23 Vibratory Communication in Treehoppers (Hemiptera: Membracidae)

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INTRODUCTION

Few insect families are as diverse in morphology, behaviour and ecology as the membracid treehoppers (Hemiptera: Membracidae). Studies of communication in membracids are uncovering a correspondingly rich variety of signals, transmitted in the form of substrate-borne vibrations. In this chapter we summarise what we have learned about vibratory communication in treehoppers, drawing on the small but growing literature and on our own recordings and observations of temperate and tropical species. We highlight aspects of their biology that contribute to an impressive diversity in communication signals. Membracids offer promising opportunities for studying the use of signals in cooperation and competition within social groups, the importance of signal divergence in the process of speciation and the evolution of communication systems.

The membracids are a clade of some 3200 species (Wallace and Deitz, 2004), with highest species diversity in the tropics and especially in neotropical lowland forests (Olmstead and Wood, 1990; Wood, 1993b). They are apparently derived from within the leafhoppers (Cicadellidae) (Dietrich *et al.*, 2001). Membracids are characterised by an expanded pronotum, which in some species forms a simple projection over the abdomen and in others takes on some of the strangest shapes ever sculpted from insect cuticle (Figure 23.1a and b).

Treehoppers are unusual not only in their morphology, but also in the diversity of their social behaviour (Figure 23.1c and d; Wood, 1993b, 1979; Lin *et al.*, 2004). Some treehoppers live

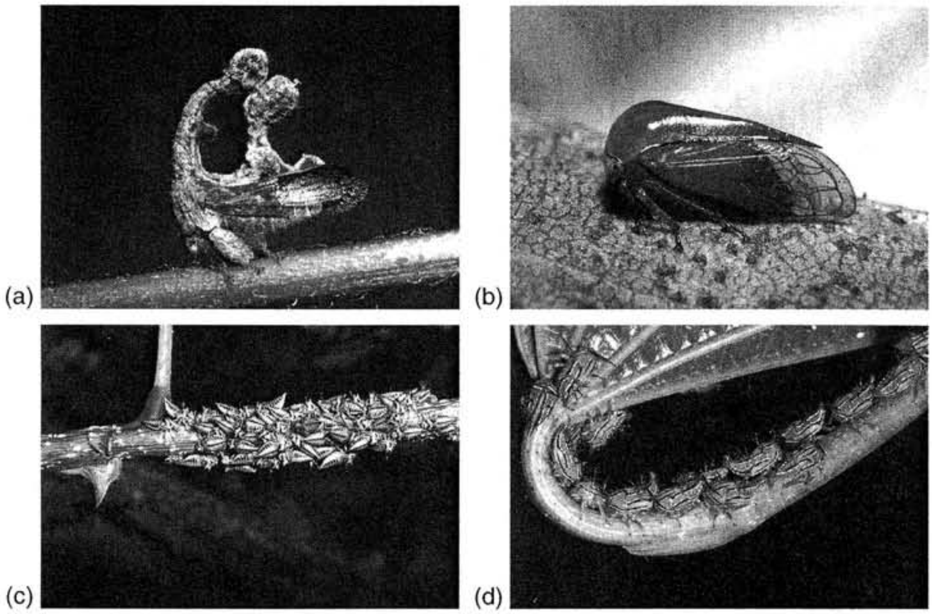


FIGURE 23.1 Membracid treehoppers. (a) *Cladonota biclavata* from Panama; (b) *Acutalis* sp. from Ecuador; (c) *Umbonia crassicornis* female and nymphs from Florida, U.S.A.; (d) *Calloconophora pinguis* nymphs from Panama, feeding on a new, expanding leaf of *Piper reticulatum* (attending female not shown). (Photos in (a) and (b) by C. P. Lin. With permission.)

essentially solitary lives, associating with others only for purposes of mating. In this regard they resemble most species in related groups such as the cicadas and leafhoppers (but see Dietrich and McKamey, 1990). At the other end of the spectrum are species in which individuals spend their lives in social groups. Some social groups are composed of related individuals; for example, many species have some form of maternal care, which ranges from guarding eggs (Lin *et al.*, 2004) to defending offspring from predators in response to specialised vibratory signals (Wood, 1984; Cocroft, 1999, 2002). Other social groups contain a mix of related and unrelated individuals that form aggregations during their nymphal development or throughout their lives (Wood, 1984). Immatures of some neotropical treehoppers even form aggregations consisting of individuals of several species (Wood, 1984). Each of these forms of social behaviour has consequences for the forms of social signalling that may occur among prereproductive individuals, and for mating systems and mate-searching strategies in adults.

Group living in membracids is often related to their mutualisms with Hymenoptera, especially ants. Ant mutualism is especially common among tropical species, and may have evolved in response to the threat of ant predation (Wood, 1993b). Although ant mutualism can occur in solitary species (Wood, 1984), it is more common in group-living species (Wood, 1993b). Indeed, there is a clear relationship between group size and the benefits of ant mutualism: ants reduce predation on the treehoppers they tend, and larger groups of treehoppers usually attract more ants and maintain more consistent ant attendance (McEvoy, 1979; but see Morales, 2000). Living in larger groups may also allow individuals to reduce their individual share of the costs of mutualism in the form of providing nutrients to attending ants (Axen and Pierce, 1998). Although ants are the most common mutualists, some stingless bees or vespid wasps also tend treehoppers (Wood, 1984). Treehoppers probably communicate with their mutualists, as do ant-attended lycaenid and riodinid caterpillars (deVries, 1991; Travassos and Pierce, 2000), but this has not yet been documented.

