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

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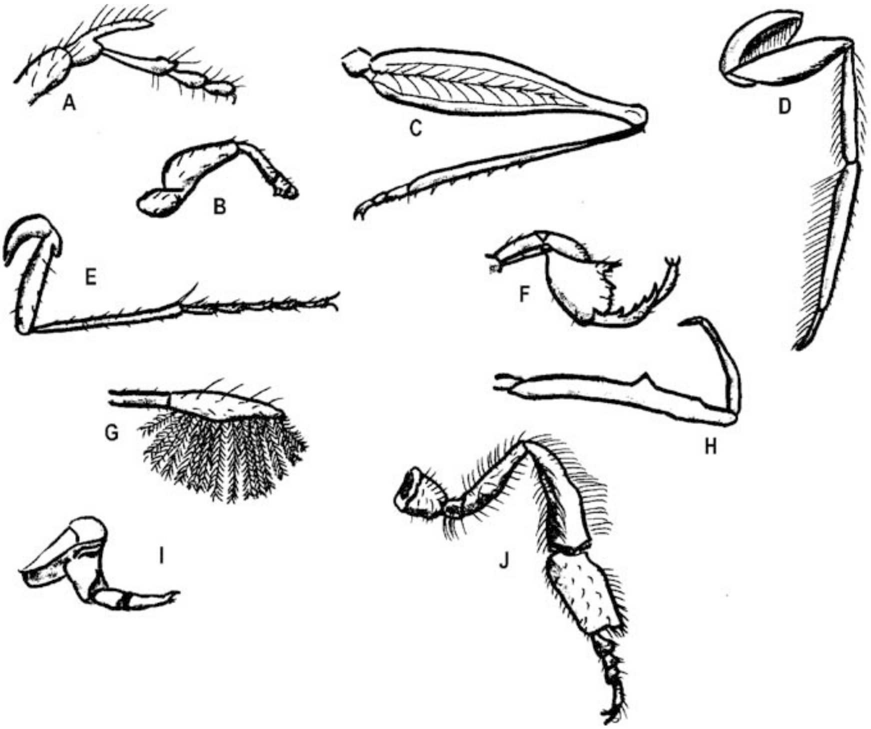

Fig. 3.1 Showing a bit of leg. Diversity of insect legs and some of the purposes of their modifications. (**A**) *Drosophila cracens* foreleg—courtship, (**B**) thrips foreleg—crawling, (**C**) grasshopper hind leg—jumping, (**D**) *Corixa* water boatman hind leg—swimming, (**E**) *Cicindela* tiger beetle 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.

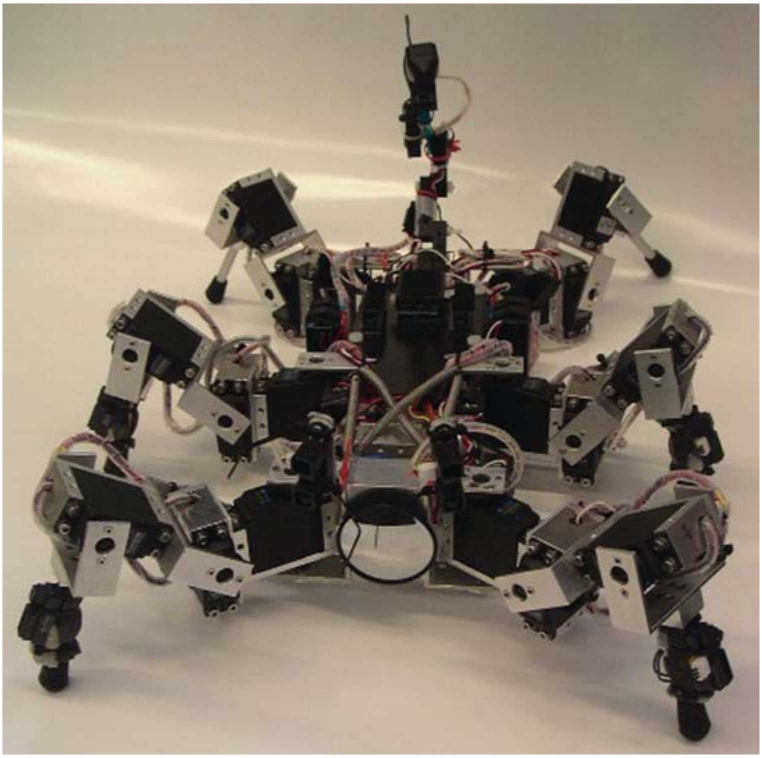

Fig. 3.2 Creating a useful mimic. Hexapodal robots have potential for performing many tasks such as exploring terrain of distant planets. Around the world, robots such as this one are being developed that mimic the analogous working morphology of common insects. The wireless camera mounted atop the robot's 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

