donor.

Kin selection can operate at any level of relatedness; although the large proportion of unlike genes carried by individuals outside an immediate family group slows the progress of selection, it does not alter its direction. Under certain situations altruism is advantageous even toward quite distant relatives.

In the Hymenoptera, many different degrees of sociality occur, and eusocial behaviors have evolved independently several times. Why has eusociality evolved so often in this one insect order? And why are hymenopteran societies organized as matriarchies in which the workers are always genetically female? Hamilton's special insight concerned the importance of haplodiploidy—the mode of sex determination in which haploid individuals derived from unfertilized eggs are male and diploid individuals arising from fertilized eggs are female. Haplodiploidy, he showed, results in relatedness asymmetries whereby sisters in ants, bees, and wasps are more closely related to each other than to their brothers or mothers (Table 10.3).

Since the father is haploid, the half of their genes which female offspring receive from him are all identical. Within the gene set they receive from their diploid mother, on average one half of the genes are identical. Thus, full sisters share through common descent an average of three fourths of their genes. As a result, a daughter is

Table 10.3 Maximal average coefficients of relationship (*r*) among close kin due to haplodiploidy in Hymenoptera

	Mother	Father	Sister	Brother	Son	Daughter
Female	0.5	0.5	0.75[a]	0.25	0.5	0.5
Male	1	0	0.5	0.5	0	1

[a] A female's relatedness to sisters (and/or nieces) will be lower if their mothers have mated more than once, which is often true in eusocial Hymenoptera

more closely related to her full sisters than she is to her own mother, a biologically unusual situation. Just as unusual is the male hymenopteran. He has a grandfather but no father. Because he receives all his genes—in one of two alleles—from his diploid mother, he shares an average of one half of his genes with his brothers but possesses only an average of one fourth of his genes in common with his sisters.

In theory, an individual's own altruistic sacrifice in fitness could be counterbalanced by an increase in the fitness of some group of relatives. Hamilton proposed that this increase must be by a factor greater than the reciprocal of the coefficient of relationship to that group (i.e., greater than 1/*r*) if an altruistic trait is to spread. In the majority of animals, when an altruistic female sacrifices her life or reproductive success for a sister or daughter, there is one half chance that the latter shares the gene for that altruistic trait. For it to be statistically probable that the altruistic gene will be fixed, the reproductive success of the sister or daughter must be at least doubled as a result of the sacrifice. However, among full sisters where there is a three quarter chance that the gene is shared, altruistic behavior is statistically probable when the recipient's gain in fitness is equal to only four thirds, or 1.33, times the donor's loss. *Hamilton's Rule* is usually stated as br-c>0, or more simply as br>c, where b = benefit to the recipient, c = cost to the actor altruist, and r is the coefficient of relationship between the two (which ranges from 0 to 1).

Thus, because of haplodiploidy, when a hymenopteran mother lives to reproduce beyond the adulthood of her first female offspring, these offspring may increase their inclusive fitness more by care of their younger sisters than by an equal amount of care given to their own offspring. Since sisters are more closely related than are brothers, altruism will be more favored among daughters than among sons. Haploid males have more to gain by fathering daughters, with whom they share an average of one half of their genes, than by assisting in the production of more sisters, with whom they share an average of only one fourth of their genes.

Thysanoptera are also haplodiploid and since 1990 a number of eusocial thrips have been discovered (see Section 10.3.5). They differ in that soldiers of both sexes actively defend the colony and can also reproduce. Colonies of some soldier-producing species have been found to have extremely high levels of inbreeding; this reduces the relatedness asymmetry between brothers and sisters. Also, unlike the hymenopteran sting that can only be possessed by the female gender,

spines and enlarged forelegs found in thrips soldiers are not sexually dimorphic traits.

All other things being equal, it would seem that Hymenoptera should all tend to become social! Yet the truth is that although apparently all of the thousands of solitary and parasitic Hymenoptera species have this same haplodiploid reproductive system, most show no trace of sociality. Why?

As new technology has made relatedness one of the easier things to quantify among social group members, the striking conclusion from numerous studies is that there is no overwhelming link between sociality and degree of relatedness. Thus, while genetic relationships and hence genetic mechanisms may be involved in furthering the initial evolution of cooperative behavior, other factors must also be considered to be important.

What might such factors be? Searching for the earliest stages of social evolution has traditionally focused on groups such as halictid bees or the aculeate wasps, because in these sociality has risen both relatively recently and repeatedly, whereas in the termites or ants all known species are eusocial and are derived from stocks that evolved eusociality long ago. However, when we step back and look at the distribution of eusociality, we find that it has arisen independently at least 13 times, mostly among the arthropods (including once in a crustacean) but also at least once in a vertebrate, the naked mole rat. At the same time it is rather striking that eusociality is relatively rare, considering the huge diversity of arthropods. Pressures inhibiting the attainment of eusociality must be extraordinary. On the flip side, one must envision some equally extraordinary set of conditions favoring flexibility that could foster cooperative breeding to overcome environmental contingencies and individual selfishness. Such a scenario seems to require selection to operate at multiple levels—genes, individuals and groups—in context-dependent ways.

A revolution in thinking about the origin and evolution of eusociality has occurred over the past decade. Facilitated by the tremendous progress in whole-genome sequencing and comparative genomics through various large-scale technologies (proteomics, epigenomics, etc.), the revolution has been driven in part from new knowledge about the interaction of genes and the environment. It is increasingly possible to probe relations between genes and social behavior. Several examples of social influences on gene expression in insects are now documented. One instance (see Case Study 1.1) involves shifts in the expression of large populations of genes in honey bee brains that relate to the point at which hive bees switch to foraging outside the nest. In particular, differences in the *foraging (for)* gene expression are related to social activity, rather than to genetic differences between individuals. Thus, emergent traits arising from interactions among group members constitute a new frontier for ultimately understanding the social evolution puzzle.

