

Vibrational Communication and the Ecology of Group-Living, Herbivorous Insects¹

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SYNOPSIS. Communication among members of a colony is a key feature of the success of eusocial insects. The same may be true in other forms of insect sociality. I suggest that substrate-borne vibrational communication is important in the success of group-living, herbivorous insects. I examine three challenges encountered by herbivorous insects: locating and remaining in a group of conspecifics; locating food resources; and avoiding predation. Studies of groups of immature treehoppers, sawflies and butterflies suggest that vibrational communication can be important in each of these contexts, enhancing the ability of these group-living herbivores to exploit the resources of their host plants.

INTRODUCTION

The ecological importance of eusocial insects such as bees, ants and termites is due in part to their remarkable ability to monitor changing resources in their environment (Hölldobler and Wilson, 1990; Seeley, 1995; Shellman-Reeve, 1997). The ability of an insect colony to efficiently exploit unpredictable resources is, in turn, based on elaborate systems of communication among colony members. Accordingly, one of the hallmarks of the eusocial insects is that colony members communicate in relation to important features of their environment (Seeley, 1995). The eusocial insects, however, represent only one end of a broad spectrum of insect sociality. Analogous communication systems can exist in very different forms of insect society, as shown, for example, by studies of trail-marking pheromones in group-living lepidopteran and sawfly larvae (Fitzgerald, 1995; Costa and Louque, 2001). Here I will suggest that for some (and perhaps many) group-living insects that feed on plants, substrate-borne vibrational communication is an important component of their ability to exploit host plant resources.

I focus on three challenges faced by group-living, herbivorous insects. First, be-

cause there often are considerable benefits to individuals of living in groups, one challenge is to locate and remain with other individuals. Second, because the location of high-quality feeding sites will vary over time within a host plant, another challenge is to locate currently profitable feeding sites. Finally, herbivorous insects must avoid predation. I will suggest that, in many species, vibrational communication among group members is important for solving each of these challenges.

BENEFITS OF GROUP LIVING

Although there are inherent disadvantages to group living, such as increased competition and risk of disease (Alexander, 1974), plant-feeding insects may benefit in various ways from being in a group. Protection against predators has been proposed to be one of the most general factors selecting for group living (Hamilton, 1971; Alexander, 1974; Vulinec, 1990; Mooring and Hart, 1992). In insects, this might occur, for example, through dilution effects (Foster and Treherne, 1981) or through enhancement of chemical defenses (*e.g.*, Adrich and Blum, 1978). For some herbivorous insects, feeding efficiency is increased by the presence of conspecifics (Ghent, 1960; Kalin and Knerer, 1977; Lawrence, 1990), resulting in faster growth rates and/or greater survivorship. Other benefits of grouping can include increased water uptake (Lockwood and Story, 1986), slower

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water loss (Friedlander, 1965), and enhanced thermoregulation (Seymour, 1974). Indeed, Costa and Pierce (1997) suggest that there may often be sufficient direct benefits of group living that grouping is favored whether or not the individuals are genetically related. One line of evidence supporting this view is that, in many species, groups that encounter each other merge into a larger group composed of individuals from different family groups, species, or genera (Carne, 1962; Wood, 1984, 1993).

LOCATING AND REMAINING IN A GROUP

In some cases, the individuals on the same plant may be in groups from the start, if they hatch from eggs laid in a cluster. However, in other cases, groups are composed of individuals hatching from eggs deposited in different locations (*e.g.*, the treehopper *Vanduzea arquata*; [Fritz, 1982]). Furthermore, groups may move from one location to another (*e.g.*, Carne, 1962). Consequently, individuals will often be faced with the challenge of locating or rejoining a group. Several lines of evidence suggest that this task can be accomplished by means of vibrational communication.

First, is it possible for a small insect to detect the location of a vibration source? In many cases, the answer is yes. There is extensive evidence that insects can locate a vibration source to one of two stems at a branching point (Latimer and Schatral, 1983; Steidl and Kalmring, 1989; Ota and Cokl, 1991; Roces *et al.*, 1993; Pfannenstiel *et al.*, 1995). This ability is not surprising, given the large number of taxa in which males localize receptive females by means of plant-borne vibrations (Michelsen *et al.*, 1982; Markl, 1983; Claridge, 1985; Gogala, 1985; Henry, 1994; Stewart, 1997). There is also indirect evidence that some insects can determine whether a vibration source is in front of them or behind them on a single, unbranched stem (Cokl *et al.*, 1999; see discussion in Cocroft *et al.*, 2000).