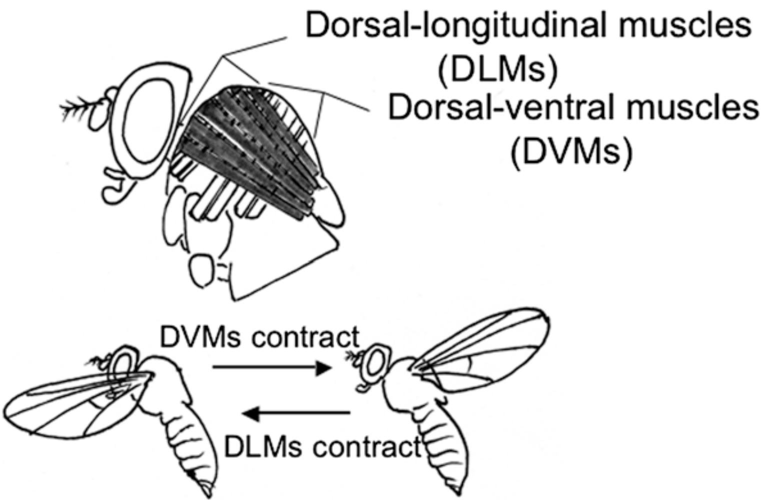

Fig. 3.3 Flapping their wings. Rather than flapping up and down, most insects wings move in a back and forth motion. This is a result of the arrangement of two groups of large antagonistic flight muscles that attach to the inner thorax walls rather than directly to the wings (thus they are called *indirect* 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'.

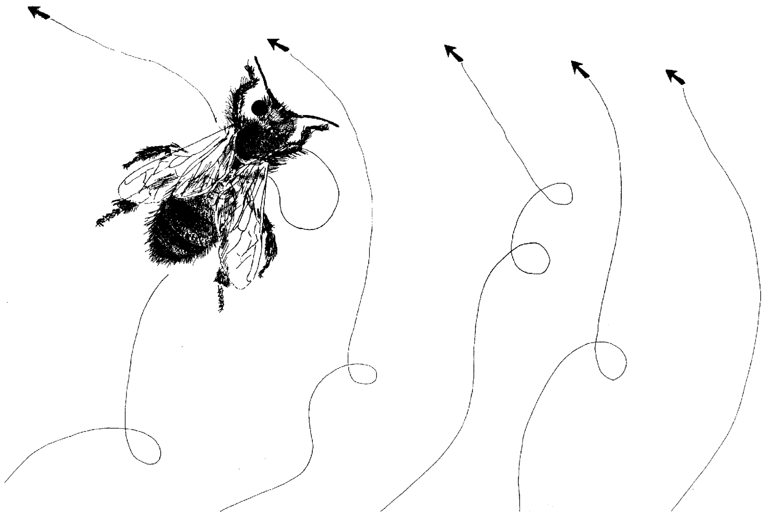

Fig. 3.4 Learning to adjust. When a honey bee's left eye is blackened, initially it circles toward the intact eye, but after 20+ repeated trials the bee learns to compensate and again moves directly toward the light. Only a sample of trials is shown; the light was directly above the starting point in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

