Manipulation of Insect Signaling for Monitoring and Control of Pest Insects

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1 Introduction

Knowledge is obtained from inherited information, information gained from learning (experience), and by information received from others through communication (teaching). The importance of the role of communication in the life histories of living organisms has been recognized since ancient times, and there are many reasons to study communication in animals. For example, reproduction in sexual animals is not possible without communication, and communication is essential for the proper functioning of all types of social organisms that live together in groups or colonies. Furthermore, the study of animal signals can be used to understand general principles of evolution, and many practical applications of communication have their origins in basic studies of information exchange between animals. The manipulation of insect signaling for monitoring and control of pest species are just two examples that illustrate some of the applications that have been developed from basic studies of communication processes in animals.

Communication may be defined in a very restricted sense as the exchange of information between sender and receiver via signals transmitted through a medium, be it solid, gaseous, or liquid. "True" or "honest" communication, as determined by benefits for both sender and receiver, includes intraspecific sexual and social signals as well as some types of interspecific signals directed towards predators, competitors, or mutualist species. Signals emitted as modifications of the physical or chemical environment by the signaler's activity are received as raw data, and are translated by the receiver to provide information about such factors as the signaler's location, identity, and physiological or behavioral state. The information is processed

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and stored in the receiver's nervous system, and together with previous experiences and/or inherited knowledge, determines the response. Eavesdropping is the process whereby a receiver exploits signals intended for another individual, and which benefit the receiver with no benefit, or negative consequences, to the sender. Thus, predators and parasitoids frequently eavesdrop on the communications of their hosts as an effective method of locating potential hosts.

In this chapter, we briefly review the use of chemical and acoustic signals in insect communication, and their actual and potential applications for insect management. Although many different types of signals mediate a wide variety of behaviors, our discussion will focus on signals connected with reproduction, because these are probably the most well studied types of insect signals, and they have the broadest potential for exploitation. Signals of different modalities are used for communication associated with reproductive behaviors. The choice of which modality is used depends on a wide variety of factors, including the size of the insect, its habitat, its daily activity patterns, the transmission mediums available to it, and the distance over which the signal has to be effective. These in turn have been shaped by evolution. An insect also may use several different types of communication during a behavioral sequence, either simultaneously or sequentially. In general, most practical applications of insect signaling have focused on the exploitation of signals intended for long-range use, because these signals can be used to draw insects in to the source of the signal. It is more difficult to visualize methods of exploiting short-range or contact signals, and such types of signals have been less widely used in insect control, unless they have been combined with a longer-range attractant. Furthermore, most practical applications of long-range signals have focused on the manipulation of a single species, for example, by attraction of conspecifics with a species-specific pheromone.

Long-range communication in insects most commonly involves chemical and/or mechanical signals, although some insects do indeed use long-range visual signals (e.g., wing patterns of diurnal butterflies, or flashing of nocturnal fireflies). Chemical signals have a number of advantages for long-range communication, including the facts that they are relatively inexpensive to produce (pheromone glands are usually a small percentage of an insect's body mass, and the chemical structures of pheromone components are relatively simple), tiny quantities (nanograms or less) are effective in eliciting behaviors, and pheromones can be detected from hundreds of meters downwind. Furthermore, even a relatively small "vocabulary" of chemical "words", with simple manipulations (changing blend components and blend ratios), can provide a virtually unlimited variety of unique messages, so that species-specific signals are easy to produce.

Contrary to well established chemical signaling mechanisms in all living organisms, communication with mechanical signals is well developed only in arthropods and chordates. With this type of signaling, the sender uses some type of mechanical force to create a disturbance in the transmission medium, and this disturbance is detected by the receiver, for example, as airborne sound or substrate-borne vibrations. Whereas long-range communication with signals transmitted through air is relatively efficient, for reasons described below, airborne communication is much less widely used by insects than substrate-borne communication, whether counted by species, families, or phylogenetic distribution (Cocroft et al. 2005). In the last few decades, the study of insect vibrational signaling on plants, the typical substrate employed by many insects, has accelerated following the development of sensitive and noninvasive methods for recording low intensity acoustic signals in relatively delicate plant structures. For some types of insects, substrate-borne communication is the most efficient method of identifying and locating a mate on a plant, as described below. Although our body of basic knowledge on such types of signaling is growing, practical applications, including exploitation for pest control, have remained elusive.

The aim of this chapter is to provide an overview of chemical and acoustic communication in insects, and how these signals are or might be exploited for insect management. Each of these signal modalities is presented separately, and we then describe how these signals might be used jointly for certain applications.

2 Chemical Signals

Chemical signals are widely used by all forms of life, from single-celled organisms such as bacteria through to the largest plants and animals. It is likely that chemical signaling was the first type of communication between organisms to evolve as early life forms developed (Wilson 1970). Such signals are highly versatile, because by adjustment of their chemical and physical properties during biosynthesis, a terrestrial organism can produce volatile molecules that transmit ephemeral messages over long distances downwind, or conversely, low-volatility signals that act over short ranges or on contact, but which can persist for long periods, and anything in between. Analogous types of signals are used by aquatic and marine organisms, generally using the alternate criterion of solubility rather than volatility to determine whether a particular signal acts on contact or over a distance. Thus, chemical signals have been shaped by evolution to suit the context in which they are used, and the types of information that they are intended to convey. The chemistry of signal molecules is very diverse, with all of the major classes of natural products being represented, including terpenoids, acetogenins, fatty acids, alkaloids, carbohydrates, and peptides.

Due to space limitations, our discussion of chemicals that mediate the behavior of insects generally will be restricted to pheromones, the subset of signal molecules (semiochemicals) that are used for communication between organisms of the same species (Nordlund and Lewis 1976). Furthermore, for the purposes of our discussion, we designate a chemical that is made by a producer for the specific purpose of communicating with a receiver as a signal, whereas compounds that are intercepted and exploited by a nontargeted receiver will be designated as cues (see discussion of these definitions in Greenfield 2002). It must be recognized that, in addition to pheromones, there are a wide variety of other types of semiochemicals that mediate interactions between organisms of different species. For example, chemical cues are widely used by insects to locate, recognize, and confirm the identification of suitable hosts or other food sources, and for location and recognition of suitable oviposition sites (Miller and Miller 1986). Furthermore, compounds that are produced in the context of pheromones for signaling to a conspecific are frequently exploited by parasitoids or predators as a means of finding their hosts (e.g., Aldrich 1999). When a receiver benefits to the detriment of the producer, such chemicals function as kairomones (Brown et al. 1970). Thus, although a chemical signal may be produced for the specific purpose of communicating with a conspecific, it can have multiple functions within an ecological community, influencing the behaviors of several different species in different ways.

Naturalists were the first to document that some insects communicated with chemicals, but systematic attempts to understand the mechanisms and identify the signal molecules occurred only over the past 50 years. In one of the first experiments that conclusively showed that insects communicate with volatile chemicals, conducted in the late nineteenth century, the French naturalist Jean-Henri Fabre demonstrated that males of the moth *Saturnia pavonia* were strongly attracted to unmated females over long distances, and that the signal had to be a volatile chemical rather than an acoustic or visual signal. Analogous observations were made with other species, but the first insect pheromone was not identified until 1959, when Adolf Butenandt and coworkers culminated a heroic 20-year effort by identifying bombykol, the sex pheromone of the silk moth, *Bombyx mori* (L.) (described in Hecker and Butenandt 1984). This generated an explosion of interest in insect chemical ecology, to the extent that pheromones of various types now are known for hundreds if not thousands of insect species, particularly for species of economic importance (e.g., El-Sayed 2008). Furthermore, the tremendous advances made in both analytical and synthetic chemistry in the past few decades, coupled with increasing knowledge of the types of pheromone molecules to expect from different types of insects, has rendered the identification of many new pheromones routine. However, this is by no means always the case, because pheromones may be produced in extremely small quantities (femtograms per insect), they may be unstable and hard to isolate in pure form, and their structures are sometimes complex. Thus, in straightforward cases, pheromones can be identified from a few or even a single individual, whereas in other cases, powerful pheromones used by economically important species (e.g., the plant bugs *Lygus lineolaris* (Palisot de Beauvois) and other *Lygus* species, reviewed in McBrien and Millar 1999, or the Australian cane beetles in the tribe Melolonthini, Fletcher et al. 2008) have eluded identification, despite intensive research over several decades.

During the late 1960s, in conjunction with the first identifications and syntheses of insect pheromones, researchers began to focus attention on the potential for exploiting these compounds for managing insect populations by manipulation of insect behaviors. This potential can be graphically illustrated with a simple bioassay for any number of species, by the attraction of hundreds or even thousands of individuals to a trap baited with a milligram or less of synthesized pheromone, and the lure will remain attractive for periods of weeks, months, or even years. Furthermore, the attraction can be so focused and all-consuming that the responding animal will seriously injure or kill itself while attempting to respond. Thus, insect pheromones might superficially appear to be powerful tools with which to manage insect populations, and major efforts have been devoted to developing reliable, practical, and economical methods of doing so. The use of pheromones for insect control, in place of insecticides, is particularly attractive for several reasons. For example, pheromones are nontoxic, highly species specific, biodegradable, and are used in relatively small amounts, so they result in no persistent environmental contamination or non-target effects. In fact, pheromones in current use are so benign that there is no reentry delay required after their application to a crop, in contrast to some pesticides, where reentry into a treated area may not be permitted for several weeks.

