The Behavioral Ecology of Insect Vibrational Communication

REGINALD B. COCROFT AND RAFAEL L. RODRÍGUEZ

Vibrational communication is widespread in insect social and ecological interactions. Of the insect species that communicate using sound, water surface ripples, or substrate vibrations, we estimate that 92% use substrate vibrations alone or with other forms of mechanical signaling. Vibrational signals differ dramatically from airborne insect sounds, often having low frequencies, pure tones, and combinations of contrasting acoustic elements. Plants are the most widely used substrate for transmitting vibrational signals. Plant species can vary in their signal transmission properties, and thus host plant use may influence signal divergence. Vibrational communication occurs in a complex environment containing noise from wind and rain, the signals of multiple individuals and species, and vibration-sensitive predators and parasitoids. We anticipate that many new examples and functions of vibrational communication will be discovered, and that study of this modality will continue to provide important insights into insect social behavior, ecology, and evolution.

Keywords: social selection, sexual selection, sensory drive, eavesdropping, insect–plant interactions

With our reliance on vision and hearing and our weak vibration sense, humans have only recently developed ways to mine the information provided by the soundless vibration of the surfaces around us (box 1). Nevertheless, the information is there: geophones show ongoing tremors of the earth's surface, stethoscopes bring the rhythm of our heart and lungs to a doctor's ears, and laser vibrometers let surveillance teams listen to conversation faithfully reproduced in the vibration of a windowpane. Vibration-sensitive species, including insects and spiders, can mine this wealth of information directly. They not only monitor vibrations to detect predators or prey but also introduce vibrations into structures to communicate with other individuals. In this article we provide evidence of the importance of this form of signaling, review what we know about vibrational signaling in insects, and discuss ecological sources of selection on vibrational communication systems.

Whether counted by species, family, or phylogenetic distribution, vibrational signaling is prevalent in insects (figure 1). Indeed, it is the most common form of communication among the insects that use some type of mechanical disturbance propagating through a medium; this includes airborne and underwater sound, substrate vibrations, and water surface ripples (Greenfield 2002). Of the insect families in which some or all species communicate using such mechanical channels, 80% use vibrational signals alone or in combination with other mechanical signals, and 74% use vibrational signals alone (figure 1). At the species level, we estimate that 92% of such species—over 195,000 described taxa—use vibrational communication alone or in concert with other forms of mechanical signaling, and that 71%—150,000 species—use vibrational signaling exclusively (figure 1). These estimates are probably low: many if not most insect species remain to be described, and vibrational communication is probably even more taxonomically widespread than the current literature suggests.

Accompanying the high species diversity of vibrational signalers is a fantastic diversity of signals. Humans can experience these signals by broadcasting them through a loudspeaker as airborne sound, a process that leaves their pitch and timing intact. One dramatic contrast between communication systems that use substrate vibration and those that use airborne sound is immediately obvious: substrate-borne signals give the impression of being produced by a large animal. This phenomenon, often startling to those listening to vibrational signals for the first time, arises from a relaxed relationship between the size of the signaling animal and the frequency (pitch) of the signal produced. When communicating with pressure waves traveling through air, small animals cannot efficiently broadcast low-frequency signals (Bennet-Clark 1998). As a consequence, only large animals can effectively produce low-frequency sounds. However, the physical constraints responsible for this relationship do not exist for substrate vibration, and thus small species are free to

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Box 1. Some methods for detecting vibrational signals.

Laser vibrometry measures the velocity of motion of a surface using Doppler shifts in reflected laser light. This is an ideal measurement method because it avoids the changes in substrate properties introduced by contact methods, but its use is largely limited to the laboratory.

Accelerometers, which use a piezoelectric material to measure the acceleration of a surface, are suitable for both laboratory and field. The mass loading imposed by attaching an accelerometer (and associated cable) to a plant stem can cause measurement problems by changing the vibration-transmitting properties of the substrate. However, use of lightweight models (with less than 5% of the mass of the structure to which they are attached) will help minimize this problem. Accelerometers have been used to study vibrational communication in the field, and are probably the best method for studying natural vibrational environments.

Phonograph cartridges that contain ceramic or crystal piezoelectric elements provide a simple, sensitive, and low-cost method of detecting vibrational signals (the more recent moving-coil or moving-magnet cartridges are much less sensitive). With the stylus in contact with the substrate, motion of the surface is transduced by a piezoelectric beam, and the output can be sent to a simple operational or differential amplifier. Disadvantages include a lack of repeatability of amplitude measurements (which can vary depending on the pressure with which the stylus is attached to the substrate) and relative difficulty of use in the field.

A *guitar or bass pickup* from a music store, along with an amplifier, provides an inexpensive method of detecting vibrational signals. The disadvantages include a lower sensitivity that may cause some signals to be missed.

produce low-frequency signals. A thornbug treehopper (*Umbonia crassicornis*), for example, has 1/10,000 of the mass of an American bullfrog, but its vibrational signals use the same low frequencies as the frog's airborne calls.

In addition to their low frequency, many vibrational signals are decidedly "un-insectlike" for listeners accustomed to the sounds of cicadas, crickets, and katydids. Many insect vibrational signals use relatively pure tones or harmonic series that change in frequency, giving the signals a haunting, melodic quality more often associated with birdsong (figure 2). Further, there are many means of inducing vibrations in a substrate, and often the same insect can use more than one of these means (Cokl and Virant-Doberlet 2003). Some insects join pure tones with noisy or percussive elements in surprising combinations, while others generate a series of percussive, rhythmic taps that recall the drumming signals of woodpeckers. Given the large number of species likely to be producing vibrational signals and the relatively small number that have been studied, we can confidently predict that most of the diversity of vibrational signals remains to be discovered.

Communication through plants

Insects are the most important consumers of plants in many terrestrial ecosystems, especially in the species-rich forests of the tropics (Coley and Barone 1996). Insect herbivores typically live on their host plants, along with many of their natural enemies. As a result, plant stems, leaves, and roots are the principal substrates used by insects to transmit vibrational signals. The use of another living organism as a communication channel provides a unique set of opportunities and constraints that shape the evolution of signaling systems. Many of the factors that arise from this relationship remain unexplored, such as daily and seasonal changes in the host plants; the interplay of selection on foraging, predator evasion, and signaling behavior; and the importance of variation in the suites of natural competitors and enemies that signaling insects may encounter on different host plants.