SIGNALS AND MATING BEHAVIOUR

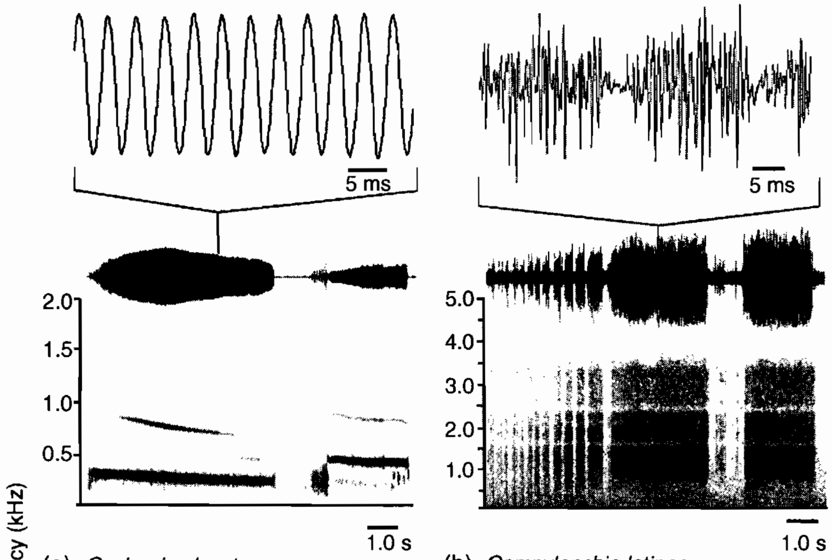
DISCOVERY OF MATING SIGNALS IN MEMBRACIDS

Although most research on communication in membracids has come in the last 15 years, evidence that membracids produced some form of mechanical signal was provided more than 50 years ago by the pioneering work of Ossiannilsson (1946, 1949). Ossiannilsson (1949) described structures similar to the tymbals of cicadas in many species of Auchennorryncha, including the European membracid *Centrotus cornutus*. Ossiannilsson (1949) recorded and described low-amplitude airborne songs from many of the same species, but he suggested that the signals were probably transmitted to other insects as vibrations travelling through the substrate rather than as airborne sound. Evans (1946, 1957) described tymbal structures in two species in the Aetalionidae, a group closely allied to the Membracidae (Dietrich *et al.*, 2001). The first sonogram of a membracid signal was published by Moore (1961). After placing several individuals of both sexes of *Anisostylus elongatus* in a small glass vial along with some pine needles, Moore (1961) detected a short, broadband signal that he speculated was produced by the wings. The first clear evidence of substrate-borne signals in membracids was not published for another 30 years, when Strübing (1992) and Strübing and Rollenbach (1992) described a complex vibratory signal produced by males of the North American membracid *Stictocephala bisonia*. Shortly thereafter, Hunt (1993) conclusively demonstrated the function of these signals in mating behaviour. Hunt (1993) found that males of the North American treehopper *Spissistilus festinus* produced complex frequency-modulated signals during mate-searching behaviour and courtship, and that individuals engaged in male–female duets prior to mating. Using methods similar to those of Ichikawa and Ishii (1974), Hunt (1993) found that vibratory duetting between a male and a female on different plants occurred only when the plants were placed in direct contact, providing a continuous vibration-transmitting pathway. The plant-borne vibratory signals of treehoppers are transmitted as bending waves (Cocroft *et al.*, 2000; also see Michelsen *et al.*, 1982) and are detected by vibration receptors in the legs (Kalmring, 1985). Most vibratory signalling interactions occur within a range of 2 m or less, between insects on the same plant or on neighbouring plants in contact through leaves, stems, or roots (Čokl and Virant-Doberlet, 2003).

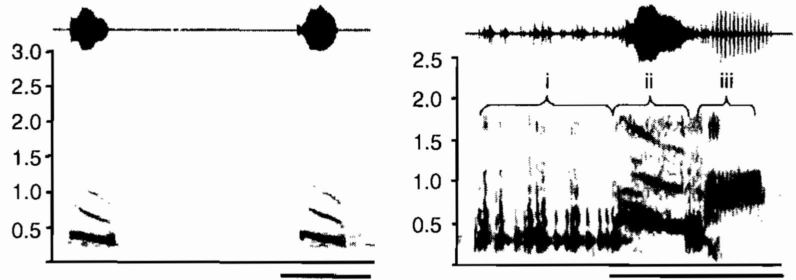
DIVERSITY IN MATE ADVERTISEMENT SIGNALS

Vibratory signalling is probably universal among the membracids. It is widespread among related taxa (Claridge, 1985b) and has been found in all membracids so far examined (we have recorded mating signals of approximately 75 species from North America and from the New and Old World tropics). With mating signals recorded from approximately 2% of the 3200 described species of membracids, it is already clear that there is a diversity of signals and signal production mechanisms. We can only guess at the diversity of signals in the other 98%, most of which occur in the tropical forest canopy. Among the species we have sampled, signals range from pure tones or harmonic series, which are usually frequency modulated (see Figure 23.2a and c), to trains of broadband clicks or other noisy elements (see Figure 23.2b). Many species produce complex signals incorporating both tonal and broadband elements, either simultaneously or in alternation (Figure 23.2d), and in combinations that can be startling when played back as airborne sound. In many species, males produce a series of low-amplitude percussive or rattling signals before each bout of advertisement signals (Hunt, 1994; Figure 23.2d).