However, some of the major benefits of exploiting pheromones for insect control via behavioral manipulation, as opposed to using insecticides that kill the target pest (and which contaminate groundwater and affect non-target organisms including humans) also turn out to be some of their major limitations. For example, because pheromones do not kill insects and remove them from the system, the pheromone treatment usually must exert its effects continuously for the entire adult lifetime of the target pest, or the pheromone must be used in conjunction with another method of killing the insect (discussed further below). Furthermore, unlike most insecticides, insect pheromones are essentially species specific. Whereas this specificity prevents effects on non-target organisms, including bees and other beneficial insects, it has both practical and economic consequences. In practical terms, if a crop is attacked by more than one major pest, then other control measures may have to be used to manage those species whose behavior is not affected by the pheromone. In economic terms, the species specificity means that the pheromone can only be used to manage one or a few species, so that the market for a particular pheromone will be relatively small, in contrast to the market for an insecticide which can kill many insect species. Thus, commercial production of pheromones is a niche market, in contrast to the much larger markets for broad-spectrum insecticides, each of which can be used to control numerous insect species.

Before detailing the use of insect pheromones and related compounds for insect control, some brief descriptions of the major types of pheromones would be appropriate.

2.1 *Types of Chemical Signals*

Insects use pheromones in various contexts in all aspects of their life histories. Whereas adult insects have been the main focus of pheromone identification and development efforts, all life stages of insects (except possibly eggs) probably use pheromones in some form. Because of the enormous range of behaviors and effects that they mediate, pheromones have been categorized in several different ways. First, pheromones are designated as either releaser pheromones, whereby reception of the pheromone triggers an immediate behavioral response (e.g., a male insect being immediately attracted by a female's volatile sex pheromone), or primer pheromones, which induce a delayed response which may be manifested as a physiological change (e.g., caste determination in termites (Kaib 1999) or honeybees (Pettis et al. 1999; Keeling et al. 2004).

Pheromones are also further classified according to the types of behaviors or effects that they mediate. A short list of the main types of pheromones used by insects follows.

Sex pheromones, which mediate behavioral interactions between the sexes, have a multitude of functions in insect reproduction, which can be viewed as a cascade of sequential behavioral steps. The most well known types of pheromones are probably the sex attractant pheromones that are released by one sex (often but by no means always the female), and which mediate the initial steps of activation and directed upwind movement of the other sex towards the "calling" individual. Over shorter distances, other sex pheromones may come into play, such as courtship pheromones, or aphrodisiac pheromones that render an individual receptive to mating. At close range and on contact, individuals verify that they have found a mate of the right sex and species with contact sex pheromones, which constitute a subset of the hydrocarbons and other lipids that coat an insect's exoskeleton. These relatively non-volatile compounds can also be used as arrestants or trail-marking compounds, to alert a walking male that a female is close by, and to lead him to her (e.g., Kainoh 1999). During mating, males may transfer substances to females that inhibit further calling behavior, so that the females do not attract other males. After mating, males also may mark mated females with an anti-aphrodisiac pheromone that renders them unattractive to other males (Schulz et al. 2007). In both cases, these male-produced compounds serve to maximize the number of eggs that are fertilized by the first mate's sperm.

Aggregation pheromones are typically produced by one or both sexes, and elicit a response from both sexes, unlike sex pheromones which only elicit a response from one sex. They are often multifunctional, for example, serving to attract conspecific individuals to a host resource, while also serving to bring the sexes together for reproduction. Probably the best known and well studied uses of aggregation pheromones are those by some bark beetle species, in which aggregation pheromones are vitally important for bringing together the critical mass of conspecifics required to overwhelm the resin defenses of host trees (review, Schlyter and Birgersson 1999). Furthermore, there is a subsequent feedback step; once the host tree has been overwhelmed by a sufficient number of bark beetles, the occupants begin to produce anti-aggregation pheromones to divert latecomers away from the tree so that it does not become overcrowded, which would result in larval competition and cannibalism. Aggregation pheromones are also known for a variety of other insects, including other beetles and flies (Hardie and Minks 1999) and some arctiid moths (Conner and Jordan 2008).

Alarm pheromones are used both to warn conspecific individuals of danger, and to recruit conspecifics for defense. As early as 1609, Charles Butler described how the scent emanating from a detached bee sting attracted more bees and stimulated aggressive behaviors. Alarm pheromones are most common in insects that live in groups or colonies such as ants, bees, and aphids, but they are also produced by species such as true bugs. Because they need to be disseminated so that receivers can respond quickly, alarm pheromones are typically small and highly volatile compounds. Furthermore, to vertebrate noses, they often have pungent odors and may be toxic or irritating, so that they serve as direct defenses as well.

Trail pheromones are used primarily by social insects such as ants and termites, as a method of guiding conspecifics to food resources (e.g. Kaib 1999). They are also used by tent caterpillars for marking trails back to food resources as the caterpillars return to the communal tent (Fitzgerald 1995).

There are many other types of marking pheromones, that are used in contexts as varied as territory marking (e.g., African weaver ants, Hölldobler and Wilson 1978) to host-marking, whereby a female insect that has laid an egg in a host (including other insects, in the case of parasitoids) will mark that host to deter further oviposition by conspecific females. Thus, the offspring of the female making the mark can maximally utilize the host resource, without competition from conspecifics (Kainoh 1999; Landolt and Averill 1999).

Pheromones are also critically important in all aspects of the organization and functioning of social insect colonies. The cuticular lipids of each individual in the colony consist of a mixture of compounds that provide information to conspecifics about its species, caste, age, and gender, so that brief antennation of one individual by another provides instant recognition and categorization of that individual. Furthermore, the blend of compounds is subtly different between nests or colonies, even for colonies living adjacent to each other, and individuals from different colonies readily recognize each other as intruders. These chemical signatures consist of a mixture of an individual insect's cuticular compounds, and compounds that are associated with each nest. However, this is just the tip of the iceberg in terms of pheromone use by social insects, and we are still in the early stages of teasing out and understanding the multitude of signals that regulate their complex societies. For example, in honeybees, we now know that the queen's mandibular pheromone inhibits reproduction by workers, but also influences behaviors as diverse as swarming, foraging, and the regulation of tasks within the hive (Breed et al. 1998; Pettis et al. 1999; Keeling et al. 2004).

This is but a small sampling of the different types of insect pheromones and their uses. Clearly, pheromones are ubiquitous signals that mediate most aspects of insects' interactions with each other, for all life stages where interactions between individuals occur. For more in-depth surveys of known insect pheromones, the reader is referred to several online resources (Ando 2003; Witzgall et al. 2004; El-Sayed 2008) or books (e.g., Mayer and McLaughlin 1991; Howse et al. 1998; Hardie and Minks 1999; Schulz 2004a,b).

2.2 Exploitation and Manipulation of Chemical Signals

Given the number and variety of insect pheromones, there are many opportunities for manipulation or disruption of these signals, using several different strategies. For example, we can attempt to replicate the insect-produced signal and its intended effects by partial or complete reconstruction of the active blend of chemicals. It may also be possible to exploit the negative behavioral effects associated with naturally occurring behavioral antagonists that are produced as minor components of some pheromone blends, and that insects use to reinforce the specificity of their pheromone channels (e.g., Bengtsson et al. 1994). Alternatively, interference with the reception or processing of chemical signals may provide opportunities for insect management (e.g., Ditzen et al. 2008). This is particularly true with the recent spectacular advances in molecular biology, whereby the genomes of a number of insect species have been sequenced, providing leads for manipulation of insect behavioral signals and mechanisms at the genetic level. To date, however, exploitation of insect pheromones has relied primarily on manipulation of conspecific attraction, although researchers are starting to explore whether other behavioral mechanisms might also be amenable to manipulation. Each of these is discussed in the following sections.

2.3 Pheromones for Detection and Sampling of Insect Populations

Volatile sex and aggregation pheromones are widely used in modern agriculture, and pheromone lures for several hundred insect species are commercially available. Pheromone-baited traps are fast and simple to use, and because of the species specificity of each pheromone, require no expertise to identify the insects caught. Pheromone-baited traps are particularly useful in providing early warning of the presence of a target species, and for following population cycles (e.g., flight phenology of adult insects) so that control measures can be accurately timed. However, it has proven more difficult to develop robust economic thresholds based on trap catches alone, for a variety of reasons (e.g., clumped rather than random distributions of target pests, and/or insufficient trap densities due to trapping costs), and so the detection of the target pest in pheromone traps often triggers secondary sampling of the crop to verify whether populations are indeed high enough to warrant control measures (e.g. Howse et al. 1998).

An equally important and rapidly growing use of pheromone-baited traps is for the detection and interception of invasive species, and the delineation of the current ranges of invasive species as populations spread outwards from the original site of introduction and establishment. Thus, semiochemically-baited traps form the cornerstone of detection efforts by regulatory agencies for notorious invasive pests such as the gypsy moth *Lymantria dispar* (L.), the Japanese beetle *Popillia japonica* Newman, the boll weevil *Anthonomus grandis* Boheman, the pink bollworm *Pectinophora gossypiella* (Saunders), and the Mediterranean (*Ceratitis capitata* (Wiedeman)) and related fruit flies (e.g., Ridgway et al. 1990; Howse et al. 1998). The importance of such sensitive trapping methods cannot be underestimated, because early detection has repeatedly enabled the eradication of small and localized populations of pests such as these, averting billions of dollars in crop and forestry losses, as well as avoiding the added pesticide load to the environment that would be required for ongoing control of invasive insects once they had become permanently established. Furthermore, insect pheromones and related compounds have often played a critical part in the eradication process, both in terms of being used to trap or kill insects, and in terms of providing a sensitive method to determine when areas have been rendered pest-free. Because of the major expansion of world trade over the past couple of decades and the consequent rapid increase in the introduction of exotic pests into new areas of the world, the use of pheromones for detection of such pests will of necessity increase.

In addition to deploying pheromones for detection of pest insects, there is increasing interest in using pheromones for detection and sampling of beneficial insects, particularly for programs in which natural enemies have been deliberately introduced into a new country for biological control of an introduced pest (e.g., Suckling et al. 1999, 2000, 2006; Stanley et al. 2000; Cossé et al. 2004). There are obvious parallels between the use of pheromones for detecting introduced beneficial insects and undesired exotic pests, i.e., in both cases, the purpose is to use the most sensitive method possible to detect the target insect at low densities.