The significance of quantifying relatedness as it relates to the evolution of eusociality is also being reevaluated. Emphasis has shifted to the other parameters of Hamilton's Rule: costs and benefits of group life. Besides haplodiploidy, several other preadaptations are now thought likely to be equally or even more important for the evolution of eusocial behavior (Table 10.4). Previously existing behavior patterns, physiological processes, and morphological structures that are already

Table 10.4 Some preadaptations that are considered to be important for development of insect sociality

Preadaptation	Leading to:
1. Reproductive ground plan (condition-dependent larval developmental pathways and shared ancestral genes)	Differentially expressed genes and resultant phenotype plasticity upon which natural selection can act in different environments; evolution of castes
2. Haplodiploid sex determination	Development of altruistic behaviors depending on coefficient of relationship
3. Chewing mouthparts	Manipulation of nest materials, brood, and other objects
4. Construction or possession of a nest in which young are reared and to which female returns repeatedly	Potential family gathering place and behavioral equipment for gathering there; central place foraging
5. Plasticity in stereotyped nesting patterns: a. altered nest and cell construction sequence	Progressive provisioning; direct contact between larvae and adults opens opportunities for reciprocal interactions
b. placement of numerous cells at one site	Clumping of brood and increased chances of neighbors being relatives
6. Increased female longevity	Overlapping lifespan of mother with young
7. Mutual tolerance of conspecifics	Communal nesting; possibility of cooperation
8. Control over sex ratio	Strong female bias; male production postponed until late in nest cycle
9. Effective channels for intraspecific communication (especially chemical)	Way to integrate and regulate multiple interactions among many individuals

functional in some other context may serve as bridges to new adaptations. For example, the *reproductive ground plan* hypothesis proposes that the gene network that once regulated the foraging and reproductive phases that coexisted in solitary ancestors was modified in the process of evolution to form the basis for the caste divisions that are evident in today's social insects. Thus, queens express genetic traits that are characteristic of the reproductive phase of solitary insects, whereas workers express traits characteristic of the foraging phase. A modification of this hypothesis suggests that in some wasps at least, the co-opted gene regulatory networks were instead from ancestors with two summer generations; workers evolved from networks switched on in early-emerging first generation individuals, whereas queens evolved from networks switched on in late-emerging, second-generation individuals that diapause.

Certainly, many studies have illustrated that relatedness alone is not necessarily the best predictor of colony success. For example, comparisons of Florida harvester ant colonies (*Pogonomyrmex occidentalis*) revealed that colonies with relatively low relatedness among the workers had strikingly higher colony growth and reproduction rates than those with high worker relatedness. Structured kin groups like harvester ants illustrate that genetic variation between colonies may be greater and of more evolutionary significance than within-colony variation. It is upon this intercolony variation responding differentially to environmental or genetic factors (e.g., disease resistance) that group selection processes can act, resulting in some groups being better adapted than others (Fig. 10.27). Indeed, the principal selective regime
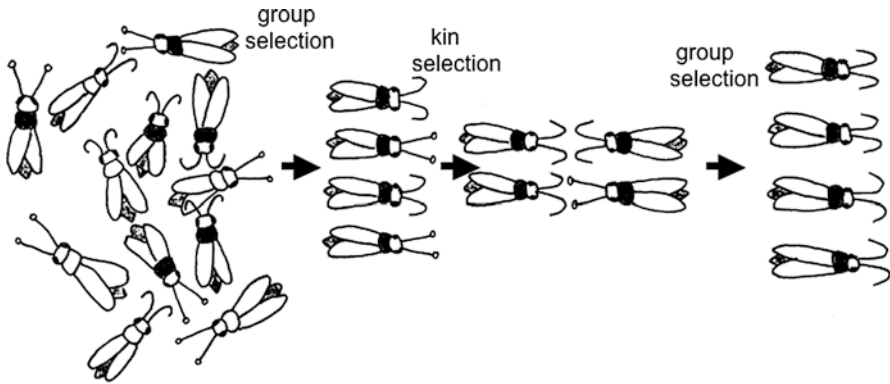
Fig. 10.27 Selecting groups. The group selection model for the evolution of eusociality. Some individuals in an initial population possess eusocial-prescribing alleles (*black thorax*) that induce cooperation, but whose phenotypic expression is flexible (*curved and knobbed antennae*). Common possession of eusociality alleles trumps relatedness in the early stages; subsequent selection based on environmental factors sorts subsequent groups without requiring a kin network. Higher related-ness in downstream populations can arise by further group selection with or without kin selection; thus relatedness is more a consequence than a cause of eusociality

leading to and maintaining sociality is differential reproductive success among colonies of a population.

In many halictid bees, individuals join in groups of females that at best may be sisters but most often are more distantly related. Suppose they are sisters; if a joiner becomes a worker, then she is enhancing the production of nieces to whom her coefficient of relationship is only 0.375. Reasoning from kin selection theory, the better strategy would seem to be to live alone and produce offspring with a relationship of 0.5. However, the balance may be tipped by enhanced nest defense and protection from parasites; early-season cooperation by adult females effectively produces an 'instant' colony with a head start in protection. Such behaviors simul-taneously increase the fitness and productivity of all individuals involved without the requirement of any close genetic relationship of the partners, although some-times such does occur. In other words, the selective effect of colony-level benefit outweighs the costs of individual fitness loss.