One important characteristic of plantborne vibrational communication is that interactions occur on a local scale. The typical range of communication varies from 30 centimeters to 2 meters (m) (Keuper and Kühne 1983, Henry and Wells 1990, Cokl and Virant-Doberlet 2003). Interactions in some spiders and large insects can occur over greater distances, on the order of 2 to 4 m (McVean and Field 1996, Barth 2002). Under some conditions, individuals may communicate over distances more often associated with airborne sound: male and female stoneflies can engage in a vibrational duet at distances of 8 m or more along a wooden rod (Stewart and Zeigler 1984). However, the scale of most vibrational interactions is probably within a human arm's length.

A number of factors limit long-distance transmission of plantborne vibrational signals. Because insects are much smaller than the structures they vibrate, the amplitude of vibrational signals is low at the source (Michelsen et al. 1982). Damping of vibrations by the plant stem further reduces signal amplitude, especially when the stem is soft and flexible (Michelsen et al. 1982). The lack of a continuous vibration-transmitting substrate can also limit the range of signals. Because soil has very different vibration-transmitting properties from plant tissue, little energy is likely to be transmitted between plants through the ground. Consequently, on a small herbaceous plant, the signaling range is limited to that plant and neighboring plants connected by roots (Cokl and

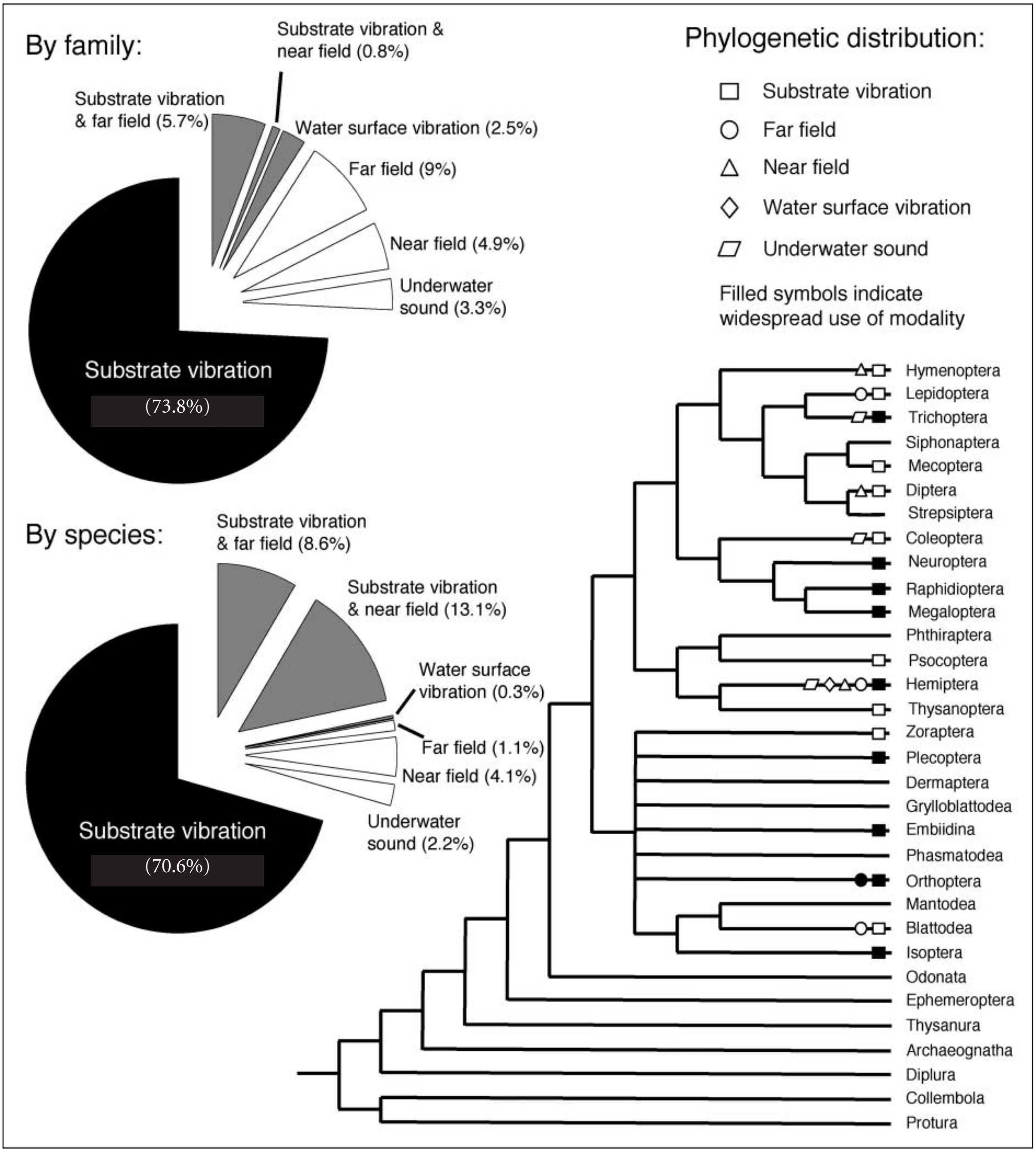

Figure 1. Prevalence of various signaling modalities among insects that use mechanical communication (categories from Greenfield 2002). The pie chart above shows an estimate obtained by tallying the number of families for which evidence of signaling in any given modality exists. The chart below shows a more speculative estimate obtained by counting the number of species for which such evidence is available; for groups in which reports suggest the use of a modality is widespread, or for which few reports exist but all have found use of a particular modality, we tallied the total number of described species in the group. We excluded instances of detection of incidental cues produced by conspecifics (e.g., we did not count detection of water surface vibrations by gyrinid beetles or of near-field vibrations by culicids and chironomids). We also excluded instances in which the vibration might be perceived through direct bodily contact (e.g., during copulatory courtship). Files with the references used to generate this figure are available on request from the authors. The distribution of signaling modalities among insect orders (phylogenetic tree from Gullan and Cranston 2000) suggests that the use of substrate vibrations for communication may be ancestral for at least some insect groups at the supraordinal level.