2.4 Management of Insects by Pheromone-Based Mating Disruption

Because many insect species are entirely dependent on the use of sex pheromones to bring the sexes together for mating, the potential for controlling insects by manipulation of this fundamentally important aspect of their life histories has been recognized for a long time. In 1967, Harry Shorey and his coworkers conducted the first successful trial of this concept, demonstrating disruption of mating of pink bollworm moths with a synthetic insect pheromone (Gaston et al. 1967). Since that landmark trial, enormous efforts have been devoted to developing mating disruption into an effective, reliable, and economical insect control tactic, with results varying from spectacular success to complete failure. Currently, mating disruption is used for insect control on approximately 660,000 ha worldwide, with the main target pests being gypsy moth *L. dispar* (forestry), codling moth *Cydia pomonella* (L.) (pome fruit), grapevine and grape berry moths, *Lobesia botrana* (Denis et Schiffermüller) and *Eupoecilia ambiguella* Hübner respectively (vineyards), oriental fruit moth *Grapholita molesta* (Busck) (peach, apple), pink bollworm *P. gossypiella* (cotton), and leafrollers (orchard crops and tea) (Witzgall et al. 2008). Development of mating disruption in various crops still constitutes a very active area of research; the types of pests and crops under investigation and implementation continually increase. For example, mating disruption of the western poplar clearwing moth *Paranthrene robiniae* (Hy. Edwards) in poplar plantations in the northwestern United States recently proved to be spectacularly successful, completely controlling a devastating problem that could not be managed effectively with insecticides (Brown et al. 2006). Mating disruption is also being attempted with insects other than moths: for example, a pheromone formulation for mating disruption of vine mealybug *Planococcus ficus* (Signoret) in vineyards came on the market in 2008 (Suterra LLC., Bend, Oregon, USA).

Overall, the history and description of research on mating disruption have been covered in a number of reviews (themselves summarized in Cardé 2008), and so only a few main points will be touched upon here. The main premise underlying pheromone-based mating disruption is that male insects are prevented from finding females by blanketing a field with the synthesized pheromone, either by releasing it from multiple point sources per hectare (e.g., microencapsulated pheromone or small, discrete dispensers dispersed throughout the crop), or by dispensing pheromone from a much smaller number of dispensers that release a correspondingly larger amount of pheromone per dispenser (e.g., plastic bags that passively release pheromone, or mechanical devices that release metered puffs of pheromone at regular time intervals). One of the points about mating disruption that must be borne in mind is its fundamental difference from management of insects with insecticides. That is, with mating disruption, the pheromone is not toxic and only interferes with an insect's behavior. Thus, to be effective, the pheromone must completely blanket a crop, with no holes or gaps, for the entire duration of the male insect's lifetime, or more widely, for the entire period that the adult stages of the target insect are present. For insects that have multiple generations per year, this can translate into a period of at least several months. In sharp contrast, with insecticides, a single contact with a lethal dose of the toxicant removes the insect from the system (although several applications may be required for season-long control). Thus, mating disruption may be inherently more difficult to use effectively than insecticides. However, this possible limitation is counterbalanced by a number of distinct advantages, not least of which is the decrease or elimination of insecticide use in crops protected with mating disruption. Furthermore, in some 40 years of use, there has only been one documented case of development of behavioral resistance to mating disruption, caused by the use of an incomplete pheromone blend (Mochizuki et al. 2002). Full efficacy was restored by simply reformulating the pheromone to include the minor components.

One of the continuing problems with implementation of mating disruption is our incomplete understanding of the mechanisms by which it works, further compounded by the fact that it is likely that different possible mechanisms are more or less important for different species, i.e., there is no "one size fits all" model applicable to all species. Three principal mechanisms have been invoked: sensory adaptation of the pheromone receptors and/or habituation of the central nervous system to the synthetic pheromone, competition between the point sources of synthetic pheromone and calling females (also known as false trail following), and camouflage of the pheromone plumes produced by calling females by the blanket of synthetic pheromone. Given good coverage of a crop with dispensers releasing quantities of synthetic pheromone equivalent to many thousand or even millions of female insects (e.g., a fraction of a gram to several grams per hectare per day), logic would seem to dictate that any one or any combination of these mechanisms should be sufficient to achieve disruption. The fact that effective control of some species has not been achieved demonstrates that successful implementation of mating disruption may not be straightforward. However, recent attempts to mathematically model mating disruption have provided insight into which mechanisms may be most important (Miller et al. 2006a,b), and may help to resolve difficulties that have been encountered in attempted mating disruption of some species.

2.5 Insect Control by Pheromone-Based Mass Trapping

Although the concept of insect control through mass trapping may be technically feasible, practical and economic considerations have limited its general use; the costs of purchasing, deploying, and servicing a sufficient number and density of traps are often prohibitive. However, under some circumstances, pheromone-based mass trapping can be both highly effective and economically competitive, and it is currently used for control of a number of species in diverse systems. For example, mass trapping of ambrosia beetles around log sorting areas and sawmills in northwestern North America has been used effectively for several decades to minimize damage to saw logs from the beetles and the blue-stain fungus that they vector (McClean and Borden 1977). In a somewhat different application, baiting of lodgepole pine trees with a combination of aggregation pheromones and host tree volatiles is used to concentrate mountain pine beetles *Dendroctonus ponderosae* Hopkins into the baited trees, which are then removed or treated with insecticide to destroy the developing brood (Borden 1989). Mass trapping for control of a lepidopteran, the brinjal borer *Leucinodes orbonalis* Guenée, was effective in India, in part due to low labor costs (Cork et al. 2003). However, the most effective and largest scale use of pheromone-based mass trapping has been in the management of large tropical weevils such as the palm weevils *Rhynchophorus palmarum* Linnaeus and *R. ferrugineus* Olivier (Oehlschlager et al. 2002; Faliero 2006) and related species, and the banana weevil *Cosmopilites sordidus* Chevrolat. One of the key factors in the success of these programs is that the weevils reproduce slowly, so that their reproduction cannot keep pace with their removal by mass trapping, and continuous mass trapping drives their populations steadily downward. Because most of the research and development on mass trapping these weevils has been done by industry rather than academic researchers, spearheaded by Chemtica International in Costa Rica, much of this work has not been published in the scientific literature, and it is difficult to estimate the total area that is mass trapped. It is clearly many thousand hectares, because pheromone-based mass trapping is a major component of IPM programs for coconuts, dates, oil palms, and bananas in South and Central America, the Mediterranean basin, and Asia. Thus, given the right sets of biological and economic circumstances, pheromone-based mass trapping can be both highly effective and economical, and in the case of the tropical weevils described above, it provided a solution to a problem that was otherwise almost intractable.

2.6 Semiochemically Based Attract and Kill Methodologies

Pheromone-based attract and kill methods involve combining point sources of pheromone with a killing agent. In theory, attract and kill may have some advantages over mating disruption; for example, the responding insect is killed or intoxicated by contact with the attracticide source, and so is effectively removed from the system. The attract and kill technique may be more economical when expensive pheromones are used, because it requires a lot less pheromone than mating disruption, i.e., it is only necessary to attract the target insects to the toxic bait, rather than overwhelming their sensory systems with pheromone. A disadvantage to attracticide technology is that it does use a toxicant as part of the formulation, and consequently, it may face more regulatory hurdles than mating disruption or mass trapping. In practice, the number of current applications of pheromone-based attracticides is relatively small, but will probably grow.

To date, attracticide technology has been most widely applied for the control and eradication of invasive tephritid fruit flies such as the Mediterranean fruit fly *C. capitata* (reviewed in Millar 1995), the oriental fruit fly *Dacus dorsalis* Hendel, the melon fly *D. cucurbitae* Coquillet, the Mexican fruit fly *Anestrapha ludens* (Loew), and the olive fruit fly *D. oleae* (Gmelin) (Metcalf and Metcalf 1992). For most of these species, the best formulations consist of food baits combined with a toxicant, but pheromone-based attracticides have now been developed for control of olive fruit fly (e.g., Mazomenos et al. 2002). Pheromone-based attracticides also form a cornerstone of effective efforts to eradicate boll weevil *A. grandis* from the United States (reviewed in Prokopy and Roitberg 2008). Whereas pheromone-based attract and kill methods have been tested for a number of insect species, such as leafrollers (Curkovic et al. 2008), diamondback moth *Plutella xylostella* (Linnaeus) and cabbage looper *Trichoplusia ni* (Hübner) (Maxwell et al. 2006), and sap beetles *Carpophilus* spp. (Hossain et al. 2007), this strategy has not been as widely adopted as mating disruption. Unfortunately, pheromone-based attracticide research has not yet been summarized in a review article, so it is difficult to obtain an accurate estimate of how widely this technology has been adopted, and how effective it is.

2.7 Exploitation of Alarm Pheromones

To date, the only well documented attempts to exploit alarm pheromones for insect control have been with aphids. The aphid alarm pheromone (*E*)-ß-farnesene induces movement and dispersal in aphids. The general concept was to use these increased activity levels to induce aphids to pick up a lethal dose of a co-applied insecticide or fungal pathogen more quickly, thus allowing lower application rates of the toxicants to be used (Pickett et al. 1992). This idea has been commercialized, but the overall efficacy and cost effectiveness for aphid control remains unclear.

There may be potential for using alarm pheromones for other types of insects that avoid or move away from sources of alarm pheromone. For example, insects such as leaf-footed bugs *Leptoglossus* spp., which can cause extensive damage in seed orchards and nut crops in western North America, disperse rapidly from a tree upon release of alarm pheromone by a conspecific (J. Nay, personal communication 2007). It might be possible to exploit this behavior to prevent infestation of nut crops, particularly as the alarm compounds have simple structures and are cheap and readily available.

