4. Vibrational communication in the "other insect societies": A diversity of ecology signals, and signal functions

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Abstract. Communication is fundamental to social life. In insects, social communication has been extensively studied in the highly social ants, bees and termites, but much less so in the "other insects societies", a diverse assemblage of species that live in groups for at least part of their life cycle. Recent research is uncovering a complex and diverse array of communication systems in these group-living insects, often involving substrate-borne vibrational signals. We provide an overview of the behavioral ecology of vibrational communication in group-living species. We organize our discussion around two fundamental ecological relationships: between group-living insects and their food resources, and between group-living insects and their predators. The relatively few studies conducted reveal both divergence among closely-related species that differ in their ecology, as well as convergence among distantly related species facing similar ecological challenges.

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Introduction

Although most of the literature on insect vibrational communication deals with sexually-selected signals and responses [1,2], many insects communicate vibrationally not just with potential mates, but also with offspring, parents, and other members of their social groups. Insects often spend more time as juveniles than as adults, and the importance of communication in the ecology of immature insects is increasingly apparent. Communication serves a range of functions: defending a territory, advertising a feeding site, soliciting resources from parents, and defending against predators. Social communication in the bees, ants and wasps often involves vibrational interactions, but communication in these eusocial species has been extensively reviewed [2-4]. Here we focus on the "other insect societies," a phrase coined by Costa [5] in his landmark synthesis of the ecology and behavior of this heterogeneous collection of group-living species.

Although far less is known about social communication in the "other insect societies" than in the eusocial insects, some general patterns are coming to light. For social herbivores, plant-borne vibrational communication is important for exploiting food resources, avoiding predation, locating a group, and interacting with mutualists [6]. For insects living in soil or wood, vibrational signaling may be involved in interactions between parents and offspring and in promoting cohesion among group members [5,7]. Species using vibrational communication provide excellent systems for the experimental study of social behavior, because vibrational signals are easy to record, quantify, and manipulate for playback experiments. Furthermore, the diversity of ecological niches exploited by group-living insects provides a remarkable opportunity for comparative study of the evolution of social communication. Here we review the role of vibrational communication in group-living species, both in social interactions among group members and in ecological interactions with predators and mutualists. We consider the role of communication first in foraging, and then in avoiding predation.

Vibrational communication and foraging ecology

The most famous signals of the highly social insects are those that recruit colony mates to a food source. Discoveries of the dance language of honeybees [8] and chemical mass recruitment in ants [9] were pivotal events, revealing the fundamental importance of communication to social life and showing how the spectacular, colony-level responses of social insects can arise from the actions of many individuals. Communication about food

resources also occurs in some of the "other insect societies", where it may be just as important in resource exploitation as in the highly social species. Recruitment signaling has been studied in only a handful of species, but probably occurs in many more. The chemical recruitment signals used by tent caterpillars are the best-known of these food communication systems [10]. Vibrational recruitment signals are currently known only from sawfly larvae and treehopper nymphs, and the role of communication in these nomadic foragers differs from that in the central-place foraging bees, ants and tent caterpillars. Here we review what is known about individual species, and provide some general comments about the communication systems that coordinate foraging behavior. Although there may be examples of food-related signaling in groups of adults, food consumption and growth occur primarily in the immature stages, and all of the examples here involve group-living immatures.

Food recruitment communication in treehoppers

Treehoppers are the only sap-feeding insects known to communicate about feeding sites. Food recruitment using vibrational signals probably occurs in many group-living treehoppers, especially in the tropics [Cocroft and Lin, unpub. data], but it has been best studied in the neotropical *Calloconophora pinguis* [11]. Communication in *C. pinguis* occurs within family groups of nymphs, which hatch from a tight cluster of 50 or more eggs deposited on the surface of a host stem or leaf midrib. Once the nymphs emerge, they remain together during their juvenile period, dispersing several days after adult eclosion. The mother remains with her eggs and offspring and defends them against predators (see Wood [12] for a study of maternal defense in a closely related species).

Nymphs of *C. pinguis* feed on sap in a tight cluster around the base of new, expanding leaves. They are not the only herbivores that prefer actively growing leaves, however; most herbivore damage to leaves occurs during this highly nutritious phase, and one escape from the herbivory targeted at young leaves is to shorten the period of leaf growth. This phenological defense likely imposes strong selection on herbivores for efficient mechanisms of discovering areas of active growth [13]. For *C. pinguis*, leaf growth in the light-gap specialist hosts is rapid enough that most family groups will need to find a new feeding site two or more times during their one-month development to adulthood. These groups thus forage nomadically, moving to a new resource every few days or weeks.

In *C. pinguis*, the exploitation of new, expanding leaves involves vibrational communication among group members [11]. While feeding on a

nutritious, growing shoot, nymphs are uncommunicative. Once that leaf grows to maturity or becomes damaged, however, nymphs engage in a behavior that looks and sounds (after converting the plant-borne vibrations into airborne sound) as if they are 'running in place' – the feet are moved as during walking, but the nymph remains stationary. Nymphs may also walk for a few millimeters, bumping into or walking over other group members. This behavior appears to be contagious; it starts with one or a few nymphs, but waves of restless movements occur every few minutes, gradually involving more and more individuals.

After half an hour or more of waves of motion within the *C. pinguis* group, one or a few nymphs will walk down the stem, though the first nymphs to leave usually turn around and quickly return to the group. Eventually at least one nymph does leave, walking down the stem and up neighboring stems, stopping occasionally to probe with its mouthparts. This explorer's behavior is analogous to that of a scout bee in a honeybee colony.