What evidence is there that insects use plant-borne vibrational cues to locate a group of conspecifics? Observations suggest that group-living sawfly larvae use vibrational signals to rejoin a moving group from which they become separated. In the

Australian sawfly *Perga dorsalis*, larvae (sometimes called "spitfires") form groups that move not only within a single tree, but also from one tree to another. According to Carne (1962), individual *P. dorsalis* larvae in migrating groups continually assess the presence of nearby individuals by "tapping" with a hardened sclerite at the end of their abdomen: "If an individual strays from the moving column and fails to make contact with another larva, it manifests disturbance by an abrupt increase in its rate of tapping. The larvae in the main body of the colony respond immediately by uncoordinated tapping for a period of 10–15 sec. There is usually an "answering" signal from the stray, then further tapping on the part of the colony. It seems certain that this is a form of communication for it invariably results in the individual rejoining its colony." Once the individual rejoins the colony, tapping activity subsides. Carne (1962) further suggests larvae respond not to the airborne sound, but to the vibration produced by tapping. Evans (1934) suggested that tapping occurs in a similar context during group movements in other species in the genus *Perga*.

A strikingly similar pattern has been observed in the chrysomelid beetle *Polychalma multicava* (D. Windsor, personal communication). In this species, groups of larvae migrate from resting positions at the base of small plants to feeding areas at the tips. When individuals become separated at a branching point, the two groups re-aggregate after back-and-forth bouts of substrate tapping.

Vibrational signaling during group movements may occur in the tingid bug *Corythucha hewitti*, in which groups of nymphs are attended by a female. Faeth (1989) observed that disturbance of the leaf containing an aggregation of *C. hewitti* caused a nymph to stop feeding and move away, "occasionally stopping and vibrating its abdomen in the vertical plane. Other nymphs in the brood followed." Because such abdominal vibrations are involved in signal production in other insects (*e.g.*, Henry, 1994), and because such movements will unavoidably produce a vibration in the substrate, these observations suggest the

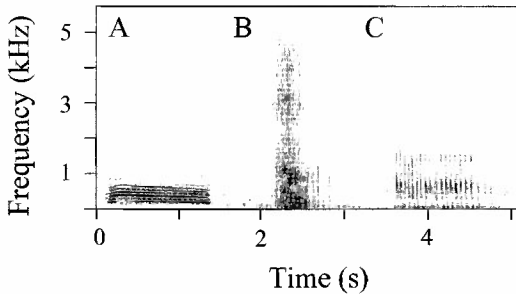


FIG. 1. Audiospectrograms of plant-borne vibrational signals. (A) A signal produced by a nymph of the treehopper *Calloconophora pinguis* after having located a high-quality feeding site; (B) A coordinated, group signal from an aggregation of nymphs of the treehopper *Umbonia crassicornis*, produced in response to the approach of a predator; (C) A series of signals produced by an (unidentified) ant-attended lycaenid caterpillar.

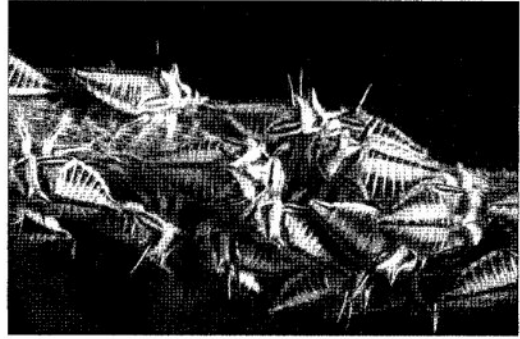


FIG. 2. An aggregation of nymphs of the treehopper *Umbonia crassicornis* on a host plant stem.

production of vibrational signals in the context of group movement.

LOCATING A FOOD RESOURCE

In the membracid treehoppers *Calloconophora caliginosa* and *C. pinguis*, nymphs develop to adulthood in tight aggregations, accompanied at least in the early nymphal stages by their mother (Wood, 1978 [as *Guayaquila compressa*]; R.B.C., unpublished data). These treehopper groups have a nomadic foraging pattern, in which the entire group moves from one feeding site to another. In *C. pinguis*, aggregated nymphs on a stem whose nutritional quality is declining (such as a maturing stem or a cut stem) eventually leave the group and explore the rest of the plant, probing with their mouthparts. When a nymph encounters a suitable feeding site (a new, growing shoot), it stops and produces a long series of vibrational signals (see Fig. 1A). These signals are used by other individuals to locate the new feeding site (R.B.C., unpublished data). Individuals in the dispersing group alternate periods of walking toward the source with periods of quiescence: they wait until a signal is perceived, then walk, then wait for another signal. Individuals that arrive at the site begin to signal in unison with the individuals already there. The alternation of walking and waiting to detect a signal was also observed in sawfly larvae locating a group (Carne, 1962). This signaling system

appears to allow sibling groups to take advantage of changing nutritional resources on the plant. It also shows that locating a feeding site can, in some circumstances, be essentially the same task as locating a group. The only additional requirement for food recruitment is that group-location signals are produced at an appropriate feeding site.