2.8 Practical Considerations for Exploitation of Pheromones for Insect Management

A number of insect pheromones and related substances are now in common use for detection, sampling, and management of insect populations, but this represents only a tiny fraction of the total number of insect pheromones known, for reasons that vary from basic biology to economics. Furthermore, the total acreage of crops in which pheromones are used as a significant or primary method of controlling pests (as opposed to detection and monitoring), is small (Witzgall et al. 2008) in comparison to the acreage on which insecticides or some other pest control method, such as transgenic crops, are used. Nevertheless, there is continuing strong interest in exploitation of pheromones, and steady growth in total acreage treated and the number of different crops in which pheromones are deployed. This interest is driven in part by the joint desires to minimize use of toxic insecticides, and to delay development of resistance to insecticides. To continue this growth trend, we need to be pragmatic about our choice of pheromones to develop. First and foremost, we need to ensure that a target pest is sufficiently economically important to warrant both the initial investment in research, and to ensure a large enough market for commercial pheromone products to be profitable. If these initial caveats can be satisfied, then there are a series of more detailed questions that need to be asked to assess whether a pheromone project is both biologically and economically feasible.

2.8.1 Biology of the Target Insect

A detailed knowledge of the target insect's biology is essential to assess whether there is a reasonable possibility that it can be controlled with pheromones. For example, an assessment of the strength of behavioral responses to the pheromone is critical. For insects such as lepidoptera, which are generally accepted to be strongly attracted to pheromones, this may seem obvious, but this is not always the case: in our experience, for some lepidoptera with long-lived adults that feed, the males may only be attracted to pheromones during a particular period in their adult lives. For other insects for which pheromone chemistry and biology is less well known, a critical and conservative examination of the pheromone-mediated behaviors (using live insects as producers and responders) should be undertaken to verify that responses are both strong and reliable.

Having determined that there is a strong response to pheromone, further aspects of the insect's biology must be considered. For example, multivoltine insects may require control for much longer periods than univoltine insects, keeping in mind that the pheromone does not remove the insect from the system, it just disrupts behavior at a critical period in the reproductive cycle. Thus, multiple generations are both more difficult to control, and may require two or more applications of pheromone. There may also be seasonal differences in response, or the adult insect may have a long sexual maturation period during which it is unresponsive to pheromones.

For some types of insects (e.g., weevils and the *Carpophilus* beetle species mentioned above), responses to pheromones are strongly synergized by food volatiles. In short, a detailed assessment of the biology of a target pest is an essential prerequisite to a pheromone development project.

2.8.2 Crop Characteristics

In theory, pheromone-based methods of insect control might be most amenable to high-value crops grown on a limited acreage, with a single major insect pest, largely due to economic reasons. That is, application of pheromone dispensers, attracticides, or traps for mass trapping is often done by hand, which becomes costly and logistically difficult for crops grown on large acreages. Thus, high-value crops grown in nurseries or greenhouses might constitute an ideal venue for pheromone use. This ideal mix of characteristics is seldom realized, and most current applications of pheromones for insect control are in orchards, vineyards, and plantations. In terms of other desirable characteristics, with other things being equal, a pheromone-based method of control will probably be less effective with tall trees versus shorter trees, because of the difficulties in getting good pheromone coverage of the much larger airspace of a crop with tall trees (it should be noted that obtaining good coverage of tall trees with insecticides also may be problematic). Similarly, pheromone control methods might be expected to be more effective when foliage is present during the main part of the growing season, to help disperse and hold the pheromone in the airspace of the crop, rather than during early spring when there is minimal foliage. Experience also has shown that pheromone-based control strategies work best when large contiguous areas are treated (so-called area-wide programs, e.g., Witzgall et al. 2008) rather than treating isolated small blocks, where immigration of mated females may be a significant problem.

2.8.3 Pheromone Chemistry

Although it is straightforward to synthesize many insect pheromones in small quantities for research purposes, only a small fraction of the known insect pheromones are amenable to synthesis in large scale at a cost that will make them economically competitive with insecticides or other control measures. To provide an idea of the scale required, in 2006 the ~160,000 ha of fruit crops that were treated worldwide for control of codling moth (*C. pomonella*) by mating disruption required 25 t of pheromone (Witzgall et al. 2008). The chemistry of pheromones may provide additional constraints. For example, the chemical and isomeric purity of pheromones can be critically important for good efficacy of monitoring lures, with trace impurities producing strongly antagonistic effects (e.g., Millar and Rice 1996). However, the effects of isomers and other impurities on the efficacy of pheromone used for mating disruption are largely unknown, and will probably vary from species to species, and with the types and proportions of impurities in the formulations. In fact, attempts have been made to exploit these strongly antagonistic effects by including known antagonists in mating disruption blends, with the aim of deterring male moth flight (Bengtsson et al. 1994). In contrast, the efficacy of insecticides generally is unaffected by chemical purity; as long as the toxicant is present, the material will be efficacious. Furthermore, some insect pheromones are rather unstable, rendering it difficult or even impossible to formulate effective blends with the required shelf and field lifetimes (e.g. Grant et al. 2003).

2.8.4 Economic and Regulatory Issues

In addition to the cost of pheromone synthesis, a series of other economic factors must be considered. One of the most intimidating may be the costs of registration of a pheromone for insect control. Although all pheromones are classified as insecticides in the United States, under the relatively relaxed requirements for toxicology and related testing of most lepidopteran pheromones, a registration for application to food crops may be obtained for a few thousand dollars. However, this may not be the case for pheromones of insects other than lepidoptera, and other types of semiochemicals. For these materials, full toxicological screening costing tens of thousands of dollars per compound may be required, although waivers of toxicological and ecotoxicological data may be granted if the materials can be shown to be identical or substantially similar to components of flavors and fragrances. Given the fact that many current pheromone manufacturers are small to medium-sized specialty chemical companies, the costs of registration alone may become prohibitive. In the United States, further costs are incurred because each product must be registered in each of the states in which it will be used. Costs are further compounded because registrations are required for each country in which the pheromone will be used, and the registration requirements have not quite been unified, although the Organization for Economic Cooperation and Development (OECD), the U.S. Environmental Protection Agency, and Canada's Pesticide Management Regulatory Agency are working towards this goal.

There are also other economic factors. For example, most insect pheromones are actually blends of compounds, rather than single components, and it is inherently more expensive to synthesize and formulate a mixture of compounds than a single component. If the components of the blend have widely differing volatilities and other properties, this may provide further complications in developing a formulation and dispenser that will release a constant blend for long periods of time. Third, depending on the crop, the application, and the insect, deployment and maintenance of pheromone devices or traps may constitute a substantial labor cost, particularly if hundreds of release devices have to be deployed by hand (mating disruption and attracticides), or large numbers of traps have to cleared and serviced (mass trapping) for extended periods of time. A fourth cost, which is generally under-appreciated, is a consequence of the fact that pheromone-based control methods may be more complex to use than insecticides, because the target pests are not killed by the pheromone. Thus, crops protected with pheromones require careful and repeated monitoring, so that if pheromone control starts to break down, for whatever reason, alternative control treatments can be applied.

Thus, there are significant biological, chemical, and economic hurdles that singly or in combination might deter the development of semiochemicals for insect control. Nevertheless, the major advantages of insect control with semiochemicals, such as the low toxicity and minimal effects of insect pheromones on nontarget organisms including humans, their biodegradability, and their expected long (and possibly indefinite) effective lifetimes before resistance develops, provide strong incentives to overcome these hurdles. Furthermore, semiochemicals will play an increasingly important role in the detection and eradication or management of exotic invasive pests, worldwide. That is, we have in general learned to live with the insect pests that are already present in our countries. Thus, the pests that represent the biggest threats may be those that we have not yet seen in our respective countries, particularly when they are released from the pressure of the natural enemies that normally hold them in check. Some examples where semiochemicals have been critically important tools in the detection and eradication of exotic pests would include the Japanese beetle, the Mediterranean fruit fly, the boll weevil, and the pink bollworm. In total, several decades of research on and implementation of insect pheromones have demonstrated that insect pheromones are and will continue to be valuable tools for the detection and management of insect pests, despite the number of hurdles that have be overcome in their successful implementation.

3 Mechanical Signals in the Insect World

Communication is a complex process of information exchange by signals transmitted through different media. Chemical, visual, and mechanically generated signals produced by arthropods travel between the signaler and receiver via defined communication channels. Mechanical and visual signals are emitted as temporally discrete packets of energy, whereas chemical signals are often persistent. Generally, the amount of information that can be conveyed by the signaler's message increases with increasing signal-to-noise ratio.

Communication with mechanical signals is only known to have developed in the phyla Chordata and Arthropoda. Such signals include contact (tactile) signals, and signals transmitted through air (airborne sound), water (waterborne sound), or solids (substrate-borne sound). Tactile signals are involved in courtship and social interactions at short distances, and are not really amenable to manipulation for insect control purposes.

Until recently, amongst the various other types of mechanical signals, airborne sounds were most intensively studied because they are mostly audible to the human sense of hearing. Waterborne signals and signals transmitted over water surfaces are restricted to relatively few and economically unimportant insect species. In contrast, counted by species, family, or phylogenetic distribution, substrate-borne sound communication is common in arthropods, using a variety of different modes of mechanical signaling (Cocroft and Rodriguez 2005). Development of sensitive devices for recording substrate-borne sounds, such as accelerometers and laser vibrometers, has greatly increased the number of species for which communication through substrates has been described (Drosopoulos and Claridge 2006). In the sections that follow, we will describe vibrational signaling in insects, and then discuss the potential for manipulation of mechanical signals transmitted through plants, because there has been virtually no research on how to use this channel as a tool for insect pest control.