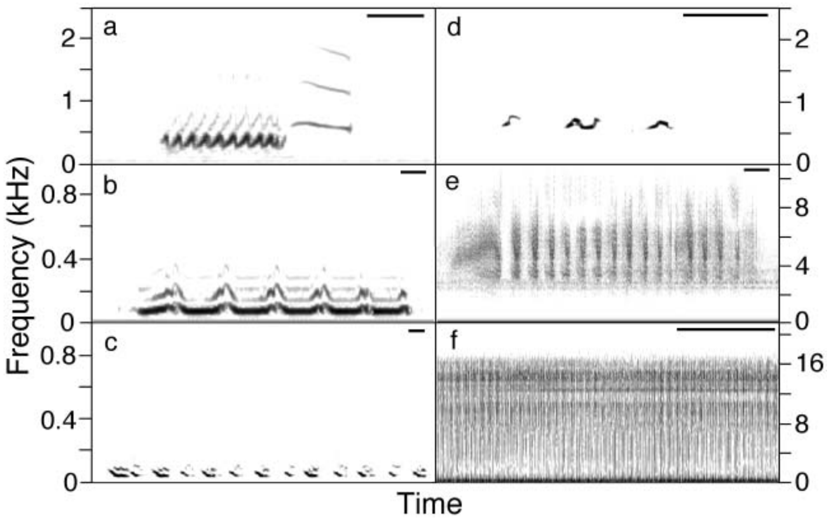

Figure 2. Examples of substrate-borne and airborne signals. Substrate-borne vibrational signals are shown for (a) the treehopper **Vanduzea mayana,** *(b) the stinkbug* **Edessa rufomarginata,** *and (c) the lacewing* **Chrysoperla carnea.** *Airborne signals are shown for (d) the plumbeous pigeon,* **Columba plumbea;** *(e) the cicada* **Fidicina mannifera;** *and (f) the katydid* **Neoconocephalus retusus.** *Note the much higher range of frequencies used by the two insect species producing airborne sounds. Scale bars = 0.5 second.*

Virant-Doberlet 2003) or by touching leaves or stems (Ichikawa and Ishii 1974). Yet another challenge for long-distance communication arises from the filtering effect of plant stems on vibrational signals: as a signal travels throughout a plant, the frequencies present in the signal will be differentially reduced in amplitude (Michelsen et al. 1982, Gogala 1985, Cokl and Virant-Doberlet 2003). Furthermore, vibrational signals are transmitted in plant stems as bending waves, for which the transmission velocity increases with the square root of frequency (Michelsen et al. 1982, Markl 1983, Barth 1997). As a result, any signal with multiple frequencies will become increasingly distorted over distance (Keuper and Kühne 1983, Gogala 1985). All of these factors limit the effective communication range of substrate-borne signals. However, although vibrational communication may be local, it often occurs in a complex social and ecological setting.

The vibrational soundscape of plant stems and leaves

Plantborne vibrational communication lends itself well to study in the laboratory. A potted host plant with a few insects provides a self-contained communication system: signalers, receivers, and the entire transmission path of the signals. Many insects will even signal on simple artificial platforms, allowing precise standardized comparisons among individuals, populations, and species. It is not surprising, then, that the study of insect vibrational communication is an almost exclusively lab-based area of research. This strength, however, is also a weakness: by eliminating wind, rain, and the signals of other individuals and other species, researchers may miss important sources of selection on these communication systems. Although field studies of vibrational communication are rare (Claridge 1985), they are feasible (Barth et al. 1988, Alexander and Stewart 1996, Cocroft 1996, 2003, Jackson and Wilcox 1998). The few studies to compare signaling interactions in the laboratory with those under more natural conditions have found close agreement (Henry and Wells 1990), but field study is clearly necessary to characterize the vibrational environments that insects encounter in nature.

It is a common perception that insects communicating via plantborne vibrations are using a "private channel," such that communication between a male and a female, for example, will be free of interference from competitors or eavesdropping predators (Bell 1980, Markl 1983, Henry 1994). This view implies that vibrational signals are free from a number of sources of natural and sexual selection faced by species using other modalities. However, although plantborne vibrations are undetected by human ears or by those of acoustically orienting predators such as bats, we suggest that vibrational communication systems are no more private than those using other modalities, such as visual signaling or airborne sound. Insects signaling through plant stems do so in a rich, complex vibrational environment containing not only interference from wind and rain but also the signals of competing individuals and other species, as well as the potential hazards of eavesdropping predators and parasitoids. Indeed, we will argue that the risk of detection by predators may be far greater for species that communicate by plantborne vibration than for those that use airborne sound or vision.

Wind is undoubtedly the major source of noise experienced by insects that communicate with plantborne vibrations (Barth et al. 1988, Casas et al. 1998). A person hearing a rustle of wind in the leaves is oblivious to the cacophony of vibrations induced in the plant by trembling leaves and colliding stems. During our studies of vibrational communication in the field, however, wind has been a nearly constant source of background noise, often interrupting attempts to record signals. Wind noise is likely to be an especially strong source of selection on species living in open habitats, such as grasslands, or in the forest canopy.

How might wind influence the evolution of vibrational communication systems? Assuming that wind of high velocity precludes communication, one response would be to restrict signaling to relatively wind-free periods, which in many environments occur at predictable times of day (figure 3a). Variation in wind noise at a finer time scale may create a need for gap detection, that is, for placing signals in silent windows that appear unpredictably in a noisy background (figure 3b;