Hograefe (1984) reported that larvae of the sawfly *Hemichroa crocea*, which live in groups on birch and alder, communicate while feeding. A signal is produced as the end of the abdomen is repeatedly scraped against the leaf surface in a characteristic rhythmic pattern. Signaling is more frequent when larvae are on new, undamaged leaves, which represent high-quality feeding sites, and less frequent when larvae are on already heavily damaged leaves. Larvae eventually move from low to high quality sites, apparently orienting by means of the vibrational signals. Again, orientation to a group and to a feeding site are closely related.

DEFENSE AGAINST PREDATORS: PARENT-OFFSPRING INTERACTIONS

In the membracid treehopper *Umbonia crassicornis*, females defend their nymphal offspring from predators. Nymphs develop to maturity in a dense aggregation of up to 100 individuals encircling a host plant stem (Fig. 2). In their exposed position near the tip of a growing shoot, the nymphs are preyed upon by a diverse array of invertebrates such as predatory Hemiptera, syrphid fly larvae, coccinellid beetle larvae, spiders,

and wasps (Wood, 1974, 1976, 1983; Dowell and Johnson, 1986; McKamey and Deitz, 1996; Cocroft, 2002). Females defend their offspring by approaching the predator from their position outside the group, fanning their wings, and kicking with their hind legs (Wood, 1976, 1983; Dowell and Johnson, 1986; Cocroft, 1999*b*). Maternal defense is an important resource for offspring: the female is their only protection against invertebrate predators, and if she disappears the nymphs' chances of survival are low (Wood, 1976; Dowell and Johnson, 1986; Cocroft, 2002).

When a predator approaches, nymphs of *U. crassicornis* produce vibrational signals (Cocroft, 1996, 1999*a, b*). The signal of one nymph is a brief series of pulses, lasting about 50 msec. However, the nymphs within an aggregation coordinate their signals (Fig. 1B). Signaling usually begins on one end of the aggregation (*e.g.*, where the predator first contacts a nymph) and travels across the group in a rapid wave as individuals respond to the signals of their neighbors. As a result, signals of individuals merge into a characteristic group display that is longer and higher in amplitude than the signal of a single nymph (Cocroft, 1999*a*). Females respond to these coordinated signals by quickly moving into the aggregation. In one field study, the combination of signaling nymphs and defending females was successful in repelling about 3 out of 4 attacks by predatory wasps (Cocroft, 2002). The coordination of signals among nymphs is necessary to elicit the female's response (Cocroft, 1996). Because obtaining the benefits of maternal defense requires collective effort, this signaling behavior contains an element of cooperation.

DEFENSE AGAINST PREDATORS: ANT MUTUALISM

Many species of membracid treehoppers, especially in the tropics, have mutualistic relationships with honeydew-harvesting ants (Wood, 1984, 1993). This relationship can have important consequences for membracid survival, because at least some ant species greatly reduce treehopper mortality from other predatory insects (McEvoy, 1979; Fritz, 1982). Ant-mutualism may

have important consequences for membracid social behavior: it is correlated with, and enhanced by, aggregating as opposed to solitary behavior (McEvoy, 1979).

Mutualism with ants, then, will often select for aggregating behavior by treehoppers. In the Neotropics, groups often consist of more than one species (Wood, 1984), again highlighting the likely importance of direct benefits to the grouped individuals. We might expect, then, that ant-attended species will have signals used in the formation and maintenance of groups. Such signals appear to be present in at least some membracid species that form mutualisms with ants (*e.g.*, species in several genera in the subfamily Membracinae; R.B.C., unpublished data).

Vibrational communication is an important component of the mutualism of lycaenid and riodinid butterfly larvae with ants (Fig. 1C; deVries, 1990; Travassos and Pierce, 2000). The signals of larval and pupal lycaenids appear to function in attracting and maintaining an association with ants (deVries, 1991; Travassos and Pierce, 2000). Travassos and Pierce (2000) also tested the hypothesis that signals were involved in the formation of groups; however, their results did not suggest a direct role of the signals in attracting conspecifics. As in these lepidopterans, signaling to attract mutualistic ants might also be expected in membracids. Whether membracids signal to attract ants is unknown, although observations suggest that this may be the case for nymphs of one ant-attended Neotropical species (*Tomogonia vittatipennis*; R.B.C., unpublished data).