3.1 Characteristics of Mechanical Signals Transmitted Through Plants, Air, or on Water Surfaces

The transmission characteristics of mechanical signals through different media are described by the physics of acoustics, the details of which are beyond the scope of this chapter. A brief overview is presented to provide a basis for understanding phenomena related to the interactions between a signaling insect and the plant substrate upon which it sits while producing signals.

Sound is described as a mechanical disturbance created in a compressible medium (air or water) and is transmitted from the source as longitudinal waves. In water, sound travels about four times faster than in air, and thus travels over longer distances: the velocity of sound waves in air at 20°C is 343.3 m/s and increases by 5.8 m/s for every 10°C rise in temperature. In contrast, the velocity of sound at the same temperature is 1,521.5 m/s in seawater and 1,482.3 m/s in fresh water. The amplitude of sound waves is measured as sound pressure level (SPL) or intensity level (ITL). Both measures are usually given in units (decibels, dB) relative to a standard value, which in air is 20 μPa (20×10^{-6} N/m^2) and at 20°C is equal to an intensity of 10^{-12} W/m^2. The decibel is a logarithmic measure, with each tenfold increase in intensity being equivalent to an increase of 20 dB. Air particle movements are described by displacement (velocity) and pressure. Close to the source (in the near field) the air particle velocity aspect is more pronounced than pressure, but with increasing distance its importance decreases rapidly. The magnitude of near field sound depends on the frequency of the sound, and the geometry and size of the sound source. Airborne sound communication in near field conditions occurs in insects that possess organs sensitive to sound in the frequency range from a few hertz to more than 100 kHz. The medium (fluid) particles absorb sound energy and scatter the sound waves. Both phenomena result in > 6 dB SPL decrease with each doubling of distance from the source. Higher frequency sound is more attenuated by absorption and scattering than low frequency sound. Near-field sound is further attenuated by diffraction by solid objects like vegetation: this phenomenon is again stronger for higher frequency signals. Consequently the time and spectral characteristics of the input signal are changed with increasing distance from the source.

Plants are the usual substrate for the production of substrate-borne signals of most insects and different kinds of waves are propagated through plant tissues.

In the first detailed introduction to the physics of structure-borne sound, Michelsen and co-workers (1982) demonstrated that insects communicate through plants with bending waves. Bending waves include longitudinal and transverse components and propagate with velocities that increase with the frequency, with only minor dependence on the mechanical properties of the structure through which they are transmitted. Low propagation velocity is the main characteristic by which dispersive bending waves are identified. For example, Barth (1985) measured group velocities below 50 m/s for 100–500 Hz signals transmitted through banana pseudostems and leaves. Thirty Hertz signals have been reported to propagate at 4.4 m/s through the apical third of *Agave americana* L. leaves, and at 35.7 m/s through the basal end where the leaf is thicker (Barth 1993). Group velocity for 2 kHz signals was 120 m/s when measured in bean plant stems (Michelsen et al. 1982) and 220 m/s in the reed *Phragmites communis* (Trinius).

Insects do not use longitudinal and transverse waves for vibrational communication. These types of waves occur in structures in which the dimensions of the structures are much larger than the wavelength of the signals. Highly damped Rayleigh waves combine longitudinal and transverse characteristics; their velocity is slightly lower than that of transverse or longitudinal waves but well above the value of bending waves. Rayleigh waves may be relevant for larger arthropods communicating through sand (Aicher and Tautz 1990).

In general, insect-produced substrate vibrations are propagated as non-dispersive bending waves (Casas et al. 2007) characterized by no correlation between propagation velocity, signal frequency, and stem diameter size; such types of waves were demonstrated in rush stems (*Juncus effuses* L., radius from 0.85 to 2.1 mm) for signals of frequencies above 5 kHz. The propagation velocity of this type of wave approaches the value of Rayleigh waves (Graff 1975). Although non-dispersive bending waves maintain their temporal and frequency structures when transmitted through plants, most plant-dwelling insects communicate with low frequency vibratory signals because green plants act as low-pass filters, efficiently transmitting signals below 500 Hz and significantly attenuating those above this value (Čokl et al. 2006, 2007). Burrower bugs of the species *Scaptocoris castanea* Perty and *S. carvalhoi* Becker (Heteroptera: Cydnidae) are an instructive example of this phenomenon. Both species feed and mate on roots of soybean plants (Lis et al. 2000) where they stridulate (Čokl et al. 2006). During transmission through the surrounding soil, signals with about 0.07 mm/s velocity (a measure of intensity of the signal, measured as a vector quantity that specifies time rate of change of displacement) at the source are attenuated approximately 3–9 dB/cm. In contrast, when transmitted from the roots to the stem and leaves of the plant, signal attenuation did not exceed 1 dB/cm. Spectra of signals recorded at the source had harmonic frequencies up to 10 kHz, with the dominant frequency at 500 Hz. Spectral units of signals above 500 Hz that were recorded from leaves and stems were significantly attenuated. In this respect, the spectra of signals recorded from above-ground plant parts resemble those characteristic of low frequency vibratory signals emitted by stink bugs such as *N. viridula* and *Murgantia histrionica* Hahn (Čokl et al. 2007).

The resonant properties of green plants also determine the spectral and amplitude characteristics of the transmitted signals. Spectra of *N. viridula* female calling songs recorded on a non-resonant substrate were characterized by a narrow dominant frequency peak around 100 Hz with harmonics not exceeding 500 Hz (Čokl et al. 2000). Spectra of the same signals recorded on a plant had new peaks below and above the dominant frequency shifted to about 20 Hz higher value (Čokl et al. 2005). Resonant spectra of signals measured from several green plants have distinct peaks below 500 Hz, with the dominant frequency between 160 and 220 Hz. This peak corresponds to the range of the first harmonic values determined in all stink bug vibratory signals recorded to date (Čokl and Virant-Doberlet 2003; Moraes et al. 2005; Gogala 2006; Bagwell et al. 2008) and corresponds to the maximum sensitivity of the middle frequency subgenual organ receptor cell in these insects (Čokl 1983).

Vibratory signals travel through green plants with low attenuation (Barth 1998). For example, signals of 75 or 5,000 Hz frequency were attenuated during transmission through monocotyledonous plants (banana, agave) by only 0.3 and 0.35 dB/cm respectively. Still less attenuation was measured for 30 Hz signals (Barth 1985). Michelsen and co-workers (1982) vibrated bean stems with short pulses and recorded significantly prolonged vibrations at some distance from the source. This means that vibration pulses reflect from the roots and apices of the plant and travel up and down the plant's rod-like structures such as stems, stalks, and side branches with low attenuation, thus creating standing wave conditions. Consequently, the amplitudes of the vibratory signals do not decay linearly with distance (Michelsen et al. 1982; Barth 1998) but are characterized by regularly repeated peaks of minimal and maximal values at nodes and internodes (Čokl 1988; Čokl et al. 2007). Regular variation of signal velocity with distance also has been demonstrated under natural conditions (Čokl et al. 2007): the distance between peaks for *N. viridula* female calling song transmitted through a *Cyperus alternifolius* L. stem ranged between 10 and 15 cm and the maximum difference between neighboring velocity peaks at nodes and internodes was 19.4 dB. The overall attenuation of naturally emitted stink bug signals of ~100 Hz was about 0.1 dB/cm at a distance of 1 m.

The distance between nodes (and internodes) decreases with increasing frequency of the signal. Spectra of signals with different frequency components have different ratios of spectral peak amplitudes at different points on the plant. The distance between nodes of the dominant frequency is double the analogous distance for its first harmonic, and at the position of the dominant frequency node (lowest dominant frequency spectral peak amplitude value) one can get the highest amplitude of the first harmonic (Čokl et al. 2007). Although the amplitude of the signal varies in phase with the amplitude of the dominant frequency, the amplitude pattern of frequency modulated signals, or those composed of different frequency components, can vary significantly at different distances from the source on the plant.

Several insects communicate with signals transmitted over water surfaces. At wavelengths above 1.7 cm, most wave motion is maintained by gravity, whereas with oscillations with frequencies above 15 Hz wave motion is mainly maintained by capillary forces (Greenfield 2002). For example, a small aquatic insect emits 25

Hz capillary waves of 10 mm wavelength traveling outward with 0.25 m/s velocity. Vibratory signals (the modulation envelope of the wave group) are transmitted over the water surface either more slowly for pure gravity waves or faster for pure capillary waves. The damping coefficient in deep water is about 0.11 dB/cm (Lighthill 1978). The coefficient between the energy and area of capillary waves is proportional to the square of frequency, and high frequency signals, like airborne sound, are attenuated to a higher degree than low frequency ones. Thus, the effective communication range over water surfaces is restricted to distances between 1 and 2 m for insects emitting vibrational signals of frequencies above 20 Hz (Wilcox 1995). A sinusoidal wave is dispersed by water into a range of wavelengths, and surface waves of different wavelengths travel at different velocities.

Only four orders of insects (Odonata, Hemiptera, Trichoptera and Coleoptera are known to communicate with specialized sounds underwater (Aiken 1985). Waterborne sounds are strongly reflected from solids and from the water surface; because of the longer wavelengths used in these signals, most communication of this type occurs in the acoustic near field.