The degree of complexity in membracid mating signals may be correlated with signalling rates. Species that produce simple signals typically repeat them relatively rapidly in bouts of 2 to 12 signals, separated from other bouts by silent intervals (Figure 23.2c). In some cases when multiple males are present, males may produce a continuous series of signals (*e.g. Notocera bituberculata*, some *Enchenopa binotata*; unpublished data). These groups of stationary, continuously signalling males are analogous to the choruses described for some leafhoppers (Ossiannilsson, 1949;



(a) *Cyphonia clavata* (b) *Campylenchia latipes*



(c) *Aphetea inconspicua* (d) *Tylopelta americana*

FIGURE 23.2 Male mating signals from four membracid species, illustrating pure tone and noisy elements as well as simple versus complex signals. The signal of the Panamanian *Cyphonia clavata* (a) largely consists of two pure tones that differ in frequency, while the signal of the North American *Campylenchia latipes* (b) contains broadband noise bursts. Male *Aphetea inconspicua* (c) from Panama produce simple signals, consisting of a short, repeated tone (two signals shown). In contrast, male *Tylopelta americana* (d) from North America produce a signal that begins with a series of clicks (i), continues with a tone that drops in frequency with simultaneous, low-amplitude clicks (ii), and ends with a series of pulses that rise in frequency (iii). The transducers used to make the recordings are as follows: (a) and (c) phonograph cartridge (PC); (b) accelerometer (ACC); and (d) laser vibrometer (LDV).

Hunt and Morton, 2001) and for many species that signal using airborne sounds (Gerhardt and Huber, 2002). In contrast to species producing simple signals, species that produce the most complex signals often produce them at more widely separated intervals. For example, *Potnia brevicornis* from Panama produces a characteristic alternation of broadband pulses and frequency sweeps terminating in a high-amplitude harmonic series that rises then falls in frequency; males (at least when recorded singly) then pause for tens of seconds before producing another similar signal. Similar signalling patterns were recorded in individually recorded males of *Oxyrachis tarandus* from India and *Campylocentrus brunneus* and *Cladonota biclavata* (see Figure 23.1a) from Panama. The apparent pattern of short, simple signals produced in series and long, complex signals produced singly represents the endpoints of a continuum, and there are exceptions.

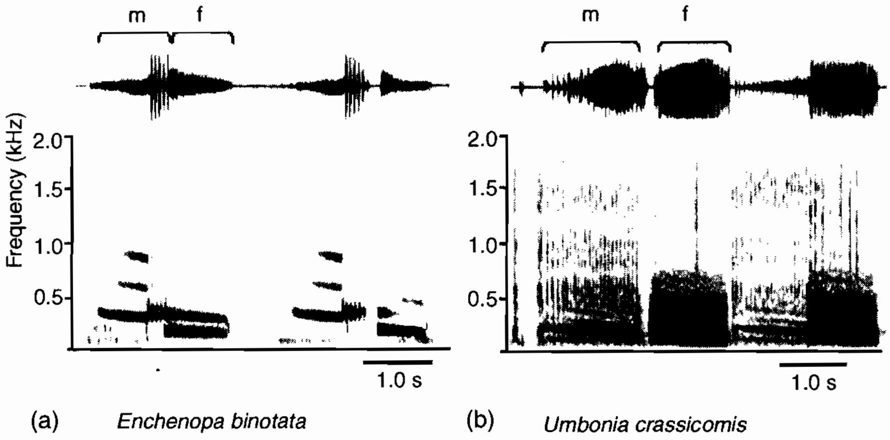


FIGURE 23.3 Male–female duets in two membracid species. (a) Duet from a member of the North American *Enchenopa binotata* complex occurring on the host plant *Viburnum prunifolium* and (b) a duet from the neotropical species *Umbonia crassicornis.* (a) and (b) both recorded using LDV.

For example, male *Tylopelta americana* produce complex signals (Figure 23.2d) but in bouts, with each about proceeded by a series of broadband clicks. In any case, establishing the relationship between signalling rates and signal complexity will require the use of a rigorous comparative phylogenetic approach.

During the vibratory duets that occur during courtship (Hunt, 1993, 1994), males may either produce typical advertisement signals or switch to different signals used only in that context (Cocroft, personal observation). The relatively few recorded examples of female response signals suggest that they are simpler than male signals and relatively similar across species (Figure 23.3). It is unclear to what extent male duetting responses may be influenced by variation in female response time or by differences in other signal features. This broad-scale pattern of diversity in the male trait and conservation in female response is suggestive of the actions of sexual selection in the evolutionary history of these signals.

After a vibratory duet during which the male locates the female, the male may then climb onto the female's pronotum and continue to signal. The signals used by males in this close-range courtship are often more complex and lower in amplitude than their longer-range advertisement signals (Cocroft, 2003). This form of signalling via direct contact may be free of some of the sources of selection on longer-range signals (*e.g.* selection for effective long-range transmission); it would be worthwhile to examine their rate of evolutionary change relative to advertisement signals.