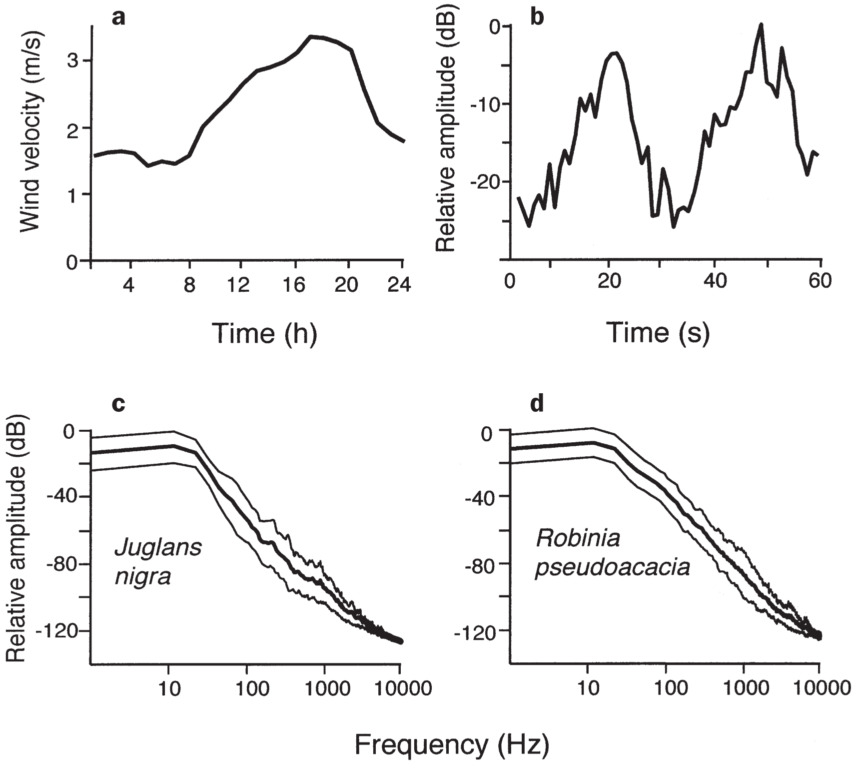

*Figure 3. Wind as an agent of selection on insect vibrational communication through plants. (a) Hourly wind speeds, averaged over one month, recorded at a weather station in Corvallis, Oregon. Wind speeds were consistently lower in the morning. Wind-speed data were obtained from the AgriMet Program of the US Bureau of Reclamation, Pacific Northwest Region (*www.usbr.gov/pn/agrimet/webagdayread.html*). (b) Short-term variation in the amplitude of wind-induced vibrations in a petiole of a black walnut tree,* **Juglans nigra.** *(c, d) Amplitude spectra ($\bar{x} \pm$ standard deviation) of wind-induced vibrations in petioles of two tree species,* **J. nigra** *and* **Robinia pseudoacacia,** *showing the predominance of low frequencies and the gradual roll-off at higher frequencies. Wind noise recordings were made at typical positions of treehoppers (***Enchenopa binotata***) on the two host plants, using a PCB U352B65 accelerometer attached to the leaf petiole and a PCB U480E09 amplifier connected to a Macintosh G3 laptop computer. Maximum wind velocity for these recordings, measured with a handheld anemometer, varied from 1 to 2 meters per second (*n *= 1 petiole per tree for 10 trees of each species).*

Gerhardt and Huber 2002). Wind of low velocity may simply provide a source of ambient noise against which signals must be detected (figure 3c, 3d). Rather than inhibiting communication, it may select for signals with higher amplitude or with frequencies not present in the noise.

There have been relatively few attempts to characterize the noise generated in plant stems and leaves by wind (Barth et al. 1988, McVean and Field 1996, Barth 1997, Casas et al. 1998). Barth and colleagues (1988) conducted a detailed field study of wind and other influences on the vibrational environment of a spider (*Cupiennius salei*) that communicates using plantborne signals. This study provides an excellent model in its use of field recordings from plants known to be used by spiders, with vibrations recorded at positions typical of those used by spiders when communicating. The authors examined two structurally different plant species. The vibrations induced by wind were primarily at low frequencies (below 30 hertz [Hz]), although higher frequencies were produced when leaves collided with each other. Most of the energy in the spiders' signals is above 30 Hz; furthermore, their principal vibration receptors are relatively insensitive to the low frequencies characteristic of wind noise (Barth 1997).

Subsequent measurements, including our own (figure 3c, 3d) and those by Casas and colleagues (1998), have likewise found that most of the energy in wind-generated noise is present at low frequencies. If this is a general pattern, wind may provide a widespread source of selection against the use of very low frequencies. There may also be enough energy at higher frequencies to mask signals in the 100–1000 Hz frequency range used by many insects (figure 3c, 3d). However, it is worth keeping in mind that wind-generated noise has only been investigated in a few species of plants. If the properties of wind noise differ between plant species or between different parts of the same plant (Barth et al. 1988, McVean and Field 1996), then differences in host use will be associated with differences in the noise environment in which communication takes place.

Rain is another important source of noise in the vibrational environment of insects on plants. The impact of a drop of water on a leaf generates a characteristic pattern of vibration consisting of a high-amplitude "pop" followed by a series of diminishing sinusoidal oscillations whose frequency depends on the position of the impact on the leaf (Barth et al. 1988, Casas et al. 1998). A heavy rainfall probably precludes the use of plant stems and leaves for communication. A light rain or percolation of drops down from the canopy after a rain, on the other hand, produces a series of high-amplitude vibrations of unpredictable timing that may simply increase the signal-to-noise ratio for communicating insects. It is possible that in environments such as cloud forests in which rain is frequent, signals that are both detectable and recognizable in the presence of raindrops may be favored (e.g., long, pure tones).

In addition to the ubiquitous abiotic sources of environmental noise, there are many biotic sources of vibration in plant stems and leaves. Some are incidentally generated, such as the vibrations produced by insect feeding and locomotion. These vibrations are conspicuous enough to be used as prey-

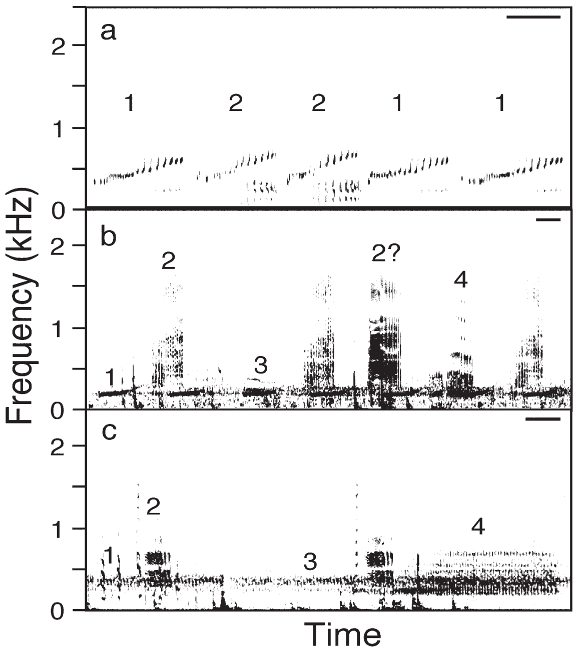

*Figure 4. Examples of complex vibrational signaling environments. (a) A male treehopper (***Heteronotus trinodosus***) producing advertisement signals in alternation with another male on the same stem. (b, c) Field recordings from two herbaceous plants in Soberanía National Park, Panama. Each recording contains signals of approximately four insect species, with one species signaling continuously (indicated with number 1 in panel b and number 3 in panel c). Scale bars = 1 second. It is difficult to gain from figures like these the impression one gets, when listening to vibrational signals in plants in the field, of an encounter with a mysterious and alien world of sound.*

locating cues by predators and parasitoids (Barth et al. 1988, Pfannenstiel et al. 1995, Casas et al. 1998) and contribute to the background noise in the environment in which insects communicate. Some sounds of locomotion may be important to detect, such as those produced by a predator. Other incidental vibrations can arise from processes occurring inside the plant, such as cavitation in water-stressed plants.