10.4.3 Interspecific Social Interactions

Scaptotrigona stingless bees make a living by plundering the nests of other species, stealing the honey and provisions for their own nest. Queens of *Vespula squamosa* intrude into established nests of *Vespula maculifrons* and either seize the queen's position or lay their own queen-producing eggs alongside those of the host, to be raised by the host's worker force.

In Chapter 4, we considered a number of symbiotic interspecific alliances in the context of feeding strategy. Here, we focus on some exploitive interrelationships between fully social species. Nest building and the care and feeding of an individ-ual's young are usually thought to be very conservative, physiologically deep-seated

behavior patterns. However, even these may be selected against if increased fitness results.

For example, various solitary Hymenoptera species (see Fig. 4.8) have lost the behaviors of nest building and provisioning and rely entirely upon the nests and labors of others. *Social parasitism* occurs when the offspring of one species are raised by another species. Among the eusocial Hymenoptera, it has evolved independently many times and in many ways. Ants show a greater diversity of forms of social parasitism than any other group of animals, with over 160 species of social parasites, no two of which are exactly alike in their adaptations for this mode of life.

The term 'social parasite' is unfortunately somewhat misleading, because the parasite does not need to be social nor does the label refer to every parasite of a social species. Rather, a social parasite is a species that uses its host as a work force (something social insect species are particularly suited for) rather than as a direct source of food. However, because many social parasites are closely related to their hosts, they often are social themselves. In its most extreme forms, social parasitism is a condition of permanent and complete dependence, in which the parasite's entire life cycle is carried out within the host's nest. Commonly, when the parasite is a social species, its own workers are nonexistent or conspicuously degenerate. Such extreme social parasites, or *inquilines*, appear to have arisen convergently via at least three evolutionary routes.

The name *Teleutomyrmex* means 'final ant,' a name most appropriate for what is probably the ultimate social symbiont. In the Swiss and French Alps, one may find this ant in small isolated populations that include no workers. Although quite an assemblage of ant species surround it, *Teleutomyrmex* is parasitic upon only one—its closest phylogenetic neighbor, *Tetramorium*. It has never been found outside the nests of its hosts. *Teleutomyrmex* queens spend much of their time riding upon the backs of the queens of their host colony. Very delicate, the symbionts seldom move independently; they apparently feed only upon regurgitates passed from workers to the host queen. Placed in an artificial nest they cannot survive, even if host workers are present. Their brains, mandibles, nervous system, and skin, in fact nearly all of their morphology, shows extensive degeneration, except in their reproductive system—each of the tiny physogastric parasites lays an average of one egg every 30 seconds. Having up to six or eight ectoparasitic ants riding upon her back may slow down a host queen; infested colonies tend to be somewhat smaller than non-infested ones. Significantly, infested colonies produce no sexual forms of the host. *Teleutomyrmex* adults, especially older females, apparently produce a very potent attractant; host workers lick them continuously. As it is circulated throughout the colony this substance may impose 'reproductive castration' upon its hosts. Such a castration phenomenon has been demonstrated in a number of similar parasite–host colony relationships, though its physiological mechanism has yet to be determined.

Two more examples illustrate the diversity of social inquilinism. One involves slavery. Red Amazon ants (*Polyergus rufescens*) with their saberlike mandibles are fierce fighters but totally inept housekeepers. In their home nest, their only activities are grooming themselves and begging for food. Living as a pure colony, they would surely perish, because they neither excavate nests nor care for their own young.
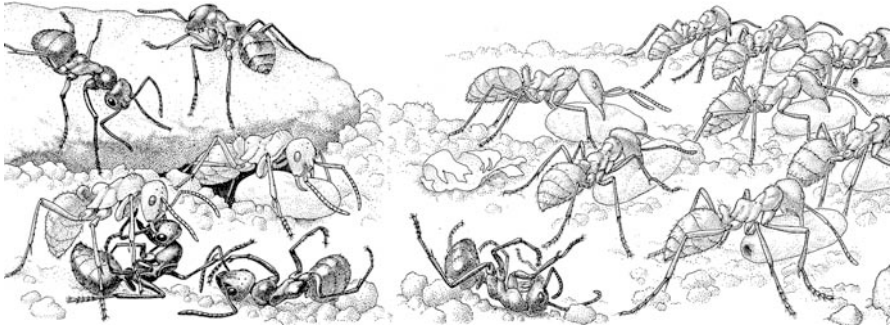
Fig. 10.28   Raiding the neighbors. Amazon ants of the species *Polyergus rufescens* (*light*) conducting a raid upon a colony of the slave species *Formica fusca* (*dark*) nesting in dry soil beneath a stone. Killing resistors by piercing them with their saber-like mandibles, the Amazons rush off with captured brood. Such behavior occurs quite often among cold temperate ant species, where slave labor is found in at least 35 species from six independently evolved groups

What keeps them alive is a unique slave-making habit. Periodically, the Amazon ants swarm out of their nest, marching swiftly to the nests of *Formica fusca* to launch a raid (Fig. 10.28). With feverish haste, they pour over the colony in a body; any defenders who resist the attack are punctured and killed. Then, like pillaging soldiers, the Amazons proceed to carry off *fusca* pupal cocoons.

Back in the Amazon nest, the pupae soon begin to hatch; genetically programmed to perform various housekeeping tasks, they begin work. Some bring food into the nest, while others tend the eggs, larvae, and pupae of their captors. Still others actually feed the adult Amazons who have made them slaves, responding to their begging by regurgitating liquid droplets. Throughout all this activity, the *fusca* slaves make no distinction between their genetic siblings and the Amazons, fully accepting their captors as sisters. Eventually, their numbers dwindle, because as members of the worker caste they cannot reproduce. In response, the slave-making Amazons set out to pillage alien colonies once again.