Males in some species also use different signals when interacting with other males, as is common in other related groups (Claridge, 1985b; Gogala, 1985a; Hunt and Morton, 2001; Čokl and Virant-Doberlet, 2003). In *Vanduzea arquata,* it is possible that these male–male signals represent a form of mate guarding and are produced by males associated with aggregations of females (Cocroft, 2003). In *U. crassicornis* the function of male–male signals is unclear as they are given when two mate-searching males meet, even in the absence of females (Cocroft, personal observation). Males do not defend territories or home ranges, and the production of signals that may or may not be as attractive to females as advertisement signals would seem to incur opportunity costs for mate-searching males.

SIGNAL RECEPTION AND RECEIVER PREFERENCES IN MEMBRACIDS

There are no published studies of the morphology or physiology of vibration sensing in membracids. Based on study of other insects (Kalmring, 1985), especially within the Hemiptera (Čokl, 1983), it is likely that membracids detect signals using subgenual organs located in the tibia.

In addition to the frequency tuning of the vibration receptors, vibration perception is also influenced by the mechanical response of the body to substrate vibration, as shown in a study of *Umbonia crassicornis* (Cocroft *et al.*, 2000). A treehopper's body resting on its legs is analogous to a mass on a set of springs, with resonant properties like other mass-and-spring systems (Cocroft *et al.*, 2000). The resonance of the body can change when the insect alters its position (unpublished data), and such changes may be important in vibration perception. In a fiddler crab, where the body likewise behaves as a mass-and-spring system, individuals alter their posture after detecting a substrate-borne signal and thereby sharpen the frequency tuning around the resonant peak (Aicher *et al.*, 1983). The mechanical response of the body to substrate vibration also provides a source of directional cues, but it is not known whether the insects use these cues (Cocroft *et al.*, 2000).

Although membracid vibration sensing has not been characterised physiologically, the signals produced by females in response to male signals provide a behavioural assay of the response to vibration. In treehoppers in the *Enchenopa binotata* species complex, vibratory playbacks to responsive females have shown that females have a narrowly tuned frequency preference; male signals are also narrowly tuned around the same frequency (Cocroft and Rodríguez, 2005). Whether female responses to variation in the frequency of male signals reflect perceived changes in amplitude or true frequency discrimination has not been investigated.

DIVERSITY IN MATING SYSTEMS

Mating systems have not been widely studied in treehoppers, but what is known suggests that their mating systems are diverse. This diversity will in turn influence the evolution of communication systems. Important determinants of mating systems include female mating frequency, the degree of spatial clumping of females and the degree of synchrony in receptivity among females (Schuster and Wade, 2004). All of these features vary widely among different treehopper species. For example, while females in a number of species typically mate only once (Wood, 1974), females in other species mate multiply (Wood *et al.*, 1984; Eberhard, 1986). In some species females are highly clumped, as in the ant-attended species *Vanduzea arquata* where there may be 100 or more individuals on a single host plant (Cocroft, 2003), while in others females are dispersed (Funkhouser, 1917). Finally, in some temperate species with one generation per year, female receptivity within the population is relatively synchronous (Wood, 1980), while in tropical species with several generations per year, there are likely to be receptive females present throughout the year.

In the *Enchenopa binotata* species complex (described in more detail below) the mating system appears to be a "cursorial polygyny" in the classification of Schuster and Wade (2004). This system is characterised by singly-mated, semelparous females that aggregate around resources, and roving males with alternative mating strategies including searching and possibly mate guarding and usurpation of other males. Within the species complex, variation in population density, synchrony of female receptivity and tendency for multiple females to be found on the same branch tip will influence sexual selection on male traits. For example, active mate searching and long-range advertisement signals may be more important in species occurring at lower densities, while mate guarding and male–male signals may be more important in species occurring at higher densities.

Alternative mate-searching strategies are widespread in membracids. When individuals are dispersed, males of many species engage in call-fly behaviour, as described for some leafhoppers (Hunt and Nault, 1991) and cicadas (Gwynne, 1987). In this form of mate searching, a male signals on a series of plants. After arriving at a new location, the male signals and then waits for a few seconds. If the male perceives a female response signal, he will begin to search locally while continuing to signal; if not, he will fly to another location and signal again. If individuals are aggregated, a male may instead remain near a group containing females and engage in close-range courtship. Finally, males may stay in one location and produce a long series of signals, often in alternation with other males (see Hunt and Morton, 2001, for similar behaviour in a leafhopper). In the aggregating treehopper *Vanduzea arquata*, males engage in both call-fly/walk searching and courtship signalling on silent females that they encounter while searching (Cocroft, 2003). In the *Enchenopa binotata* complex, males of at least some species can engage in call/fly searching, extended courtship in contact with silent females and extended chorusing, which involves remaining stationary near other males and signalling in alternation (L.E. Sullivan, personal communication). These different mate-searching strategies are thus not fixed, species-typical behaviour patterns, but rather an aspect of phenotypic plasticity that may be adaptive for individuals which encounter a wide range of social environments. A corresponding plasticity in signal may be equally important.