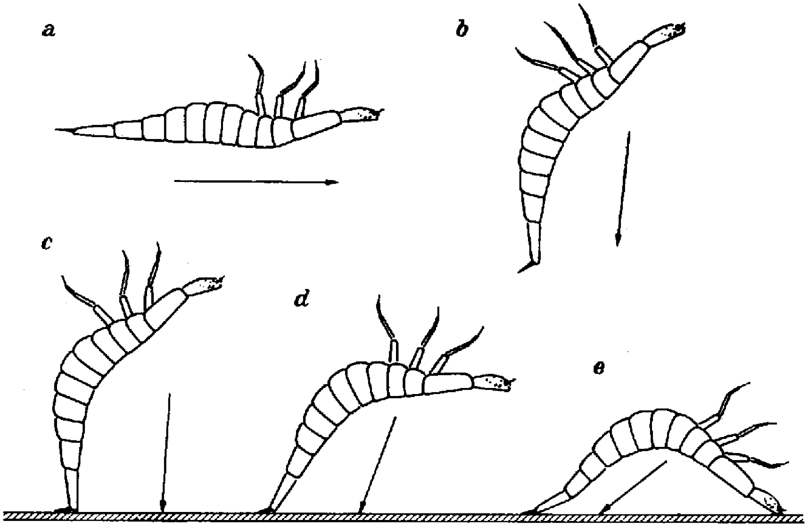

Fig. 3.5 Heeding unnatural cues. The larva of the diving beetle *Acilius* normally swims to the surface for air, cued by its dorsal light reaction; placed in an aquarium lit from below, it will descend with its back down, attempting to get air at the *bottom* as though it were the surface. *Arrows* indicate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

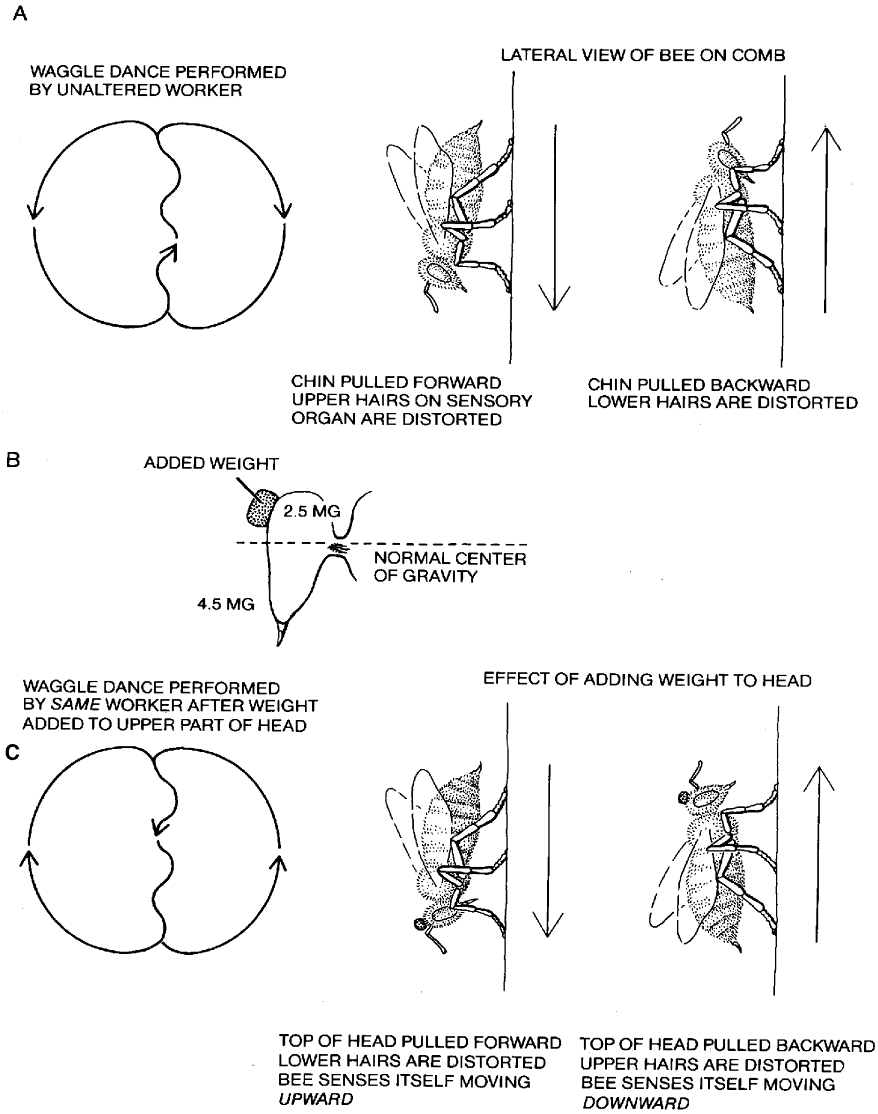

Fig. 3.6 Turning gravity on its head. Proper orientation during the honey bee waggle dance depends on gravity perception. Because of the way it is connected at the neck, the lower half of a honey bee's head weighs almost twice as much as the upper half. (**A**) When an unaltered bee is dancing on the 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