The nest-raiding techniques of slave makers are among the most sophisticated behavior patterns found in the insect world. Some physically overpower their victims. Others depend on various chemical ruses. Workers of two species of *Formica* spray acetate chemicals at resisting nest defenders; these chemicals act as 'propaganda substances' that imitate the alarm pheromones of the slave species so powerfully they throw the resistors into utter helpless panic. In addition to this disruptive effect, the acetates serve as an attractant to workers of the slave maker, quickly assembling them where fighting has broken out.

A second example shifts our focus to queen behavior. Sexual forms of most social Hymenoptera leave their home colony for their mating flights. Some mated queens fail to find their own colony again following such flights, or after hibernation fail to successfully initiate their own nest the following season. Should they locate a colony of another species and somehow eliminate the host queen, however, they gain an established nest complete with a work force. For a brief period, when the

usurper queen has begun to reproduce but not all the original queen's brood have reached old age and died, the colony consists of workers of both species. Eventually, however, the nest will come to contain only the usurper and her offspring. This situation, termed *temporary parasitism* may evolve from a facultative affair to an obligatory one where usurper queens depend entirely upon this method to found new colonies. Temporary parasites have increased their chances of successfully entering the host nest in a variety of ways, from stealth to aggression to deceptions involving chemistry, morphology, or behaviors such as 'playing dead.'

The apparent ease by which symbionts have repeatedly intruded themselves into their host's colony is somewhat surprising, particularly in view of the exceptional ability of social insects to defend themselves from larger predators. The clue to understanding this paradox lies in the organization and integration of insect societies. As stressed in Chapter 6, insect societies are integrated primarily by non-personal colony odors, an easier code to break than the visually based individual recognition or learned roles and dominance-based interactions characteristic of vertebrate societies. Furthermore, organization into castes results in role specialization in which the individuals of one caste largely lack a broad awareness of the roles of other colony members. These combine to lend an impersonal nature to social insect organizations, which has apparently made it relatively effortless for social symbionts to insert themselves into the colony regime.

Credits

Chapter One

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Plates
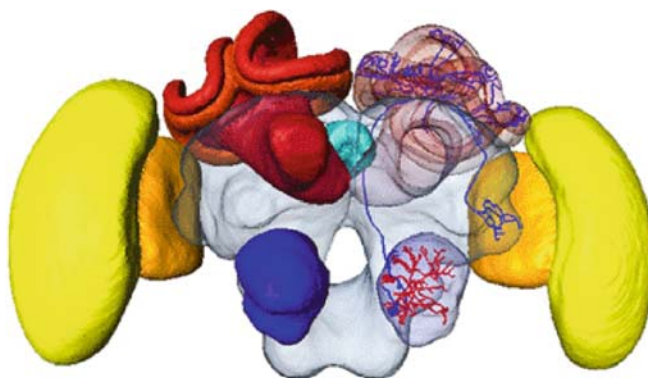
Plate 1 Proximal analysis of honey bee foraging. (*above*) A foraging worker depends on its highly developed spatial navigation abilities to search for pollen and nectar outside its hive or nest, return home, and communicate this information to others. (*below*) Clusters of neurons called mushroom bodies (*shown in red*) located at the top front of its brain are involved in spatial learning; the yellow globes are the optic lobes of the bee brain
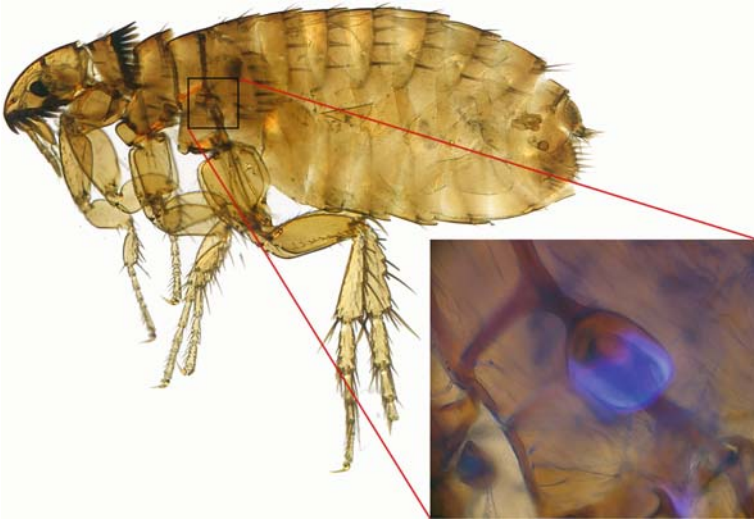
Plate 2 Amplifying power for a remarkable jump. As the flea crouches before takeoff, a resilin pad (insert) at the base of the leg is squeezed and two cuticular catches are cocked. When these let go, all of the energy imparted via the leg muscles is released from the pad in about a millisecond, thrusting the flea's hind trochanters against the substrate

Plate 3 Two monarch butterflies, *Danaus plexippus*, on their host plant, the milkweed *Asclepias tuberosa*

Plate 4 Swarming behavior. (*top*) Two morphs of *Schistocerca gregaria*; the gregarious form is on the left, the solitary form is on the right; (*bottom left*) locusts swarming in Africa; (*bottom right*) a group of adults and nymphs feeding on cabbage in a laboratory colony

Plate 5 Aggregating for hibernation. (*above*) Paper wasps, *Polistes carolina*, move to sheltered sites in the fall, then eventually disperse to establish new nests in the spring. (*below*) Some coccinelliid beetle species gather in large numbers before hibernating, as this aggregation from Arizona illustrates