3.2 The Use of Different Mechanical Signal Modalities

Several analogies can be drawn between chemical signaling and communication with mechanical signals. For example, mechanically produced signals are transmitted with high velocity over relatively long distances, analogous to wind-borne volatile chemicals. Because mechanical signals can be emitted in temporally defined bursts in distinct patterns, they can be highly species and sex specific, in parallel with many chemical signals. Furthermore, insects detect the position of the signaler by homing in on the signal transmitted through the air or through a substrate. Airborne acoustic signals are less dispersed into different wavelengths and velocities than substrate-borne signals when traveling through acoustic free-field. Nevertheless, compared with lower frequency sound, higher frequency signals are more attenuated by absorption and scattering, and more attenuated by diffraction by solid objects like vegetation. Thus, low frequency airborne signals should be more effective for long distance communication by plant-dwelling insects, but insects cannot efficiently emit low frequency airborne sound because of their small body sizes. An object oscillating in an elastic medium (air or water) radiates compressional sound waves efficiently when the vibrating body is large compared with the wavelength of sound in the transmission medium (Markl 1983). Thus, insects can communicate efficiently with airborne sound in the frequency range in which their body size (radiator's diameter) equals or is larger than one third of the radiated wavelength. For example, a one cm insect can efficiently radiate sound waves only above 10 kHz in air and above 50 kHz in water. This is one of the major reasons why most small plant-dwelling insects communicate through the substrate. Furthermore, higher frequency sound and ultrasound signals that are transmitted through air in the acoustic free field expose the signalers to discovery by flying predators and parasitoids. In contrast, substrate-borne signals can only be exploited by predators and parasitoids if they are on the same substrate as the signaler. The same restriction applies to intended receivers (i.e., conspecifics), but may be overcome by using the vibrational signal in tandem with other, longer-range signaling modalities such as volatile pheromones.

Contact vibration and near field medium motion are widely used in insects but because they are only effective over very short ranges, they are not discussed here. Instead, we will focus on possible manipulation of long range calling signals as a method for insect management.

3.3 Signal Types and Behavior

Signal features are designed according to the communication range, the positions of the signal sender or receiver, the duty cycle of the signal (the ratio between the signal being “on” and “off”), the sender identification level, the modulation level (the amount of inter-individual variation measured by the position of the signal along a scale from stereotyped to graded), and the degree of form-content linkage, defined as the degree to which signal form is dependent upon signal content (Bradbury and Vehrencamp 1998). The design rules have been generally examined for signals emitted in the context of mate attraction, courtship, territorial defense, threat, and alarm.

In the mate attraction process, questions about species and sex identification, receptivity, and location are important (Bradbury and Vehrencamp 1998). In most insects, mate attraction is relatively simple, with one sex producing calling signals when it is receptive. In this case, the signal only needs to carry information about species and location of the signaler. The signal has to be readily repeated from one place, has to carry the information over long distances, needs to be complex enough to retain its species specificity, and has to have a high duty cycle (long “on” time). In contrast, courtship signals are emitted when conspecifics are in close proximity, and function during mate assessment and mating synchronization (Bradbury and Vehrencamp 1998). Because of the short distances over which they act, signals used in courtship are different in structure than those used in long distance communication; they mediate a specific sequence of events, each triggered by specific signals carrying different information. Usually males are less choosy and more motivated to mate than females, and use courtship to induce the female to mate. In addition, errors in species recognition (and mate choice) are more costly for females, and thus females evaluate males’ signals carefully. Acoustic courtship signals are generally more species- and sex-specific than long-range signals, and have a high duty cycle. Thus, insect courtship signals are characterized by long pulse trains with complex temporal patterns, and often have frequency modulated subunits. Because of the short distance over which the signals are used, these characteristics are not significantly changed during transmission through the medium. They also do not need to carry directional information because at that point, prospective mates are usually in visual and/or tactile contact.

Threat signals are emitted during direct competition of two individuals at close range for resources like food, mates, or territory (Bradbury and Vehrencamp 1998).

Threats are produced when a sender and receiver are competing for a resource, and serve as a way of minimizing actual combat which can result in damage to both competitors. Threat signals are in some ways similar to courtship signals because they are intended for short range use, the threats are directed at a specific individual, and the signals need to convey honest information as to the quality of the signaler. On the other hand, the duty cycle is usually shorter, with threat signals usually being short and of high intensity.

Bradbury and Vehrencamp (1998) also describe territorial defense and alarm signals. The territorial defense signals are known only from insects and the alarm signals are found primarily in some social species. Alarm signals can be differentiated into those that stimulate flight (if a group is in immediate danger), assembly signals (dispersed individuals are called to the signaler), and alerting signals, when a threat is perceived but danger is not imminent. The design of each type of alarm signal is different. Signals that stimulate flight do not have to be species specific, their duty cycle is low, and they should carry as little information as possible about the position of the signaler. In contrast, assembly alarm signals can be longer, are usually species specific, and should allow location of the sender. Although alarm signals of different modalities have been described, auditory alarm signals show the greatest complexity, employing repetition rate, duration, frequency and intensity characteristics of the signals to encode information about danger, urgency, or other important details.

3.4 Sound Communication in Stink Bugs

Stink bugs, particularly those in the subfamily Pentatominae, represent one of the insect groups that has been most intensively studied, in large part because of their economic importance as agricultural pests. They can be difficult to control, and in the search for novel methods of managing these pests, researchers have investigated numerous aspects of their biology, ecology, and behavior (Panizzi et al. 2000). Pentatominae, and particularly the southern green stink bug *N. viridula* (L.), form useful models for studies of chemical and substrate-borne sound communication because these insects make use of both of these methods of communication, providing an opportunity to understand how interruption of basic communication processes can be used as a tool for insect pest control. The general use of chemical signals for insect control are described in sections 2.2 to 2.8. Because olfactory and substrate-borne sound signals are both involved in communication in *N. viridula*, these types of signals will be described in tandem, in the context of stink bug mating behavior.

3.4.1 Biology and General Statement of Stink Bug Economic Importance

Stink bugs, family Pentatomidae, with about 4,100 described species, form the third largest heteropteran family, after Miridae and Lygaeidae (Panizzi et al. 2000). The family Pentatomidae comprises eight subfamilies: Asopinae, Cyrtocorinae, Discocephalinae, Edessinae, Pentatominae, Phyllocephalinae, Podopinae, and Serbaninae

(Schuh and Slater 1995). Many stink bugs are herbivorous, with some species in Edessinae and Pentatominae being regarded as major pests worldwide. They feed by piercing plant tissues with their maxilliary and mandibulary stylets, then sucking up plant fluids with nutrients from the food source. Thus, they cause loss of fluids and decrease in turgor pressure, and they also inject destructive digestive enzymes, transmit plant pathogens, and delay plant maturation (McPherson and McPherson 2000). The edessine species *Edessa meditabunda* (F.) is a pest of many Solanaceae and Leguminosae, feeding also on cotton, tobacco, sunflower, papaya, and grapes (Panizzi et al. 2000). Major pests among the Pentatominae include *N. viridula*, *Oebalus pugnax* (F.), *Acrosternum hilare* (Say), *Euchistus servus* (Say), and *Euchistus variolarius* (Palisot de Beauvois) (McPherson and McPherson 2000).

The southern green stink bug, *N. viridula*, originated from eastern Africa but it has been introduced into tropical and subtropical regions of Europe, Asia, Australia, Africa, and the Americas by global commerce (Hokkanen 1986; Jones 1988; Kavar et al. 2006). The recent expansion of this species in South America is the result of increased acreage for soybean production (Panizzi and Slansky 1985), and climatic change is the probable cause of this invasive species becoming established on the Galapagos islands (Henry and Wilson 2004), in Hungary (Redei and Torma 2003), and in Britain (Barclay 2004; Shardlow and Taylor 2004). The northern border of the range of this species has moved 70 km in Japan within the past few decades, related to the movement of the 5°C isotherm of the average temperature in January (Musolin and Numata 2003). Because of its economic importance, the southern green stink bug is one of the most intensively investigated pentatomid species in the world (Todd 1989).

N. viridula is highly polyphagous, feeding on both monocotyledonous and dicotyledonous plants from more than 30 families, with a distinct preference for legumes (Todd and Herzog 1980; Todd 1989; Panizzi and Slansky 1991; Panizzi 2000; Panizzi et al. 2000). As with other multivoltine stink bugs, *N. viridula* switches from one host to another, taking advantage of differences in temporal patterns of fruiting in their various hosts (Panizzi 1997). In addition to being one of the major global pests of soybean (Kogan and Turnipseed 1987), *N. viridula* also damages many other economically important crops including cowpea, pecan, macadamia, rice, wheat, sorghum, corn, tomato, tobacco, and cotton (Hoffmann 1935; McPherson and McPherson 2000). Plants with developing fruits or pods appear to be more attractive than those with mature ones (McPherson and McPherson 2000).

Damage to soybeans is of particular current importance because of recent increases in acreage of this crop in many areas of the world. Southern green stink bugs quickly adapted to soybean, and the damage from increasing numbers of this species has spilled over into other crops like cowpea and pecan.

3.4.2 Signals Involved in Communication During Mating Behavior of Stink Bugs

The mating behavior of *N. viridula* and many other pentatomine bugs consists of two phases, long range mate location, followed by short range courtship interactions

(Borges et al. 1987). These authors confirmed the presence of a sex attractant pheromone in *N. viridula* that had been reported earlier by Mitchell and Mau (1971), and demonstrated that odors from males elicited long range mate location behaviors from females. Thus, the male-produced pheromone appears to attract females to the vicinity of the odor source (Aldrich et al. 1987), at which point shorter range acoustic signals that are transmitted through the plant substrate take over. The stereotyped short range courtship phase of stink bug mating behavior was described first for *Chlorochroa ligata* (Say) and *Cosmopepla bimaculata* (Thomas) (Fish and Alcock 1973), and in *N. viridula* it includes male–female antennation, abdominal vibration by the male, and head-butting of the female to induce her to lift her abdomen to the position required for coupling of the genitalia, genital coupling, and copulation (Kon et al. 1988). Courtship is preceded by the medium range calling phase which serves to bring the two sexes together. This phase starts with the emission of the female calling song (FCS) (Čokl et al. 2000). The signals or cues that stimulate the female to begin calling are not yet fully known, but preliminary experiments suggest that the male pheromone may be involved. FCS emission activates a male to move towards the female, mediates directionality at branch points on the stem (Ota and Čokl 1991; Čokl et al. 1999), triggers male emission of the calling (MCS) and courtship (MCrS) songs (Čokl et al. 2000), and increases the rate of pheromone emission by the male (Miklas et al. 2003).