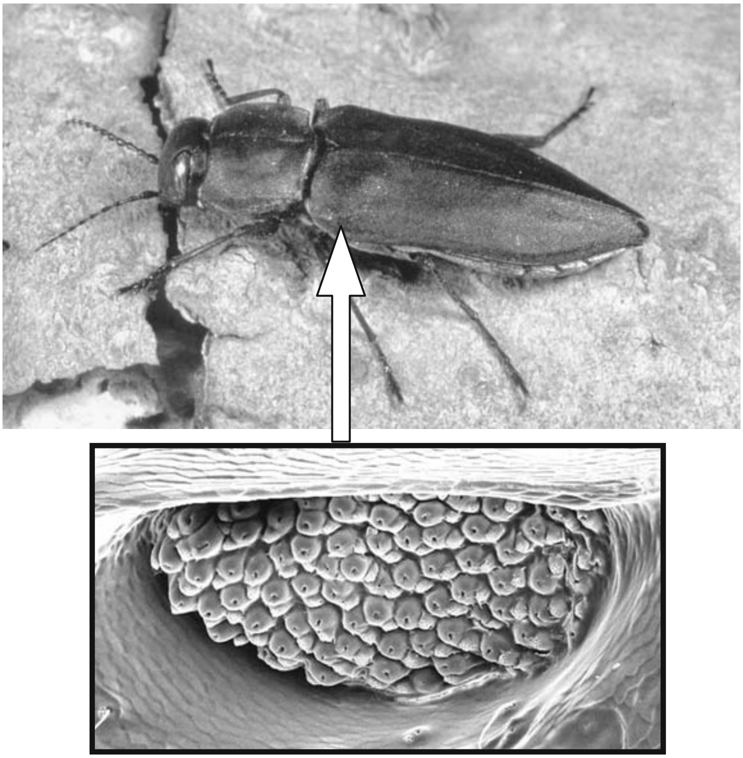

Fig. 3.7 Finding fires. The jewel beetle, *Melanophila acuminata*, possesses a pair of infrared detector organs in pits next to the junction of its middle legs and body. Each organ contains a cluster of about 70 individual dome-shaped sensilla (*below*, highly magnified), which are exposed during flight. 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