Plate 6 Stylopsized paper wasp. Three strepsipteran parasites protrude from between the abdominal segments of this *Polistes exclamans* worker. The parasites modify the behavior of the wasp to their benefit

Plate 7 Cuckoo wasps such as this one, *Stilbum cyanura*, attack their host, in this case a mud dauber wasp, by first chewing through the nest wall to reach the helpless offspring. They then lay a egg on the host using their telescoping terminal abdominal segments. If disturbed, the heavily armored cuckoo wasp can retract its abdomen into a tight ball; its thick cuticle is relatively impenetrable

Plate 8 Living in a thorn. (*above*) Nest of *Pseudomyrmex* ants in a swollen thorn of the bull's horn *Acacia*, which the ant hollows out to house its brood. The entrance hole near the tip is clearly visible, as are extrafloral nectaries (three swellings on the adjacent leaf petiole). (*below*) Portion of an *Acacia* leaf, showing the protein-rich yellow Beltian bodies on the leaflet tips being collected by a *Pseudomyrmex* worker ant

Plate 9 The carrion plant, *Stapelia*, produces a strong odor like decaying carrion; this is highly attractive to calliphorid and sarcophagid flies that are duped into depositing their eggs at the flower's base. Two flies are visible at the flower base here

Plate 10 An ant, probably *Formica*, tends a batch of black bean aphids

Plate 11 Vivid aposematic colors characterizes these nymphs of *Oncopeltus fasciatus*, the milkweed bug; this warning is backed by chemical defenses gained from the milkweed plant

Plate 12 Two adults of the willow leaf beetle, *Plagiodera versicolora*; their larvae practice both group feeding and cannibalism
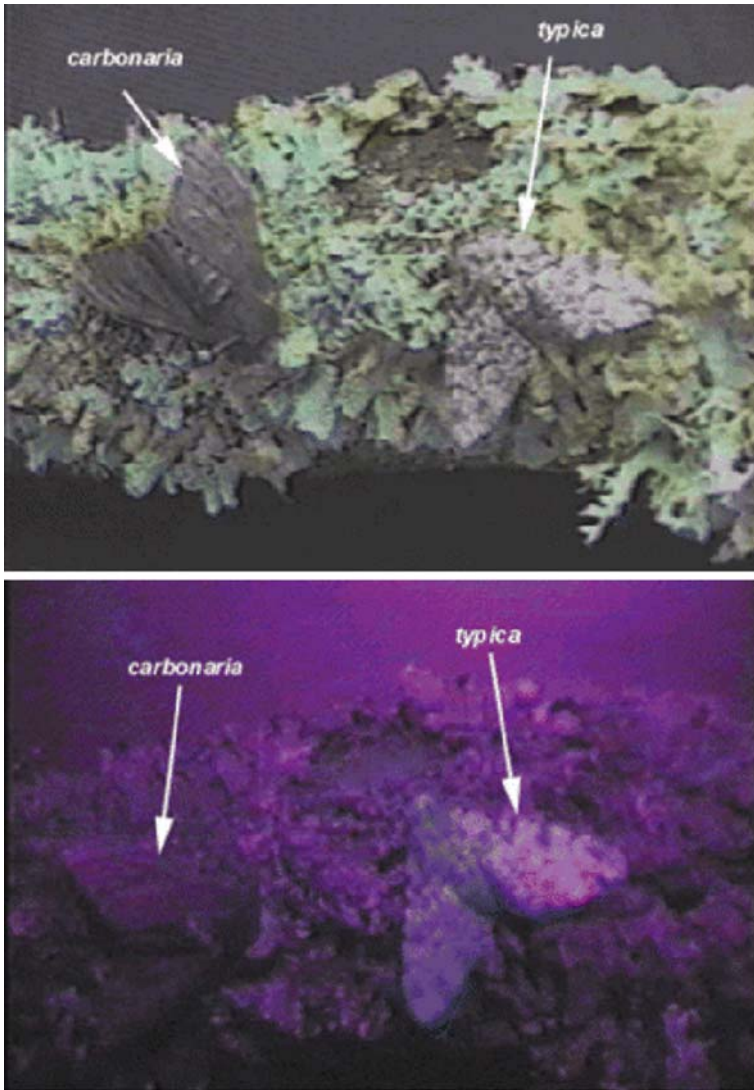
Plate 13 The two forms of peppered moths, *Biston betularia,* on foliose lichen, (*above*) as they would look in normal 'visible' light, and (*below*) under UV illumination