Male rivalry singing has been recorded and described for *N. viridula* and other phytophagous stink bugs (Čokl et al. 2000; Čokl and Virant-Doberlet 2003; Moraes et al. 2005a; Bagwell et al. 2008). A pair of male rivals alternate singing in an a-b-a-b-a-… fashion with short signals of high intensity and low species specificity, which inhibit singing of the competing male. The song is produced when two (or more) males are courting the same female. Female *N. viridula* are silent during male rivalry. A male emits the rivalry song to silence the rival and afterwards resumes calling and courting the female, who in turn resumes emitting her calling and courtship songs.

A broad-band repelling song emitted by females (FRS) has been recorded only in *N. viridula* as a vibration of several seconds duration, without a pulsed pattern (Čokl et al. 2000). The song was recorded within the courtship phase when a female rejected a courting male, and the song inhibits male singing.

The *N. viridula* male pheromone (Aldrich et al. 1989) and vibratory songs (Čokl and Virant-Doberlet 2003) are species specific. Nevertheless, they do not completely prevent interspecific copulations. In areas of sympatry in Japan, interspecific copulations frequently have been observed between *N. antennata* Scott and *N. viridula* (Kiritani et al. 1994; Kon et al. 1994), although no viable offspring result (Kiritani et al. 1963).

To date, calling and courtship songs have been described in more than 20 pentatomine species (Gogala 2006). Mating behavior, as described for *N. viridula*, is similar in all these species except for stink bugs of smaller body size such as *M. histrionica* (Hahn) (Čokl et al. 2004) and *Holcostethus strictus* (Fabricius) (Pavlovčič and Čokl 2001). In the latter two species, males initiate communication with vibratory signals, and females do not emit a long calling song with steady repeated pulses or pulse trains. The female courtship song is triggered by male courting and no regularity in the exchange of courtship songs has been observed. Differences in the calling phase between these species and *N. viridula* and the other larger pentatomids may be a consequence of shorter distances between the legs of the smaller species, which do not enable the smaller individuals to determine the direction of a signal from the time difference between the moving vibration hitting the first and subsequent sets of legs; for these smaller bugs, the time interval may be too short for the individual to be able to discriminate which legs were vibrated first (Virant-Doberlet et al. 2006).

Contrary to the well-expressed temporal structure of the species and sex specific pentatomine songs, the spectral characteristics of these signals are similar between species, reflecting the shared mode of sound production. Vibratory signals are produced by synchronous contraction of the tergal longitudinal (TL) and lateral compressor (LCr) muscles attached on one end to the side of the tergal plate formed by fusion of the first and second abdominal tergites, and on the other to the thoracic (TLI) or abdominal wall (TLII, LcrI, and LCrII) (Maluf 1932; Kuštor 1989). Muscular contractions vibrate the abdomen versus thorax in a 1:1 fashion according to electromyiogram potentials recorded by implanted electrodes (Kuštor 1989). The dominant (fundamental) frequency of all known songs of pentatomine bugs ranges between 80 and 150 Hz. Spectra differ in the number of higher harmonics, which do not exceed 1 kHz, and in the presence (or absence) of frequency modulated units. As described above, such spectral properties are well tuned to the resonant frequency of green plant hosts as the medium for transmission of vibratory communication signals.

3.4.3 Insect–Plant Interactions During Substrate-Borne Communication

Vibrational signals are characterized by their time (pulse duration, repetition time, number of pulses per pulse train, etc.), frequency (fundamental frequency, higher harmonics, frequency modulation), and amplitude characteristics. The amplitude variation with distance depends on the signal's frequency characteristics. According to the dispersive nature of bending waves transmitted through a substrate under standing wave conditions, the amplitude of vibratory signals transmitted through green plant stems varies, with regularly repeated peaks of minimal and maximal values at nodes and internodes. The distance between peaks decreases with increasing signal frequency. The velocity of signals measured at the body of a singing *N. viridula* ranged between 0.3 and 0.7 mm/s (Čokl et al. 2007) and decreased by less than 0.5 dB/cm. Because the threshold sensitivity of leg vibrational receptors lies 20–40 dB below this value (Čokl 1983), bugs can efficiently communicate over distances greater than 1 m when on the same plant. The fundamental frequency remains stable, but at different distances from the source, different ratios of spectral peak amplitudes determine the amplitude of frequency modulated or spectrally different signal subunits.

Michelsen and coworkers (1982) demonstrated that sine wave pulses of a few milliseconds, when transduced into a plant's stem, persisted for more than 20 ms.

Signal duration is prolonged because the vibration pulse reflects from apices and roots, and due to low attenuation, the signal may travel up and down the stem several times, creating standing wave conditions in which the signal pattern is frequency dependent and often complicated. The repetition rate of vibratory signals or of their subunits remains the parameter that generally is not changed during transmission. Thus, this characteristic of the signal may transmit the most reliable information about sex, species, and location within the calling phase of mating behavior.

Recently, Cocroft and coworkers (2006) measured the influence of the substrate on frequency and temporal characteristics of vibratory signals of male treehoppers, *Umbonia crassicornis* (Hemiptera: Membracidae), on two woody plants, *Albizia julibrissin* Durazz. (Mimosaceae) and *Viburnum lentago* L. (Adoxaceae). At a distance of 10 cm between the measuring points (5 and 15 cm from the source) the authors found that the influence of the substrate on temporal parameters was relatively small. The distance influenced signal duration, but the effect varied among individual plants and the difference was slight. As expected, the signal repetition rate was not influenced by the plant species, individual plant, or distance. The dominant frequency was not different for different plant species but varied among different plants of the same species. The authors found no overall effect of distance on dominant frequency.

Miklas and coworkers (2001) demonstrated that the inner time structure of a pulse train may change during transmission when prolonged pulses are repeated with such high repetition rates that they fuse. This is the case in *N. viridula* male–female calling duets (Miklas et al. 2001). The *N. viridula* female calling song sequence is composed of pulse trains with two or more pulses (Čokl et al. 2000). The non-pulsed type (FCS-np) is characterized by a short prepulse followed by a long pulse of about 1 s. The pulsed type (FCS-p) contains three or more pulses that are quickly repeated. The duration and repetition rate of pulse trains of both types are similar. On a non-resonant substrate, males respond only to the FCS-np pulse trains. When stimulated with these signals on a plant, males responded to pulse trains of both types. The analyses of plant recorded FCS-p signals has shown that short FCS-p pulses become prolonged by transmission through a plant and fuse to such an extent that males cannot differentiate them from the FCS-np pulse trains and respond to them. Results of investigations with *U. crassicornis* cannot be directly compared with those with *N. viridula* because experiments with the two species were conducted on different substrates (woody and green plants respectively).

Acoustic communication by plant-dwelling insects over longer distances through a plant occurs predominantly or exclusively through the substrate. Determination of the informational value of calling songs is easier than similar determinations with songs involved in the courtship phase, where signals of different modalities are involved. According to expected signal parameter changes during transmission through a plant, signal design follows general rules including steady repetition rate of simple and less amplitude modulated units, the spectral properties of which are tuned to the mechanical properties of the transmission medium. The necessity to provide information about the signaler's position seems to be more important than information about the signaler's identity. For example, *N. viridula* males responded when stimulated with calling songs of females of the sympatric pentatomine species *Palomena prasina* (L.) and *P. viridissima* (Poda) (Čokl et al. 1978). Results of this early study revealed that *N. viridula* males recognized and responded to synthesized female calling songs in which the changes in spectral and temporal characteristics that would be expected during transmission through a green plant had been simulated.

3.5 Disruption or Manipulation of Acoustic Signals as a Potential Method for Insect Management

The study of vibrational communication in insects is relatively recent, following development of recording instruments that are sensitive enough to detect and measure signals of low intensity from mechanically delicate biological substrates such as plants. Although substrate-borne acoustic communication is widespread in insects, data about basic phenomena are still lacking. With the accumulating body of basic research in this field, scientists can begin to think about practical applications of substrate-borne communication for management of insect pests.

A good basic knowledge of the biology of the target species is critically important in order to be able to exploit or manipulate aspects of the insect's life history for our own purposes. In this context, investigations should be focused on species of sufficient economic importance to warrant the costs of basic research and development. A number of stink bugs fit this criterion, and both the economic importance and the extensive knowledge of the basic biology of *N. viridula* renders it a good model species for such studies. The reliance on both chemical and acoustic communication during mate location in this species provides opportunities for disruption of these communications to achieve pest control. We shall discuss the following phenomena: (Section 3.5.1) attraction of parasitoids and predators, (Section 3.5.2) interruption with induced vibrations, (Section 3.5.3) combination of signals with sub-lethal doses of insecticides, and (Section 3.5.4) combination of acoustic signals with chemical or other signals.

3.5.1 Attraction of Parasitoids and Predators

All life stages of *N. viridula* and other phytophagous stink bugs are subject to attack by a variety of parasitoids, predators, and entomopathogens (Panizzi and Slansky 1985; Todd 1989). For example, Jones (1988) listed 57 parasitoids attacking *N. viridula*. The most important are the wasps *Telenomus podisi* Ashmead and *Trissolcus basalis* Wollaston (Hymenoptera: Scelionidae), *Trichopoda pennipes* F. (De Groot et al. 2007), and *T. giacomelli* (Blanchard) (Diptera: Tachinidae). Predatory stink bugs of the pentatomid subfamily Asopinae, including *Picromerus bidens* L., *Podisus maculiventris* Say (De Clerq 2000; De Clercq et al. 2002; Vandekerkhove and De Clercq 2004), and *P. nigrispinus* (Dallas) (Saini 1994) are among numerous arthropod predators that feed on *N. viridula*, and the fire ant *Solenopsis invicta* Buren (Hymenoptera: Formicidae) is a significant predator of eggs (Kryspin and Todd 1982; Stam et al. 1987).