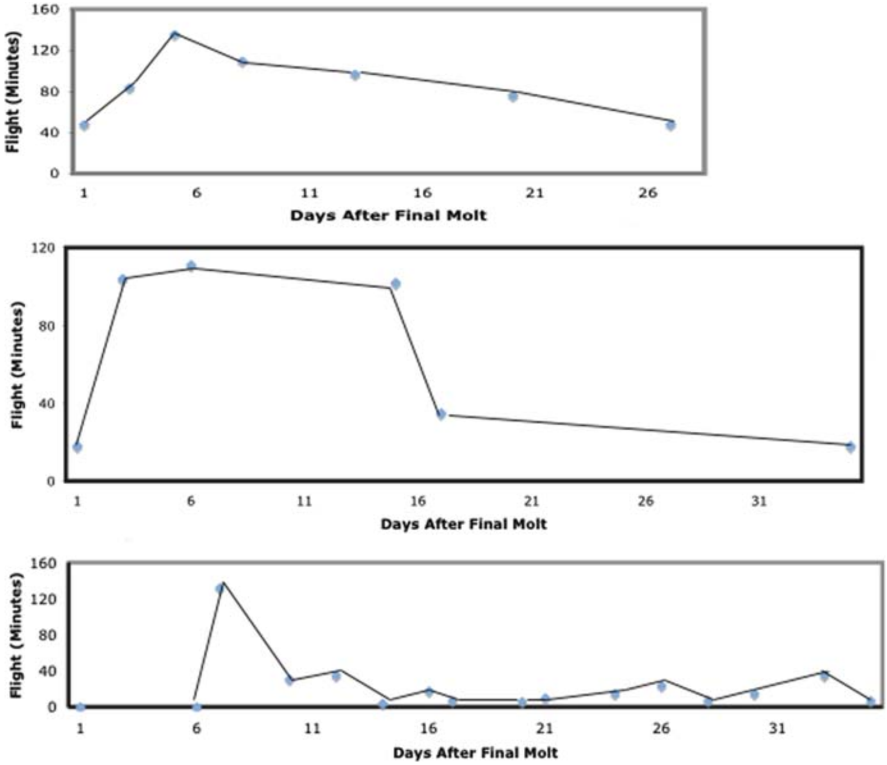

Fig. 3.9 Making trade-offs. Duration of tethered flight as a function of age in three insects: (*top*) the frit fly, *Oscinella frit*, (*middle*) the fruit fly, *Drosophila funebris*, and (*bottom*) the milkweed bug, *Oncopeltus fasciatus*. The decline in flight occurs concurrently with an increase in 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 following 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 succession 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 requirements 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 relationship 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 migration, 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 surprise 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 anticipated 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 geography. 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,

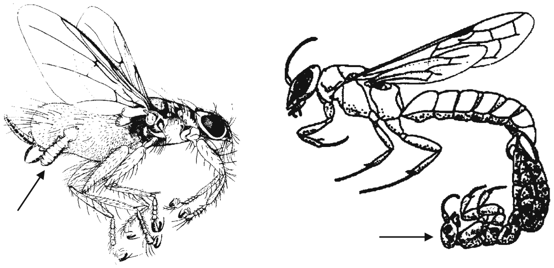

Fig. 3.10 Hitching a ride. Two examples of insect phoresy. (*left*) Feather lice firmly attach their mandibles to the abdomen of hippoboscid flies, obtaining transport to new bird hosts; it is not unusual to find 20 lice (*arrow*) upon a single fly. (*right*) Phoretic copulation in a parasitic wasp, *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