Insects often communicate in complex social environments. In the treehopper *Vanduzea arquata,* a single host plant can contain hundreds of individuals (Cocroft 2003). At the peak time of signaling during the day, a quarter of the males on the plant may be producing advertisement signals. In some species, multiple signalers coordinate the timing of their signals (figure 4a) to form a chorus like those that occur in species using airborne sound (Hunt and Morton 2001, Greenfield 2002).

The vibrational soundscape of a single plant stem will often include a number of different signaling species (figure 4b, 4c; Heady and Denno 1991, Claridge and De Vrijer 1994). The assemblage of individuals and species signaling together is likely to be highly variable in time and space, because the local density of signaling males of a given species is variable (Cocroft 2003), and many species of vibrationally communicating insects use a "call–fly" strategy in which males signal on a succession of different plants or parts of the same plant (Cokl and Virant-Doberlet 2003). The presence of other signaling species can be an important source of selection on communication systems (Gerhardt and Huber 2002).

One source of noise in plant stems and leaves that is sometimes overlooked is the vibration induced by airborne sounds in the environment. One could, for example, obtain a representative sample of the birdsong in an area by using a vibration transducer on a plant stem. The potential importance of this source of noise is illustrated by a study of two vibrationally communicating species in which mating was prevented by broadcasting the sound of a musical instrument in the vicinity of the plants (Saxena and Kumar 1980). Similar conditions might occur in the vicinity of loud sound sources, such as a pond full of singing frogs or a tree full of cicadas.

Sensory drive in vibrational signals?

In considering the evolution of diversity in vibrational signals, one unresolved question stands out: does the use of different host plant species generate divergent selection on signals? If signals are under selection for efficient transmission between signaler and receiver, then populations inhabiting environments that differ in their effect on signal transmission or detection are expected to evolve different signals—a process known as "sensory drive" (Endler 1993). A wide diversity of plants are used as transmission channels for insect vibrational signals. If plant species differ in their transmission properties, host plant use may have important consequences for the role of signals in assortative mating and speciation, especially in cases of sympatric speciation through host plant shifts.

Plants act as frequency filters for the signals traveling through them: a signal with equal energy across a wide range of frequencies will have unequal energy among frequencies after propagating along a plant stem (Michelsen et al. 1982). In this discussion we assume that selection will favor signals that transmit with less attenuation (Endler 1993)—that is, signals that use frequencies that match the filtering properties of the substrate (but see McVean and Field 1996). We also need to consider frequency selectivity on the part of receivers, whose responses may be strongly influenced by signal frequency (figure 5). We can thus think of selection on signal frequency as driven by two filters: the filter imposed by the receiver's sensory system and the filter imposed by the properties of the plant along which the signal propagates (figure 6).

Here we explore how signals are expected to evolve in response to the interaction of substrate filtering and receiver selectivity for spectral properties of signals. The actual filters imposed by receivers and plant substrates may be complex, but to illustrate their potential influence on signals, we consider a simple scenario in which receiver frequency selectivity is either narrow or broad, and in which the average substrate filter encountered by a population of signaling insects favors all frequencies equally (flat), favors lower frequencies (low-pass), or favors a narrow frequency band (band-pass).

When might insects experience a flat frequency filter? This could occur if all frequencies transmit equally well in individual substrates (which is unlikely), or if the variability among substrates is so unpredictable that on average all frequencies transmit equally well. This scenario might apply to insects that use many different species of plants as communication substrates. If receiver frequency selectivity is broad, then one solution to unpredictability in transmission environments, suggested by Michelsen and colleagues (1982), is to use signals with a broad frequency range (figure 6a). Use of such broadband signals will increase the likelihood that at least some frequencies reach the receiver. However, if receivers are selective for a narrow frequency band (figure 5), use of broadband signals will provide no advantage; instead, we would expect signalers to use a narrowband signal matched to the receiver's preferred frequency (figure 6b). Similar arguments apply to the case in which the substrate, on average, imposes a low-pass filter; within the frequency range that transmits well, selection for transmission efficiency may favor relatively broadband or narrowband signals, depending on the selectivity of the receiver (figure 6c, 6d). Finally, where the average filtering properties of the substrate favor a particular frequency (more likely for insects that specialize on one plant species), the expected signal spectra again depend on the receiver. If the receiver's frequency selectivity is broad, we would expect the signal spectrum to match the substrate filter (figure 6e). If receivers are selective for a narrow frequency band, and if the preferred frequency matches the substrate filter, then selection will favor signal spectra centered on the frequency that transmits best (figure 6f). If, in contrast, the frequency preferred by the receiver does not match the frequency transmitted best by the substrate, then selection will favor the signal frequency that best balances the joint effect of stem filtering and receiver selectivity. The above predictions, of course, consider only two factors affecting signal transmission and ignore other sources of selection, such as environmental noise or predation (Endler 1993).

Our knowledge of the filtering properties of plant substrates is limited. In particular, few studies of vibration transmission have characterized a large enough sample of natural substrates to allow an inference of how selection might act on signal frequency. The need for large sample sizes is underlined by the finding that substrate filtering properties can vary within a single stem or leaf, depending on the distance from the source and on the relative positions of the signaler and receiver (Michelsen et al. 1982, Keuper and Kühne 1983, Barth et al. 1988, Magal et al. 2000, Cokl and Virant-Doberlet 2003). Filtering during transmission may not be entirely unpredictable, however. Some studies have found that lower frequencies may be better suited than higher frequencies for longer-distance transmission along plant stems (Michelsen et al. 1982, Barth 1997, Magal et al. 2000, Cokl and Virant-Doberlet 2003), although others have not (McVean and Field 1996). There may also be cases in which a plant substrate best transmits a narrow frequency band. Different plant parts—main trunk, side branches, twigs, and leaves—may each have characteristic frequencies at which vibrational energy will propagate especially well (McVean and Field 1996). Insects are often found on only a single type of plant part, such as leaf petioles or young stems, and may thus regularly encounter environments that are similar in their filtering properties.