It has been demonstrated recently that females of the egg parasitoid *T. podisi* responded with oriented movements towards vibratory signals of the Neotropical brown stink bug, *Euschistus heros* (F.) (Laumann et al. 2007). The reaction was sex specific, and was triggered by female but not male songs. The *E. heros* female song is a typical pentatomine calling song characterized by repeated pulses of the fundamental frequency around 145 Hz (Moraes et al. 2005a), and is similar to the FCS of *N. viridula* (Čokl et al. 2000). We can expect that female calling songs of different species with similar time and frequency characteristics will also attract this (and possibly other) parasitoids, but further experiments are needed to determine the specificity of the reaction. Overall, the parasitoids exploit these signals for medium to short range location of hosts; the initial host finding steps consist of longer range orientation to a plant that might be infested with hosts, mediated by chemical signals from the plant (Colazza et al. 2004; Moraes et al. 2005b). Host-produced kairomones are also involved in longer range orientation (Mattiacci et al. 1993; Medeiros et al. 1997; Borges et al. 1998; Colazza et al. 1999; Conti et al. 2003). Over shorter ranges, parasitoids then locate and recognize their hosts using both chemical and visual cues (Sales et al. 1980; Bin et al. 1993; Borges et al. 1999, 2003; Colazza et al. 1999; Conti et al. 2003).

Thus, one potential method of exploiting stink bug acoustic signals would be to vibrate a plant with a stink bug female calling song, with the aim of stimulating parasitoids to search for hosts more intensively. Although such experiments could be conducted relatively easily in the laboratory, it is difficult to visualize how this might be used in the field as a crop protection strategy. There are at least three problems. First and most obvious is the problem of how to vibrate a whole field of plants. The second problem is that artificial vibration of the whole plant will probably disrupt the ability of parasitoids to locate real calling hosts, so that parasitoids would find hosts only by chance. Finally, vibration of a plant may silence calling host females. Thus, it is difficult to see how the the oriented movement of parasitoids in response to vibrational signals from their hosts might be manipulated for practical purposes.

3.5.2 Interruption with Induced Vibrations

The emission of different songs in a male-female *N. viridula* duet follows defined rules. All the songs are triggered by songs emitted by the opposite sex, except for the female calling song which is triggered by the presence of a male (unknown triggering signal), and also emitted in the absence of male responses. The response of males with the courtship song stabilizes the repetition rate of female calling signals. Increasing ambient temperature up to 28°C increases the repetition rate of the FCS pulse train, but further temperature increase results in a decreased repetition rate (Čokl and Bogataj 1982). This early experiment also pointed to the important role of chemical communication in the courtship phase of mating behavior: antennectomized males readily courted and copulated with normal females but females without antennae ignored male courting, rarely responded with the courtship song, and never copulated.

Recently Polajnar and Čokl (2008) studied the possible disrupting effect of a 100 Hz signal on vibrational communication between male and female *N. viridula*. The artificial signal significantly decreased the number of males responding to female calling songs, and significantly fewer males responded with the courtship song. However, the disturbance signal did not change the time that males needed to locate calling females. Females still produced calling songs during disturbance with the continuous 100 Hz signal, but some of them changed the rhythm by skipping one or more signal intervals or emitted the repelling song. Females did not change the time characteristics of their calling signals but varied the dominant frequency when the disturbing frequency was similar; the number of females which changed the dominant frequency increased with decreasing difference between the dominant frequencies of their own and the disturbing signal.

These experiments need confirmation under field conditions. As stated above, a major practical problem is how to vibrate plants in the field. If this can be worked out, there are several possible ways in which communication could be interrupted. For example, played back female repelling song might be used to silence males and inhibit their courting, although further experiments are needed to confirm the hypothesis that the repelling song causes males to leave the plant. Another possibility is to disorientate males by reproducing female calling songs with unnatural signal repetition rates, to give stochastic and interfering signals at branch points, with the aim of disrupting males' ability to orient to calling females. Finally, stimulation with the male courtship or rivalry songs may induce rivalry and inhibit courtship.

Thus, use of artificial signals to disrupt normal acoustic communication may have some promise from a theoretical viewpoint. However, its potential only can be tested properly if we can surmount the technical challenges posed by the problem of vibrating large numbers of plants under field conditions.

3.5.3 Communication and Insecticides

Sublethal doses of neurotoxic insecticides directly affect the peripheral and central nervous systems of insects, which may result in indirect effects on their behaviors. The neuronal basis of behavior has been studied in insects at several levels, mainly in the context of a single neuron's responses to stimulation with signals with parameters that mimic those characteristic of natural communication signals. To our knowledge, the effect of insecticides on the activity of neuronal nets underlying communication have not been explored thoroughly. Nevertheless, we can expect that sublethal doses of neurotoxic agents will affect insect communication by their direct action on receptors and the underlying neuronal networks. This hypothesis has been confirmed in *N. viridula* treated with sub-lethal doses of imidacloprid, which has been shown to act on synapses as an acetylcholine agonist (A. Žunič, personal communication 2008). Doses 10–100 times below the lethal level significantly decreased calling, resulting in fewer successful mate locations and copulations. Thus, insecticides may have some potential for insect control by disruption of behavior when applied at sublethal levels. However, this potential benefit must be weighed against the increased risk of enhancing the development of insecticide resistance by challenging the population with sublethal doses of insecticide.

3.5.4 Calling Signals in Combination with Pheromone Traps

One of the most important factors in effective management of stink bugs is knowing when and where bugs are present, and in what numbers. Because many species are oligophagous and highly mobile as adults, they can migrate from crop to crop in response to senescence or harvesting of one crop, or they can migrate into crops from surrounding uncultivated land as the natural vegetation senesces. Thus, efficient monitoring is crucial for stink bug management. Unlike most insects, which use a single communication mode for long range attraction of mates or conspecifics, stink bug communication is bimodal, with chemical signals probably acting over longer ranges to bring individuals together on the same plant, and vibrational signals becoming predominant to actually bring the individuals together. Thus, for many phytophagous stink bug species, including *N. viridula* (Aldrich et al. 1987), *Acrosternum hilare* (JGM, unpublished data 2001), *Thyanta* spp. (McBrien et al. 2002), *Chlorochroa* spp. (Ho and Millar 2001a,b), and *Biprorulus bibax* (James et al. 1996), monitoring traps baited with pheromones caught few bugs. However, all of these authors noted that the plants in which traps were placed had many more bugs on them than control plants. Thus, as expected, the pheromones did indeed act as long range attractants, but once attracted to the vicinity of the pheromone lure, bugs require the secondary vibrational signals to locate and enter the trap. Thus, a combination trap that incorporates both pheromonal and vibrational signals may provide the solution, and this concept is under active investigation (JGM, unpublished results). What is required is a small playback device with bug songs prerecorded on a chip, a power source to drive it, and a transducer to transmit the signal into the trap substrate. All of these components are cheap and readily available, and we are currently working with prototype devices to obtain proof of concept. In short, a vibrating pheromone trap may provide an effective method of monitoring stink bug populations. Furthermore, it should be possible to extend this concept to other insects that communicate with both acoustic and pheromonal signals, such as clothes moths (Takács et al. 2003) and the peach twig borer moth (Hart 2006).

4 Summary

Insect pheromones and related semiochemicals are much more than scientific curiosities. Because of their critical role as essential intraspecific signals, without which insect species cannot live and reproduce, pheromones have tremendous potential for exploitation for insect control, and they can and should be developed in our ongoing struggle to protect crops and forests from insects. The identification of the first pheromones some 50 years ago resulted in an initial period of great excitement and tremendous expectations for pheromones, followed by disillusionment and some loss of interest in pheromones when practical applications were slow to develop. However, steady progress in recognizing and understanding the complexities of semiochemically-based insect management, coupled with the development of reliable formulation and dispenser technology, has positioned us for continuing growth in practical applications of semiochemicals. This growth will be enhanced by the increasingly restrictive regulatory climate for insecticides, and by increasing public pressure for foodstuffs that have not been treated with insecticides. Semiochemically-based insect control methods cannot and will not be developed for all crops, for reasons described above. However, for those crops and insect pests for which both the biology is favorable and the economics are at least competitive with current management practices, semiochemicals may have a strong future.

Furthermore, acoustic signals transmitted through substrates have now been described in numerous groups of insects, and these signals are essential mediators of insect behaviors. The signals are relatively short range, being restricted to one plant or to two or more plants that are in direct contact with each other. These acoustic signals, alone or in concert with signals of other modalities, enable efficient and precise mate location and recognition in a complex environment over distances of several meters. The use of laser vibrometry technology for recording and measuring low intensity vibratory signals from delicate biological substrates has enabled deeper insight into the basic phenomena underlying the interactions between the calling insect and the plant substrate during communication. Stink bugs form an instructive model system for illustration of efficient bimodal communication systems that use both pheromones and substrate-borne signals. Whereas no methods of exploiting or manipulating vibratory signals for insect pest control have been commercially developed to date, this is currently an area of active investigation, for several types of insects. With our expanding knowledge of this widespread mode of communication in insects, it is certain that new possibilities will arise. To date, the most promising use of vibrations may be in combination with pheromone traps for pest insects, but as discussed, there also may be possibilities for using vibratory signals to manipulate the behaviors of beneficial insects such as parasitoids. Thus, substrate-borne acoustic communication in insects represents a virtually untapped field for both basic research and for practical applications in insect control.

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