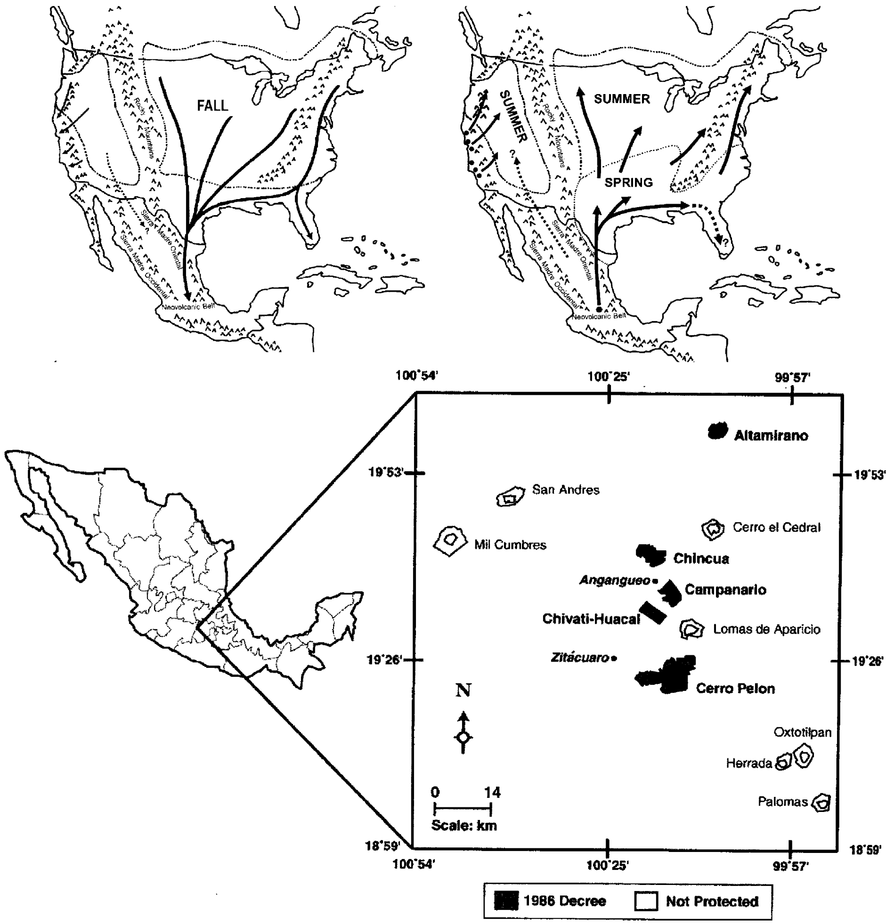

Fig. 3.11 Migrating monarchs. (*above*) The fall, spring and summer migratory routes of North American populations of the monarch, *Danaus plexippus*. Fall migrations take the butterflies to congregation sites in coastal California and central Mexico; marked individuals have been documented to fly over 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

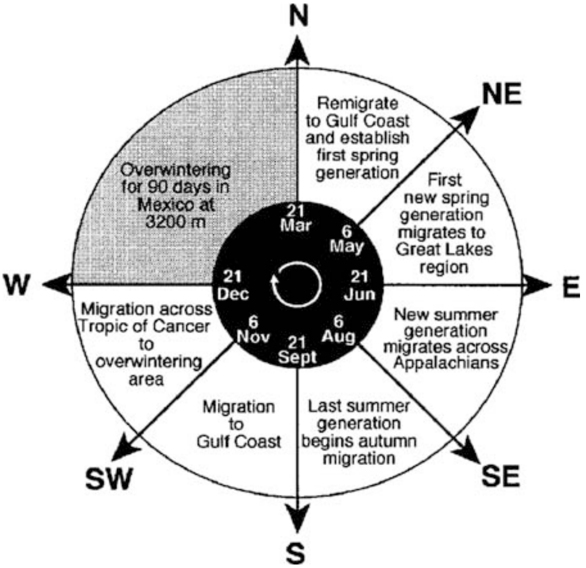

Fig. 3.12 Shifting direction. The rotational orientation hypothesis holds that monarch butterfly orientation shifts clockwise at a rate of 1 degree per day throughout the year for all generations of the annual migratory cycle. The spring equinox at overwintering sites apparently triggers northward migration 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

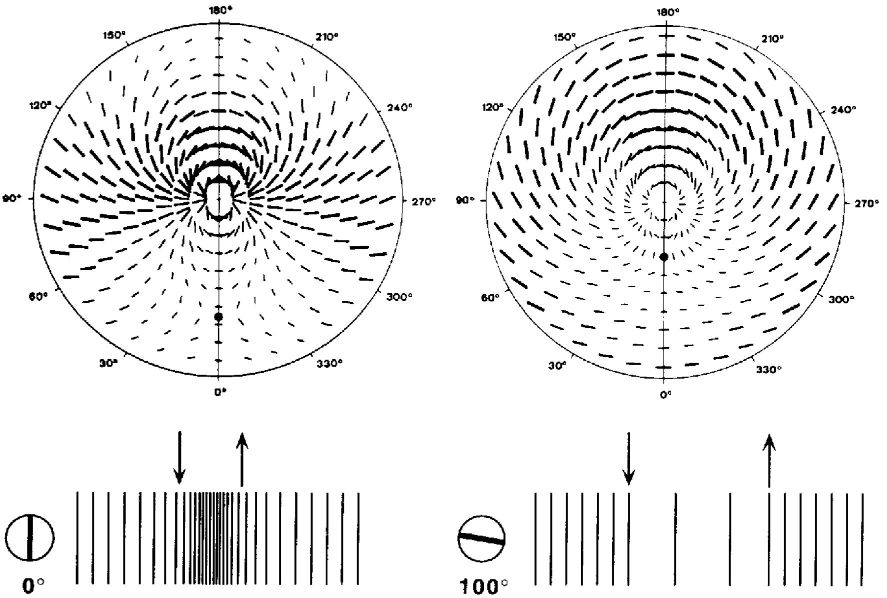

Fig. 3.13 Polarizing cues. Two representations of the e-vector sky or plane of polarization pattern of light with the sun in different positions above the horizon (24° left and 60° right) represented by the *black dot* on the axis. Orientation of each black bar gives the e-vector direction for that bar, 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.