Plate 14 Three examples of crypsis among insects of the tropical rain forests. *Top*: nymph of an unidentified preying mantis. *Middle*: a well-camouflaged walking stick. *Below*: a katydid resting on a moss- and lichen-covered branch demonstrates both crypsis and disruptive coloration
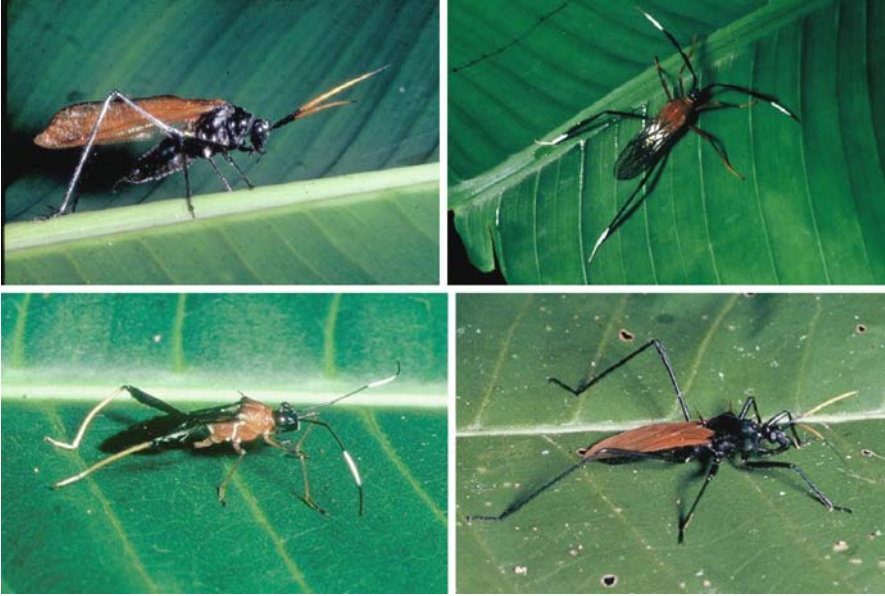
Plate 15 Four examples of apparently Batesian mimics resembling many tropical 'tarantula hawk' wasp species. (*upper left*) a carnivorous katydid from Panama; (*upper right and lower left*) two different coreid bugs from Ecuador; (*lower right*) an assassin bug from Panama

Plate 16 The expanded coremata of a displaying male of an arctiid lekking moth, *Creatonotos*

Plate 17 A cluster of
Neodiprion sawfly larvae on a
pine branch exhibit their
characteristic defensive
posture, with the anterior
parts of their bodies tilted
backward and droplets of
regurgitated fluids exposed
from their mouths. Vigorous
jerking movements enhance
the effectiveness of this group
display. The secretion
contains primarily
plant-derived substances

Plate 18 The Japanese hornet *Vespa mandarinia japonica* preys on worker honeybees that it captures at the hive entrance; instead of attempting to sting or succumbing as most domestic honeybee species would, workers of the native *Apis cerana* honeybees grasp the intruder, and dozens more quickly surround and engulf it into a living, buzzing ball of warm bees, producing a temperature the bees can withstand but the hornet cannot

Plate 19 Green tree ants build nests by stitching leaves together with larva-produced silk. Dominant canopy ants throughout the Old World tropics, *Oecophylla* form colonies many thousands strong and can be ferocious when their nests are disturbed

Plate 20 Attracting a crowd. The secret to creating a bee beard lies in knowing that the honey bee queen's pheromones makes her the center of attention. To make the beard, the queen must be located in a bee swarm and moved into a small screen cage with an attached string that can be quickly hung like a necklace. Within minutes the workers sense that their queen is missing and take flight in a huge cloud; when they discover her, the workers quickly settle as close as possible to their queen. (She is under the author's chin, hidden by the swarm.)

Plate 21   Dinner by glowworm light. (*above*) The predatory Australian glowworm *Arachnocampa flava* inhabits caves, where the larvae spin silk hammocks adorned with glistening droplets. (*below*) A time-lapse photo of a group of glowworms; the source of one glowworm's luminescence is spotlighted in the upper photo

Plate 22 Playing *femme fatale*, a female *Photuris* firefly has seized a male of another firefly species in a fatal embrace after attracting him by mimicking the mating signal of females of that species. *Photuris* are such significant predators on other fireflies in the Americas that they are thought to be the driving force that has caused several firefly species to become diurnal
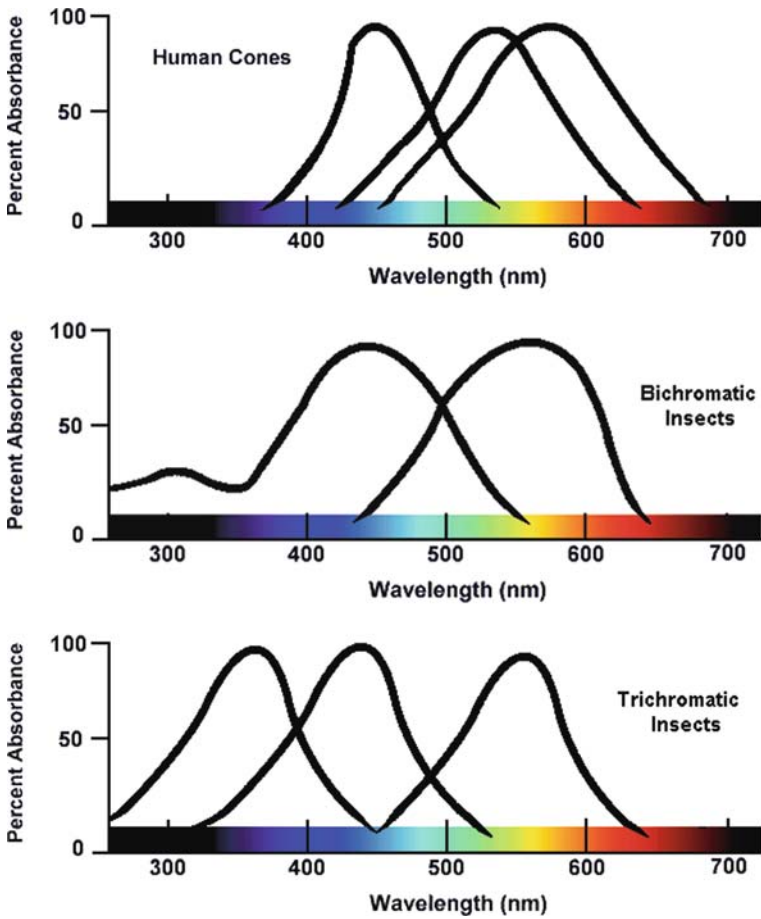
Plate 23 Perception of color by humans (*top*), bichromatic insects (*center*), and (*bottom*) trichromatic insects such as honey bees