Treehopper species vary not only in mating systems, but also in their level of inbreeding and outbreeding. Masters (1997) studied two closely related species in Costa Rica (*Umbonia ataliba* and *U. crassicornis*), both of which have extended maternal care of aggregated offspring. *Umbonia crassicornis* is an outbreeding species with high population densities, with mating taking place after dispersal from the natal aggregation (Masters, 1997; see also Wood and Dowell, 1985). In contrast, *U. ataliba* is an inbreeding species with low population densities, with mating taking place between siblings before dispersal from the natal aggregation (Masters *et al.*, 1994). Masters (1997) found that, while *U. crassicornis* experiences inbreeding depression when siblings mate, *U. ataliba* experiences outbreeding depression when nonsiblings mate. She concluded that inbreeding in *U. ataliba* was a form of mating assurance in light of the high costs of mate searching associated with outbreeding in this relatively rare species. Furthermore, sex ratios within broods of *U. ataliba* are female-biased, probably reflecting an adaptation to local mate competition (Masters *et al.*, 1994). These breeding systems will have important consequences for sexual selection and communication, with active mate searching by roving males in *U. crassicornis*, but highly localised competition among siblings in *U. ataliba*. Different traits and signalling behaviour are likely to be important for male mating success in the two species.

MATING SIGNALS AND SPECIATION IN THE *ENCHENOPA BINOTATA* COMPLEX

The *Enchenopa binotata* species complex is a clade of nine closely related species, each occurring on a different species of host plant. The species have not yet been given formal names, and here we refer to them by reference to their host plants. This group has been a model system for the study of sympatric speciation resulting from shifts to novel host plants (Wood and Guttman, 1983; Wood *et al.*, 1990, 1999; Wood, 1993a). The combination of divergent selection and assortative mating facilitates sympatric speciation (Schluter, 2000; Coyne and Orr, 2004). Host shifts result in divergent selection: survivorship of *E. binotata* can drop dramatically when individuals are transferred to a nonnatal host (Wood, 1993a). Changes in host use also lead to assortative mating because life history timing in the *E. binotata* complex is dependent on the phenology of the host plant (Wood *et al.*, 1990). Use of different host plants can thus cause an allochronic shift in the timing of mating, which, in combination with high host fidelity, can reduce mating between populations on different hosts (Wood *et al.*, 1990). However, some interbreeding is still possible due to partial overlap of mating periods and occasional dispersal, especially of mate-searching males. This possibility for gene flow between *E. binotata* populations on different hosts highlights the potential importance of mating signals, which, because of their role in assortative mating, have often been implicated in the process of speciation (West Eberhard, 1983).

Hunt (1994) described the mating signals of one species in the *E. binotata* complex. Males produce complex frequency- and amplitude-modulated signals, and receptive females respond with a simpler signal of their own. Rodríguez *et al.* (2004) used vibratory playback of signals recorded from several species in the complex to ask whether variation among the signals of different species in the complex was important for assortative mating. The authors showed for one species in the complex (*E. binotata* from *Viburnum lentago*) that females responded to signals of conspecific males but discriminated strongly against those of males of the most closely related species in the complex. Given that signals can contribute to assortative mating among extant species, studies are now underway to examine variation in male signals and female preference curves within and between species (unpublished data). These studies will reveal which signal traits are most important in assortative mating, and set the stage for further studies to examine how host shifts influence the evolution of those traits.

Research on *E. binotata* also suggests that the communication system can contribute to assortative mating in the early stages of a host shift before divergence in signals or preferences has occurred. For example, the communication system might contribute to assortative mating if host fidelity is reflected in male mate-searching behaviour, such that males invest less in signalling on nonnatal hosts. Sattman and Cocroft (2003) found that signalling behaviour is indeed influenced by plant identity: male *E. binotata* from *Ptelea trifoliata* produced fewer, shorter signals when on a nonhost plant. This host fidelity in advertisement signalling should have the consequence of reducing the likelihood of mating between host-shifted populations because females prefer males that produce more signals per bout (unpublished data). Mate-searching behaviour is also biased towards host rather than nonhost plants in *U. crassicornis* (Masters, 1997), although males do not alter their signals on nonhosts (unpublished data). Other aspects of phenotypic plasticity could also influence gene flow between host-shifted populations. Because mating periods of populations on different hosts are allochronic (Wood, 1980), interbreeding among host-shifted populations will only be likely between older males from the early population and receptive females from the late population. A decrease in the attractiveness of the signals of older males would reduce this probability. However, Sattman and Cocroft (2003) found no influence of male age on signal variation.

SIGNALS AND GROUP LIVING

FUNCTIONS OF SOCIAL SIGNALLING

For many group-living insect herbivores, vibratory communication may be important for solving the challenges of life on a plant, including avoiding predators and finding feeding sites (Cocroft, 2001). The first evidence that vibratory signals played an important role in treehopper social behaviour came from studies of group-living nymphs of the thornbug treehopper, *Umbonia crassicornis* (Figure 23.1c; Brach, 1975; Cocroft, 1996). Nymphs in this species develop to adulthood in dense, cylindrical aggregations on their host plant stem. Aggregations are attended by their mother, who typically remains stationary at the base of the group. In their exposed locations at the growing tip of a host plant stem, nymphal aggregations are vulnerable to invertebrate predators including syrphid fly larvae, predatory Hemiptera and vespid and sphecid wasps; and because aggregations are stationary, predators can either remain near the aggregation or make repeated visits (Cocroft, 2002). For most predators, the nymphs' principal or only protection is the mother's active defence, which involves wingbuzzing, approaching the predator and kicking the predator with specialised hind legs (Wood, 1983). Mothers travel rather slowly, however, and thus early information on the presence of a predator is critical. Coordinating signalling among the nymphs provides this early information.