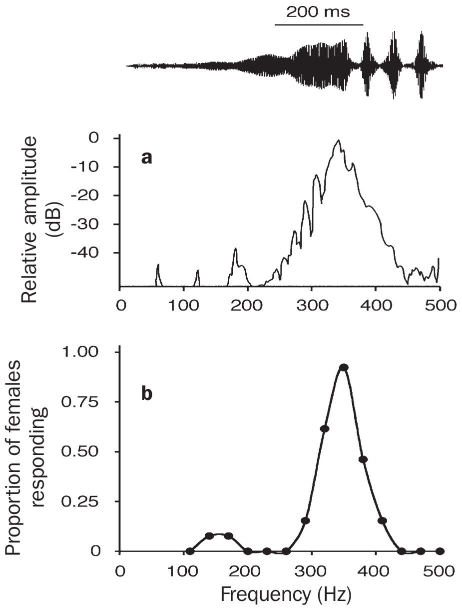

Figure 5. Female preference curve for signal frequency compared with the amplitude spectrum of a male advertisement signal for a treehopper (a member of the **Enchenopa binotata** *species complex occurring on the host plant* **Ptelea trifoliata** *in central Missouri). (a) Amplitude spectrum of a male advertisement signal that closely matches the mean frequency for the population. The waveform of that signal is shown above. (b) Proportion of females (***n** *= 15) that responded to digitally generated signals that varied in carrier frequency while keeping all other traits at the mean value for the population. Playback stimuli were delivered by means of a magnet attached to the host plant stem and an electromagnet placed 2 millimeters away from the magnet. The stimuli and the female response calls were monitored with a PCB U352B65 accelerometer and U480E09 amplifier connected to a recording computer. Playback intensity was set to the median peak acceleration of the signals of nine males recorded on the playback plant.*

Few studies have explicitly addressed the hypothesis that vibrational signals are adapted for transmission through particular plant substrates. One approach has been to characterize the filtering properties of the substrate used by signalers and investigate whether the frequencies used transmit better than other frequencies. In the spider *C. salei,* males and females exchange low-frequency vibrational signals during courtship

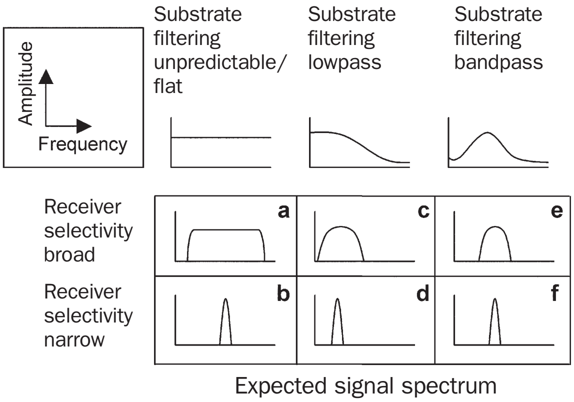

Figure 6. Frequency spectra of vibrational signals (a through f) predicted to evolve in response to different combinations of receiver frequency selectivity and average substrate filtering properties. For example, when the substrate filtering is unpredictable or flat, use of signals containing a broad range of frequencies may ensure that some energy reaches the signaler (a). However, this strategy will only be successful if receivers are also broadly tuned; if receivers are selective for a narrow band of frequencies, signals should likewise be narrowly tuned (b). Use of hosts with different filtering properties (such as lowpass vs. bandpass filters, or bandpass filters with different best frequencies) may favor the evolution of different signals, a process that could contribute to speciation.

(Barth 1997). Barth and colleagues (1988) found that the spiders' signal frequencies were among those that transmitted especially well in two of their plant substrates. Michelsen and colleagues (1982) measured the signals of seven species of Hemiptera with varying degrees of host specificity. The authors also measured the frequency transmission properties of eight plant substrates, including some of the substrates used by five of the insect species. Although frequency filtering was presented in detail for only one plant species, the authors reported a lack of correlation between the signals of different insect species and the transmission properties of their plant substrates. Indeed, the authors suggested that filtering properties of the various plants were similar, although this similarity was not clarified in detail.

A second approach to testing the hypothesis that signals are adapted to transmit through particular plants is to play back insect signals (box 2) through the plants they use and through those they do not use. A pioneering study by Bell (1980) showed that artificial stimuli approximating the vibrational signals of tree crickets (Orthoptera: Gryllidae) transmitted with less attenuation through the stems of plant species used by calling crickets than through the stems of plant species the crickets did not use. This is the only study in the transmission literature to report values for a large enough sample ($N = 10$ stems per species) to allow an estimate of the mean and standard deviation for attenuation values, and it may be significant that this is one of the few studies to conclude that stems of different plant species differ in their frequency attenuation properties. In an experimental study designed explicitly to test whether signals are adapted for transmission through their usual plant substrates, Henry and Wells (2004) used signals of two species of lacewings that communicate on different substrates. One species is found on coniferous trees, while the other is found on herbaceous plants and grasses. For both species, Henry and Wells (2004) measured changes in the signals of males when played back through exemplars of both types of substrate, using two stems each of a conifer species and a grass species. They then tested the responses of females to signals that had been transmitted through both substrate types. The authors concluded that there was no evidence for substrate-specific adaptation, as measured either by changes in signals over distance or by responses of females. The authors were cautious in their conclusions, however, in consideration of potential mass loading effects on their measurements.

Which of the scenarios depicted in figure 6 would lead to signal divergence among species using different plant substrates? Widespread selection for broadband signals or use of low frequencies (figure 6a, 6c, 6d) would lead to convergence. In contrast, if there are plant substrates that consistently favor a particular frequency (figure 6e, 6f), then shifts between host plants that favor different frequencies could result in divergent selection on signals, contributing to assortative mating and evolutionary differentiation. Other ecological shifts could also influence signal evolution; in particular, one might expect differences between host specialists that communicate using only one kind of plant substrate and generalists that communicate using many different kinds of substrates. It would also be fruitful to compare the signals produced by different species that use the same plant (Claridge and De Vrijer 1994), especially in a phylogenetic context where convergence on similar signal properties can be evaluated (Henry and Wells 2004).