Plate 24 A bumblebee, here just leaving a Mexican zinnia, sees a very different color palette than the human who planted the flower. (*above, left*), human view; (*above, right*), the same flower under ultraviolet (UV) light. *(below)* Simulated bee vision shows the way a flower with a visiting bumblebee would look to humans if our light sensitivity were like that of the bees. In this photograph of a bee on a yellow flower, colors have been remapped so that UV reflectance is shown as violet/blue and the whole image only contains UV-blue-green

Plate 25 Butterflies drinking at a mud puddle. When disturbed, they will swirl up together to form a confusing mass of colorful forms
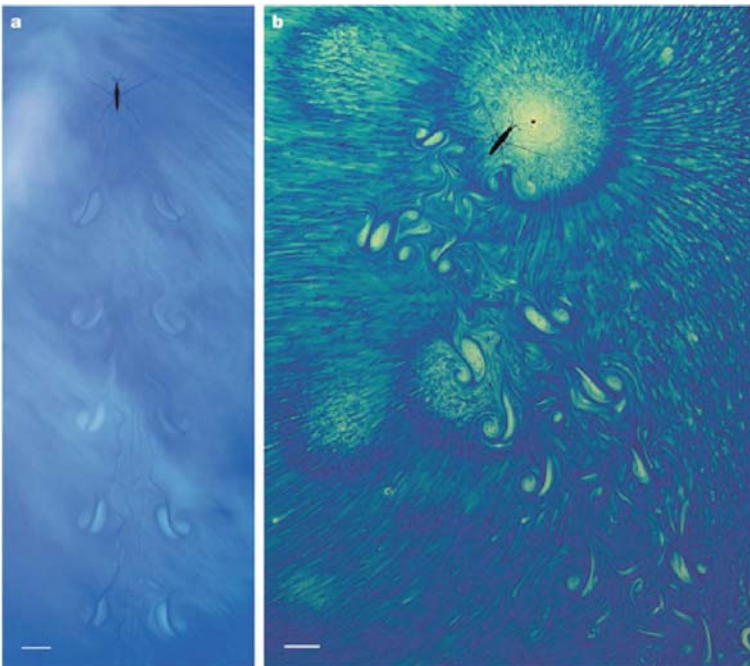
Plate 26 Using a thin layer of thymol blue on the water surface reveals the way in which a water strider (Gerridae) propels itself across the surface of a pond or river by hemispherical vortices shed by its driving legs

Plate 27 An adult female thorn bug treehopper (*Umbonia crassicornis*) guards her nymphs. They will use substrate vibrations to signal her as a group if a predator such as a coccinellid beetle should approach, and she will respond by blocking the invader, fanning her wings aggressively, and sometimes buzzing
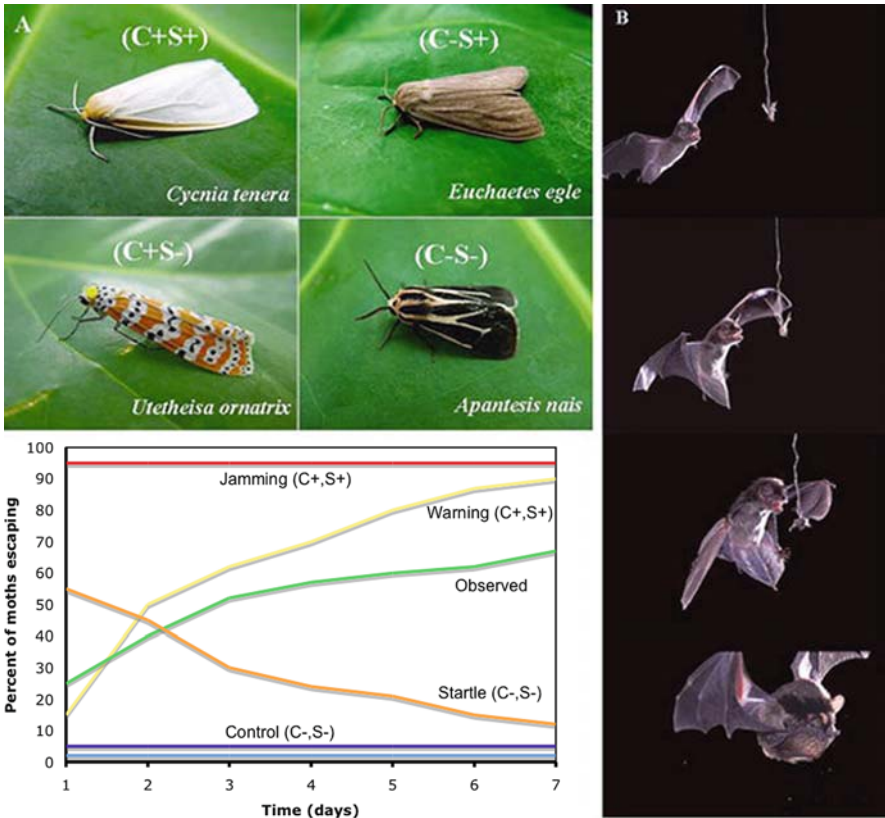
Plate 28 'Speaking' to bats. (A) All possible combinations of palatability and sound production traits occur naturally in four different species of sympatric North American tiger moths: C+ and C– refer to presence or absence of defensive chemistry and S+ and S– refer to ability or inability to produce ultrasonic clicks. (B) Four stages in prey capture. (graph) Predictions arising from three alternative hypotheses for the function of moth sound (jamming, startle, or warning) are depicted; any would result in a trained bat aborting its usual prey capturing sequence. Results were consistent only with a hypothesis of acoustic mimicry ('observed' line on graph); apparently the sounds are a warning to bats that the moths are unpalatable, and the bats quickly learn to ignore clicks that are not associated with distastefulness