When a predator approaches an aggregation of *U. crassicornis* nymphs, the first nymphs to perceive the predator each produce a short vibratory signal. This elicits additional signals from siblings and signalling rapidly spreads across the group, resulting in a coordinated group display. Coordinated displays, to which each individual contributes only one signal, are produced every 1 to 2 sec (Figure 23.4a). In response to a series of group displays from her offspring, a female leaves her usual position at the base of the aggregation and walks into the group attempting to locate and drive away the predator. The offspring continue to produce coordinated signals as long as the predator is present, suggesting that they continue to provide information to the female throughout a predator encounter. The potential fitness benefits of rapid offspring–parent communication are high: a field study in Costa Rica showed that when a female disappeared from an

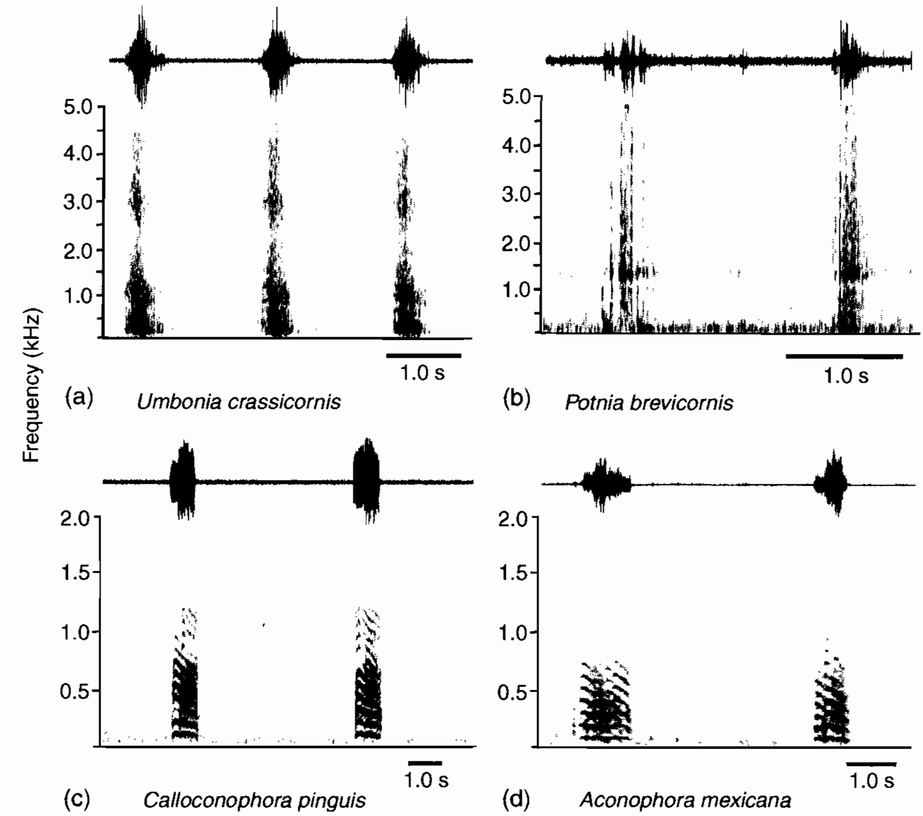


FIGURE 23.4 Signals of membracid nymphs showing conservation of signal form in two pairs of closely related species. *Umbonia crassicornis* (a) and *Potnia brevicornis* (b) are members of the tribe Hoplophorioni; in response to the approach of a predator, aggregated nymphs of both species produce brief, noisy pulses that are synchronised into group displays. *Calloconophora pinguis* (c) and *Aconophora mexicana* (d) are close relatives within the tribe Aconophorini; nymphs in both species produce relatively long, harmonically rich signals that function to recruit siblings to a feeding site. (a–c) recorded using ACC; (d) recorded using PC.

aggregation, attacks by predatory wasps were always successful; while in contrast, when a female was present, she was able to drive away wasps in about 75% of the encounters (Cocroft, 2002).

Although parent–offspring groups in *U. crassicornis* communicate largely or exclusively in relation to predators, the context of communication is very different in family groups of another neotropical treehopper, *Calloconophora pinguis*. Nymphs of this species likewise develop to adulthood in aggregations of siblings (Figure 23.1d), which are usually attended by the mother. Aggregations feed at the base of young, expanding leaves and, as one leaf matures and becomes unsuitable, the group must find another. The process of locating and moving to a new feeding site involves vibratory communication: individuals begin leaving the group and when one locates a suitable feeding site it produces a series of signals (Cocroft, 2005). Other individuals respond to these signals by approaching, and once at the site begin signalling in synchrony with the individuals already there (Figure 23.4c).

It is notable that in both *U. crassicornis* and *C. pinguis*, individuals produce coordinated group displays. One likely causal factor is that in both cases a group of individuals is producing signals that function to influence the behaviour of receivers outside the group. Synchronised signalling is not optimal for within-group communication because other potential receivers within the group would be producing signals at the same time. However, the superposition of multiple signals may increase overall display amplitude and enable receivers outside the group to assess the amount of signalling taking place. Such assessments might be important if female *U. crassicornis* need to assess the degree of threat or if dispersing *C. pinguis* nymphs are faced with deciding among more than one advertised feeding site.