Much work remains to be done to assess the contribution of differences in host use to the evolution of diversity in insect vibrational signals. Progress is likely to come from studies that address substrate transmission, signal properties, and receiver preferences in the same system (Barth 1997, Henry and Wells 2004). It will also be important to consider variation among substrates in their effect on the temporal features of signals, an aspect of signal transmission that has been little explored (Keuper and Kühne 1983, Cokl and Virant-Doberlet 2003). Characterization of substrate transmission properties should begin with careful description of where on the plant communication takes place in nature, and over what distances. It will be critical to characterize a large enough sample of appropriate substrates to provide robust estimates of both the average substrate properties and the extent of variation among substrates. For example, for insects that specialize on the stems of one plant species, we suggest characterizing stems from 10 to 20 plants, depending on the level of variation among stems. For species that use a range of different plant species as substrates, characterizing the selective envi-

Box 2. Some methods for playback of vibrational signals.

Electrodynamic shakers are used in industry and come in a wide range of sizes, the smallest of which are suitable for vibrational playback of insect signals. A shaker works like a loudspeaker, but without a cone coupling the vibrations to the air; instead, it is attached directly to the plant stem. Shakers provide a high-fidelity means of reproducing insect vibrational signals, although they are relatively heavy and can be difficult to position if the playback is done on a plant substrate in a natural position.

An *electromagnet* can be positioned opposite a small, strong magnet attached to a plant stem (Michelsen et al. 1982); sending a stimulus signal to the electromagnet through an amplifier vibrates the stem. This method is very effective in re-creating the fine structure of vibrational signals, but one caveat is that the frequency response of the system depends on the distance between magnet and electromagnet.

Piezoelectric stacks have not been widely used (see Cocroft et al. 2000) but offer ease of positioning and a wide frequency range. Disadvantages are the need for an offset voltage, requiring specialized (and expensive) amplifiers or custom-designed DC couplers.

A number of studies have used a *loudspeaker* from which the speaker cone has been removed, and with a pin inserted into the coil to make contact with the plant. This method is inexpensive and suffices for reproducing the signals of many insects. A disadvantage is that the output is not flat across different frequencies, and that the characteristics of the system may alter depending on the pressure with which the pin contacts the substrate.

Regardless of the playback method used, whenever the stimulus contains more than one frequency, it is necessary to compensate for the filtering imposed by the plant or other substrate as well as for the frequency response of the playback device. If this issue is addressed, all of the above methods can reliably reproduce insect signals; otherwise, if one simply records an insect signal and plays it back through a substrate, the played-back signal at the location of the receiver will depart in unknown but possibly dramatic ways from the original signal. This distortion can be compensated for by introducing a noise stimulus into the plant and recording it, calculating the change in the amplitude at each frequency, and then modifying the experimental stimuli accordingly (Cocroft 1996). This compensation is best done using digital signal processing, but it could be roughly approximated with a graphic equalizer.

ronment for communication will require correspondingly greater effort. Finally, we suggest that a match between signal and substrate is most likely for insects or other animals that use a single species of host plant, rather than those that use a range of species—a possibility that remains unexplored apart from one species in the classic study by Michelsen and colleagues (1982).

Unintended receivers

Communication systems using light, pheromones, and airborne sound are vulnerable to exploitation by predators and parasitoids that use their prey's signals to locate them (Zuk and Kolluru 1998). There are no known examples of such exploitation for plantborne vibrational communication, perhaps because of the lack of field-based research; however, vibrational eavesdropping by predators is very likely. Spiders, given their exquisite sensitivity to vibration and their ability to locate a vibration source (Barth 1997), are especially good candidates for eavesdropping on vibrational signals. Morris and colleagues (1994) suggest that when tropical katydids avoid bat predation by switching from airborne sounds to plantborne tremulations, they may instead attract spiders, a diversity of which have been observed preying on katydids. The jumping spider *Portia fimbriata* illustrates the potential for sophisticated use of vibrational prey signals: it can mimic the vibrational signals of males of other spider species to lure females into range (Jackson and Wilcox 1998). The importance of predation by vibration-sensitive spiders is underscored by the phenomenon of "vibrocrypticity," described for some insects that move so slowly and generate so little vibration in the substrate that they can walk past a spider without eliciting an attack (Barth et al. 1988).

The exploitation of prey-generated vibrations is not limited to spiders. The predatory stinkbug *Podisus maculiventris* homes in on the vibrations produced by feeding caterpillars (Pfannenstiel et al. 1995), and parasitoid wasps find hidden hosts by orienting to incidental vibrations produced by feeding and locomotion (Casas et al. 1998). In fact, a wide range of insects can locate a source of vibrational signals (Cocroft et al. 2000, Cokl and Virant-Doberlet 2003). We can see no reason why insect predators could not locate prey on the basis of their vibrational signals, rather than relying only on incidental vibrational cues.

A vast number of predators could exploit insect vibrational signals. There are 40,000 species of spiders (Barth 2002), and the density of individuals can be astoundingly high; as Bristowe (1971) put it, "Picture a small defenceless insect in an acre field surrounded by 2,000,000 pairs of spiders' jaws" (p. 55). If we also consider predatory ants and true bugs, other predatory insects, and parasitoid Hymenoptera, it is clear that a signaling insect is never far from an enemy capable of eavesdropping on its signals. However, in keeping with the dearth of field research, we do not know of a single study that has explored the potential for predators to exploit insect vibrational communication.

Social selection

Vibrational signals play a major role in pair formation and other stages of reproduction. Much research has focused on the species specificity of vibrational signals and their contribution to reproductive isolation. Female choice based on between-species variation in male signals has been widely documented (Heady and Denno 1991, Claridge and De Vrijer 1994, Henry 1994, Wells and Henry 1998, Cokl and Virant-Doberlet 2003, Rodríguez et al. 2004). Female signals can also vary between species, and male choice of female signals has been found in planthoppers, including discrimination between sexual and triploid pseudogamous females (Claridge and De Vrijer 1994). Interestingly, male *Ribautodelphax* planthoppers exposed to conspecific signals during development favored conspecific female signals more strongly than males exposed to heterospecific signals (De Winter and Rollenhagen 1993).