Plate 29   Mating pair of snowy tree crickets, *Oecanthus fultoni*. For as much as an hour, the female (*above*) will remain in position, chewing on a thick glutinous liquid from the male's metanotal gland; later she will also consume the white spermatophore that is visible here. Mating in this subfamily is entirely female-controlled

Plate 30   An aphid giving birth to live young, one of the ways in which aphids reproduce

Plate 31 Stalk-eyed flies, *Cyrtodiopsis dalmanni,* gather to roost. A male (*above*) will fight off other males to be the sole male in such aggregations, in which mating occurs at dusk or dawn. Males with wider eye spans usually win these altercations, and females prefer to group with males with the longest eye spans

Plate 32 *Heliconius hewitsoni* butterfly male, guarding a pupa (attached to a *Passiflora* vine in a Costa Rican rain forest) from which his future mate will soon emerge

Plate 33 Ebony jewelwing damselflies, *Calopteryx maculata*. (*above*), a male on his territorial perch. (*below*), a mating pair in the classic "wheel" position; the female has white wing spots
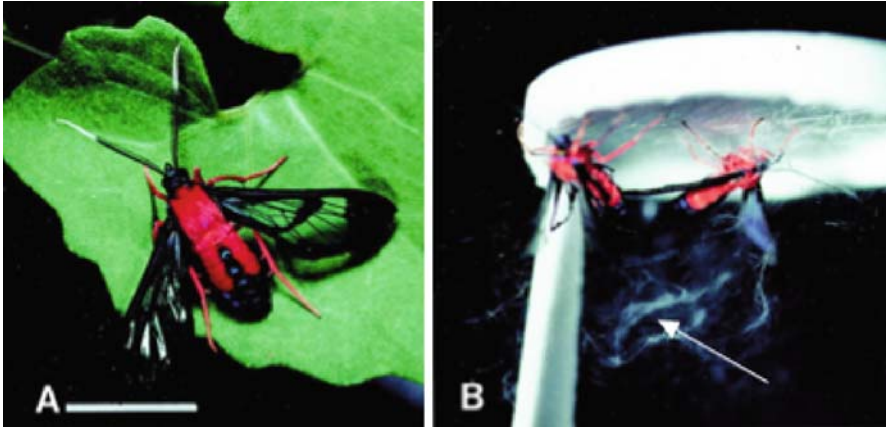
Plate 34 Chemical defense in the arctiid moth, *Cosmosoma myrodora*. (**A**) An aposomatic male rests on its larval food plant, a source of pyrrolizidine alkaloids (PA). (**B**) A courting male has just ejected a flocculent cloud (*arrow*) that will festoon the female in PA-rich fibers

Plate 35 Mud nest of a large Australian potter wasp, *Abispa ephippium*. Strictly solitary, one female builds this fortress and progressively provisions each of up to seven cells. The nest entrance funnel, thought to play a role in parasite deterrence, is dismantled and constructed anew with each added cell

Plate 36 A tumblebug (Scarabaeinae) rolls its ball of dung carved from manure. The flesh fly (Sarcophagidae) riding on the ball also breeds in dung and is a competitor for this rich food resource. After rolling the ball for some distance, the pair of beetles will cooperatively excavate a burrow and bury it, thereby making it inaccessible to flies. Underground in their burrow, the pair may spend long periods preparing the ball to receive their egg

Plate 37 *Phelypera distigma* weevil larvae in their 'circle the wagons' (cycloalexic) defensive formation between feeding bouts

Plate 38 *Mastotermes darwiniensis* worker being attacked by three green tree ants, *Oecophylla* sp. Worldwide, ants undoubtedly pose the single greatest threat to termites

Plate 39 Parental care in a wood-feeding cockroach, *Cryptocercus punctulatus*. The mother protects a clutch of offspring that infect themselves with needed cellulose-digesting symbionts by feeding on the mother's feces as well as on fluids from the mother's hind gut

Plate 40 (*left*) Australian gall-making thrips, *Kladothrips morrisi,* display striking polymorphism, shown by a stout foundress female and her more heavily sclerotized soldier daughter (*right*) A foundress female (*black*) and her offspring inhabit a domicile (here opened) formed from gluing together two phyllodes of an *Acacia*

Plate 41 Golden egg bugs, *Phyllomorpha laciniata,* carry one another's eggs, keeping them safe from ant predation. The odd, leafy spines help the bug blend in with dried parts of its host plant

Plate 42 A *Manduca* hawk moth paying a night visit to a moonflower, *Ipomea alba*. The flowers have coevolved for moth pollination; they do not open until evening, and they close the next morning

Plate 43 Maternal care in the earwig, *Forficula auricularia.* Here, a female retrieves displaced eggs and returns them to her nest. In addition to guarding the eggs, she will bring food to her nymphs while they are very young

Plate 44 After spending most of their life feeding on roots underground, cicada nymphs emerge from the soil in great numbers, split their exoskeleton, and become short-lived adults whose sole purpose is reproduction. Males produce noisy songs, using their tymbals, and receptive females respond with timed wing flicks that attract males for mating

Plate 45 Termites swarming from a railroad tie

Plate 46 To a human observer, all bumblebees and carpenter bees appear quite similar, but to a female *Xylocopa virginica*, this yellow face mask indicates a conspecific carpenter bee male

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