GENERAL DISCUSSION

One common feature of many of the communication systems described here (especially in sawfly larvae, membracids, and chrysomelid beetle larvae) is the simultaneous production of signals by multiple individuals. This process also occurs in the chemical signals produced during recruitment communication in some eusocial insects and in tent caterpillars (Costa and Pierce, 1997; Hölldobler and Wilson, 1990). This coordination of signaling may provide a means by which individuals with

a common interest can enhance the signals of other colony or group members (see Costa and Pierce, 1997). However, although group members will often have an overlap of reproductive interests, this will not always be true. Although there may be benefits of group living, these benefits will often be unequally shared among group members (reviewed in Krause, 1994). The nymphal aggregations of *U. crassicornis* treehoppers provide an illustration. Although maternal defense is important in reducing predation, the distribution of predation risk in offspring aggregations is far from uniform. Individuals on the edges of aggregations, and those farther from the female at the time they are contacted by a predator, are substantially more likely to be preyed on than individuals in the center of the aggregation and/or closer to the female (Cocroft, 2002). While there is a clear element of cooperation in offspring signaling, then, the finding that predation risk is unequally distributed suggests that cooperation may have its limits. This would be especially true if offspring are able to influence the female's position during an attack. Although it is currently not known whether competition for access to maternal defense is even possible in this species, it is clear that there is at least the potential for conflict among group members. A divergence of interests may also occur in other groups, such as those of migrating sawfly larvae. For example, if edge individuals are more vulnerable to predators or parasitoids, individuals in that position may be more likely to signal to attract 'strays' than individuals in the center. Indeed, if strays will become edge individuals, shielding those currently on the edges, it is conceivable that edge individuals could compete among each other to attract strays to their location. Carne (1962) reports that after strays had rejoined a migrating group, the only individuals that still signaled were those on the edges of the group.

In other cases, such as in the food recruitment signals of nymphs of the treehopper *Calloconophora pinguis*, it may be in the interests of all of the individuals recruited to a food source to recruit the remaining individuals in the group. If so, then

the joint signaling of these nymphs may indeed represent a case of signal enhancement. Further examination of the costs and benefits of group living, and of the dynamics of signaling, will be needed to resolve the issue. In general, resolving the interplay of cooperation and conflict in the signaling interactions of group members will probably require a case-by-case examination.

In many insect groups, chemical communication plays a role similar to that of the vibrational communication systems described here. In some group-living insect herbivores, chemical cues attract individuals to groups of conspecifics (Aldrich and Blum, 1978). In group-living lepidopteran and sawfly larvae, a complex system of chemical trail-marking underlies their foraging behavior (Fitzgerald, 1995; Costa and Louque, 2001). Chemical cues are often important in anti-predator defense in group-living species, in which alarm pheromones and/or cues associated with injury alert other group members to the presence of a predator (Nault and Phelan, 1984). In some insects with parental care (e.g., the treehopper *Umberia crassicornis*), both chemical cues (Wood, 1976) and vibrational signals (Cocroft, 1999a) can elicit parental defense of offspring, and there is likely to be an interaction between the two kinds of signals in their effect on parental responses to predators.

Although evidence for the role of vibrational communication is anecdotal or lacking for many group-living herbivorous insects, studies of membracids, sawflies, and lepidopteran larvae suggest that this form of communication may represent an important set of adaptations to herbivory. Analogous communication systems may be present in other groups, many of which are known to use vibrational signals in communication in at least some contexts. Parent-offspring communication in response to predators might be especially likely in social Hemiptera, chrysomelid beetles, and sawflies with maternal care (Dias, 1975, 1976; Windsor, 1987; Kudo, 1990; Kudo *et al.*, 1995; Tallamy and Schaeffer, 1997). Vibrational communication among group members might also be expected in taxa such as many lepidopterans (Costa and

Pierce, 1997), some aphids (Williams, 1922; Eastop, 1954), Neuroptera (Henry, 1972), tingid bugs (Faeth, 1989), and ant-attended cicadellids (Dietrich and McKamey, 1990) and fulgoroids (Bourgoin, 1997). Only further study of communication in these fascinating insect societies will reveal the extent to which vibrational communication is a widespread adaptation to the challenges of herbivory in group-living insects.

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