Within species, geographic differences in male and female vibrational signals can influence mate choice (Gillham 1992, Claridge and De Vrijer 1994, Miklas et al. 2003). Individual differences in male signals also influence female choice, suggesting the operation of sexual selection (Hunt et al. 1992, Butlin 1993, Rodríguez et al. 2004). In meadow katydids, male vibrational signals are indicative of body size, and females favor signals associated with larger males (De Luca and Morris 1998). In scaly crickets, males in good condition are more likely to signal and have higher rates of spermatophore transfer (Andrade and Mason 2000).

The mechanism by which females exercise mate choice will vary according to male and female mate-searching strategies. Males of many species use a "call–fly" strategy (Cokl and Virant-Doberlet 2003), in which males visit and signal on a series of plants. Receptive females respond with a vibrational signal that elicits searching by the male (Hunt and Nault 1991, Claridge and De Vrijer 1994), and the pair may then engage in a prolonged duet. For species using this mate-searching strategy, the first stage of female choice lies in the decision to signal in response to a particular male. In other species, males signal repeatedly from one location, and females may exercise choice by approaching a signaling male (Tishechkin and Zhantiev 1992). Females may also initiate interactions with vibrational signals (Heady and Denno 1991, Ivanov 1997, Cokl and Virant-Doberlet 2003) or pheromones (Ivanov 1997).

Vibrational signals may influence mate choice after pair formation. Female signaling during rejection of male mating attempts has been documented in various groups (Ryker and Rudinsky 1976, Markl et al. 1977, Manrique and Schilman 2000, Cokl and Virant-Doberlet 2003). Furthermore, males sometimes continue to signal after finding the female (Cocroft 2003), during copulation (Claridge and De Vrijer 1994), and even after copulation (Brink 1949).

Interactions under high population densities may favor strategies more complex than call–fly and duetting. Vibrational signals are involved in male–male competitive interactions in many species (Gogala 1985, Claridge and De Vrijer 1994, Hunt and Morton 2001, Cokl and Virant-Doberlet 2003). These interactions may include signal timing strategies to deal with competition in choruses, such as jamming and avoidance of signal overlap (Greenfield 2002, Bailey 2003). "Rivalry calls" often occur in species that also engage in the call–fly strategy, suggesting that these signaling systems may be adapted to a range of social environments (Cocroft 2003). Signaling during male fights is taxonomically widespread (Morris 1971, Ryker and Rudinsky 1976, Crespi 1986, Choe 1994, Ivanov 1997).

Vibrational communication also underlies many social interactions outside the context of reproduction. Vibrational signals are widespread in the highly social insects, including ants, termites, and bees (figure 1). For example, plantborne signals are fundamental to the ecological success of leafcutter ants, which are the dominant herbivores at some sites in the New World tropics (Wirth et al. 2003). Colonies monitor and exploit a changing set of resources by means of communication among colony members. Some of this communication is vibrational: foragers produce vibrational signals while cutting leaves, especially if the leaf represents a high-quality substrate for growing fungi, and these signals recruit other foragers (Hölldobler and Roces 2000).

For many plant-feeding insects, vibrational communication is important for meeting the challenges of life on a plant. One challenge is to gain access to feeding sites, and here vibrational signaling can underlie competitive or cooperative interactions. Solitary drepanid moth larvae use vibrational signals to defend their leaf from other larvae (Yack et al. 2001). On the other hand, larvae of other insects attract conspecifics to feeding sites with vibrational signals (Cocroft 2005), and may convey feeding site quality with higher signaling rates (Cocroft 2001). Another challenge of life on a plant for some species is to find and remain in a group. In the group-living sawfly larvae known as "spitfires," individuals form groups to make relatively long-distance moves; tapping signals assist stragglers in rejoining a moving group (Carne 1962). Likewise, Greenfield (2002) observed that, in response to a disturbance, larval tortoise beetles quickly formed tight aggregations after an exchange of vibrational signals.

Vibrational communication can help herbivores avoid predation. Female thornbug treehoppers defend their aggregated offspring. When a predator approaches, the nearest offspring produce brief vibrational signals; this signaling spreads through the group in a chain reaction, generating a group signal that is longer and higher in amplitude than an individual signal (Cocroft 1996). In response to group signals from offspring, mothers move into the aggregation and attempt to drive off the predator. Within an aggregation, there is variation among offspring in their probability of participating in a group signal, and a recent study (Karthik Ramaswamy, working with R. B. C.) has revealed that an individual's probability of signaling is closely correlated with its relative risk of predation.

Signals of butterfly larvae in the Riodinidae, and of larvae and pupae in the Lycaenidae, also function in avoiding predators, but by means of an intermediary. Vibrational signals, in concert with chemical signals, attract mutualistic ants that provide protection from predators (DeVries 1991, Travassos and Pierce 2000). Ant-attracting signals are widespread in the Riodinidae and Lycaenidae, but there is an interesting change of function in the lycaenid genus *Maculinea.* Here the relationship is not one of mutualism but of predation: *Maculinea* larvae produce signals to attract ants, gain entry to the nest, and feed on ant brood (DeVries et al. 1993).

Future directions in the study of insect vibrational communication

We have argued for the importance of the vibrational channel in insect communication. Our estimate of 195,000 species using vibrational signals is probably too low: we included only described species, and excluded likely cases that have simply not received enough study—such as fleas, whose stridulatory organs suggest the likelihood of vibrational signaling (Smit 1981, Henry 1994). Accordingly, we encourage exploration of the possible use of vibrational signals in insects in which such communication is unknown, particularly in group-living species. Ecological sources of selection on vibrational communication systems have been underresearched, and there is much opportunity for groundbreaking studies of how the evolution of vibrational communication is influenced by the nature of the substrate, sources of environmental noise, interference from competitors, and eavesdropping by predators and parasitoids. Given the number of vibrationally communicating insects, as well as the large number of vibrationally orienting predators and parasitoids, we expect further study to reveal many evolutionarily important interactions between vibrational signalers and their natural enemies. All of these areas will contribute to our understanding of the evolution of a mechanical signaling modality that dwarfs all others in its taxonomic breadth and diversity of signaling species.

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