DIVERSITY IN SOCIAL SIGNALS

Social signalling is widespread in membracids and may occur in all group-living species. Where social signals have been recorded from immatures, the signals and signalling behaviour of closely related species are similar, suggesting that social signals are more evolutionarily conservative than male advertisement signals (Figure 23.4). For example, *Umbonia crassicornis*, in which immatures produce group displays in an antipredator context, is a member of a clade with similar forms of offspring aggregations and maternal care (the Hoplophorionini; McKamey and Deitz, 1996). Signals very similar to those of *U. crassicornis* have been recorded not only in congeners including *U. spinosa* and *U. ataliba*, but also in other related genera including *Alchisme* and *Potnia* (Figure 23.4b). All were produced by maternally-defended immatures in response to disturbance (unpublished data). The signals of *Calloconophora pinguis* nymphs (Figure 23.4c; Cocroft, 2005) are very different from those of *U. crassicornis*. However, they are very similar to those of species in the closely related genera *Guayaquila* and *Aconophora* (Figure 23.4d), which are also produced by immatures aggregating at a feeding site (unpublished data). The consistent association of signal form and function is striking — the antipredator signals of *Umbonia* and its close relatives are brief, high-pitched, noisy pulses, while the recruitment signals of *Calloconophora* and its relatives are longer, lower-pitched harmonic series (Figure 23.4). Whether these differences are adaptive given the time scales and distances involved in each communication context remains to be tested.

Social signals are produced not only by immatures, but also by adults. In *U. crassicornis*, as mentioned above, females defending their offspring produce a series of short, percussive "clucks" after the predator has left (Cocroft, 1999). Similar signals are produced by adults in predispersal aggregations (Cocroft, personal observation). Unlike the synchronised signalling by nymphs attempting to elicit their mother's defence, signallers in these adult aggregations actively avoid signal overlap, which suggests that the intended receivers are other group members.

In addition to vibratory signals, group-living membracids also can use chemical cues to assess the presence of a predator (Nault *et al.*, 1974). These cues are released when an individual is injured. It is not known whether the chemical cues involved represent an evolved signal, favoured by selection because of its effect on the behaviour of receivers, or whether receivers have simply evolved the ability to detect incidentally-produced cues from injured conspecifics. It is likely that in social species such as *Umbonia crassicornis*, there is an interaction between vibratory signalling and chemical cues. For example, perception of cues from an injured sibling may trigger vibratory signalling.

SIGNAL PRODUCTION MECHANISMS

While signal production in Membracidae has received little rigorous attention, it is clear that multiple mechanisms underlie the diversity of signals. It is characteristic of the vibratory modality that multiple signal-producing mechanisms can easily be incorporated into an individual signal. Vibratory signals are known to travel with little attenuation along woody stems (Michelsen *et al.*, 1982; Čokl and Virant-Doberlet, 2003). As a consequence, nearly any movement of a body part can result in a signal or cue being propagated a reasonable distance and, hence, detected by other individuals. This is much less likely in airborne signals, where there exist inherent constraints in coupling a mechanical disturbance to air (Bennet-Clark, 1998a). This should leave airborne signallers with fewer signalling options and make it less likely for them to incorporate multiple mechanisms into an individual signal since most movements do not translate into a signal or cue that is loud enough to be biologically useful. Thus, complexity in the airborne signals of insects may be more restricted to variations in temporal pattern (see Bailey, Chapter 8), while complexity in vibratory signals may also involve variation in spectral features where different signal components are produced by different means.

Most of what is known about signal-producing mechanisms in membracids is based on the work of Ossiannilsson (1949), who described a signal-producing system including striated tymbals in the first abdominal segment with associated muscles and muscle attachment points. The tymbals and associated muscles described by Evans (1946, 1957) for two aetalionids closely match those of Ossiannilsson. This tymbal system appears to be homologous with that of cicadas, perhaps representing the ancestral condition from which the dramatic tymbal structures of cicadas evolved.

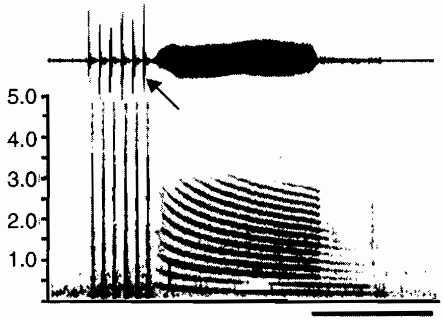
The tymbal mechanism described by Ossiannilsson (1949) and Evans (1946, 1957) presumably is responsible for click-like portions of vibratory signals. Yet as we described above, many membracids also incorporate pure tones or harmonic series which are likely produced by a different mechanism. Tonal signal elements are typically accompanied by the dorso-ventral abdominal tremulation (Virant-Doberlet and Čokl, 2004), which may be powered by the wing muscles. Additional signal production mechanisms in Membracidae are also evident from observations of signalling males (Figure 23.5). In *Vanduzea arquata*, for example, the signal consists of an initial series of taps produced by the male rocking forward and backward and apparently striking its head on the stem, followed by a harmonic series that is accompanied by abdominal tremulation (Figure 23.5a; Cocroft, 2003). In *Atymna querci* the signal contains percussive elements that appear to result from the male striking the substrate with his abdomen (Figure 23.5b). Another example can be found in *Tropidaspis affinis*, where signal production is accompanied by a rapid vibration of the wings (Figure 23.5c). It is clear from examination of the advertisement signals of some species that more than one sound production mechanism is used simultaneously. For example, male *Umbonia crassicornis* produce a frequency-modulated tonal component lasting about a second while simultaneously producing a series of higher-pitched clicks (Figure 23.3b).

Whether variation in pronotal shape has any relationship to variation in the properties of communication signals remains untested (see Montealegre and Morris, 2004, for a relevant study in Tettonigoniidae). A direct relationship between pronotal shape and signal variation seems unlikely given the lack of an airborne sound signal for which the hollow pronotum could serve as a cavity resonator. Furthermore, qualitatively similar signals are produced by species in related groups that lack expanded pronota.

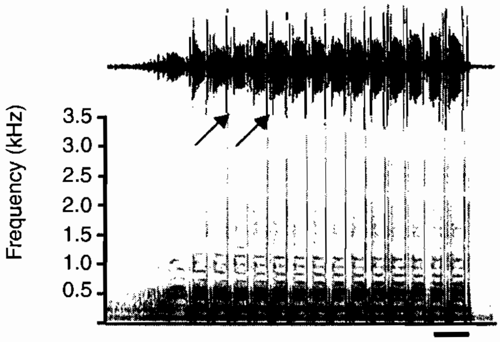
Nymphal treehoppers likely have a diversity of vibration-producing structures given the range of signals they produce. The tymbals of the treehopper *Aetalion reticulatum* (Evans, 1957) are present not only in adults but also in every nymphal instar except the first. Evans (1957) inferred the production of social signals that might function in maintaining group cohesiveness; nymphs and adults in this species do indeed produce rather similar high-intensity, broadband vibratory signals (unpublished data) but their function has not been studied. A different mechanism must underlie the harmonic series produced by nymphs of *Calloconophora pinguis* and relatives. It would be interesting to investigate whether these nymphs use novel means to produce their signals, or whether they are simply using a form of the adult structure at an earlier ontogenetic stage as in *Aetalion*. It can safely be stated that the field of vibratory signalling in general would benefit from more detailed investigations of signal-producing mechanisms.

VIBRATORY COMMUNICATION IN THE FIELD

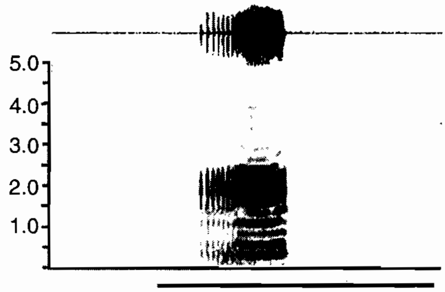
Most research on vibratory communication in insects has been conducted in the laboratory (Claridge, 1985b; Cocroft and Rodríguez, 2005), and studies of membracids are no exception. However, field research is necessary for understanding the social and ecological context in which communication takes place. Although solitary membracids might be difficult to study in the field,



(a) Vanduzea arquata 1.0 s



(b) Atymna querci 1.0 s



(c) Tropidaspis affinis 1.0 s

FIGURE 23.5 Mate advertisement signals of male membracids that illustrate a diversity of signal production mechanisms. In *Vanduzea arquata* (a), a male first produces a series of taps (arrow), apparently by striking its head on the substrate, then a harmonic series accompanied by abdominal tremulation. In *Atymna querci* (b), male signals incorporate percussive elements (arrows) that apparently result from the male striking the substrate with his abdomen. In *Tropidaspis affinis* (c), signal production is accompanied by rapid vibration of the wings. (a and b) recorded using ACC; (c) recorded using PC.

the high density and site fidelity of social species make them excellent subjects for field study. Research on mating behaviour and dispersal in the aggregating *Umbonia crassicornis* (Wood and Dowell, 1985) shows the potential for field study of membracids, as does the career-long series of studies by T. K. Wood on the biology of the *Enchenopa binotata* species complex (see Wood, 1993a). However, to date only one study has examined mate-signalling behaviour in a field study of treehoppers (Cocroft, 2003). This study found a high degree of spatial and temporal variation in the social context experienced by both males and females of the aggregating, ant-tended membracid *Vanduzea arquata*. This variation may be important in influencing the mating decisions of females and the mate-searching strategies of males.

The prospects for field study of antipredator or recruitment signalling are even more promising than for mating behaviour, especially among the immatures where dispersal is limited and groups can persist in the same location throughout nymphal development. Field studies of social behaviour and ant mutualisms have been conducted in several species, but so far only one study has examined social signalling in the field. Cocroft (1999) examined the signalling behaviour of offspring and mothers of *Umbonia crassicornis* during attacks by predatory wasps. This study revealed that, as predicted by laboratory studies, *U. crassicornis* nymphs produce group displays as soon as a predator arrives and continue to display until after the predator leaves. It also revealed behaviour not noticed in laboratory studies, such as signalling by the defending female after the predator had left, or sporadic signalling by mother and offspring at a low rate throughout the day. Furthermore, study of the details of predator attacks revealed which individuals in the group were at highest risk, allowing predictions of how signalling behaviour should vary within groups. Such fieldwork then provides additional predictions that can be experimentally studied in the lab, and the potential for this interplay of laboratory and field studies is one of the attractive features of research on membracids.

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