If a scouting nymph encounters a mature leaf during its exploration, it probes briefly and moves on. When it encounters a growing shoot, however, it settles in and begins producing a short vibrational signal, rich in harmonics, every several seconds (Fig. 1a). The scout's signals propagate along the host plant stems, reaching the group at the old site. Recruits home in on the signals, walking for a few cm after each signal, then waiting to update their directional information with the next signal before walking again. Once a recruit finds the new site, it begins signaling in time with those already there, producing a growing chorus of synchronous signals at the new site. This pattern of group signaling at the new site, alternating with short bursts of walking by searchers, continues until all the nymphs have arrived at the new site. Eventually the group stops signaling, possibly after they no longer receive feedback from the walking vibrations of searchers.

There is no evidence of trail pheromones in *C. pinguis*, although chemical trails are commonly used in other group-living species [5]. Playback experiments show that vibrational cues are sufficient for orientation [11]. Trail pheromones are unlikely in any case: scouts often walk up and down a number of stems before finding a suitable site, and some may fail to find a site. Trail following would only be efficient if scouts laid down chemical cues while returning to the group, but scouts stay and feed at the new site. Under these conditions, vibrational signals that propagate along a direct path between old and new sites provide an efficient means of advertising a feeding site.

Groups of *C. pinguis* nymphs are often, though not always, accompanied by the parent female (Fig. 1a). The adult's role in group moves was not studied by Cocroft [11]. However, in the case of one family observed during

a move in the field (RBC pers. obs.), the female walked to the base of the plant and remained there during the move, potentially to intercept nymphs that walked toward the base. The behavior of female *C. pinguis* is similar to that of females of the chrysomelid beetle *Acromis sparsa*, in allowing offspring to locate new feeding sources [14]. This is as expected, since mobile offspring far outnumber adults in these insect families, and as a group can gain more information about the location of feeding sites.

Food recruitment occurs in a number of other membracid species, including species in the same tribe as *C. pinguis* (Cocroft & Lin, unpublished data [15]). Even among close relatives there is wide variation in the behavioral ecology of food signaling. For example, in a species of *Erechtia* in Amazonian Ecuador (Cocroft & Lin, unpub. data), nymphs feed in small ant-tended groups along leaf midribs (Fig. 1b). A single host plant will often harbor multiple groups. Although all of the individuals in a group may move if the leaf is damaged, it is more common for a single individual to move from one group to another. There does not appear to be any signaling prior to leaving the group, but once the individual begins walking away it produces a regular series of short, harmonically rich signals. If the searcher finds a new site it does not produce recruitment signals. However, when a walking, signaling searcher is near a leaf with one or more feeding nymphs, the searcher's signals are answered by a short series of signals from the feeding individuals (Fig. 1b). These responses appear to function as short-range recruitment signals, elicited by signals from a searching nymph.

Food recruitment communication in sawflies

In sawflies, communication involved in food recruitment and/or group movements to foraging sites is probably widespread, but the use of vibrational signals has only been studied in a few species. In the European sawfly *Hemichroa crocea,* larvae develop in groups of 20-60 siblings, which feed communally on several nearby leaves. Hograefe [16] found that larvae produce vibrational signals while feeding. They extend their normally rolled-up abdomen outward and rapidly bring it back, dragging the modified tip along the leaf surface. These 'substrate-stridulations' produce broad-band scrapes rather than distinctive, harmonically-structured signals like those of *Calloconophora* nymphs, and as a result are probably distinguished from the vibrations produced by wind-driven leaves or falling twigs by their characteristic temporal patterns.

Hograefe's pioneering study provides the only evidence, for vibrational recruitment signals in the "other insect societies", that signals indicate feeding site quality. This is also the only species in which signaling is

continuous throughout the feeding period. Larvae of *H. crocea* feeding on undamaged leaves stridulated at a higher rate than those on leaves that had been mostly consumed. Signaling rate depends not only on leaf quality, but also on the number of individuals feeding on a leaf. As more *H. crocea* larvae joined a group on a leaf and began to signal, the individual signaling rate declined, such that the rate of scraping emanating from that leaf remained relatively constant. A consequence of this adjustment of signaling rate is that searchers will receive a similar amount of recruitment signals from a leaf of a given quality, independent of the number of individuals feeding on that leaf [16]. Once leaf quality declines, signaling rates will presumably drop. Importantly, this information about leaf quality is used by receivers, since searching larvae oriented preferentially toward leaves with larvae signaling at a higher rate.

In larvae of the Australian sawfly *Perga affinis*, studies by Fletcher [17, 18] reveal a fascinating interplay of signals and responses that initiate group movement, maintain cohesion while the group is traveling, and (though this is less well studied) recruit other individuals to a foraging site. Larval *P. affinis* (known as 'spitfires' in reference to their communal defense of ejecting a noxious yellow-green secretion) live in groups that are initially composed of siblings but later include both related and unrelated individuals, as groups frequently merge. Groups feed on *Eucalyptus* leaves at night, spending the day in a tight resting cluster around a stem at a distance from the feeding site. These larval groups thus move daily between a series of different foraging and resting sites, in contrast to the sporadic one-way group movements of *C. pinguis* treehopper nymphs. The first published account of communication in *Perga* is by Evans [19], who observed that individuals rapidly tap the sclerotized portion of their anal segment on the substrate when separated from a group. He also observed that group members respond by tapping, and that the separated individuals relocate their group. Carne [20] suggested that the vibrational component of tapping might provide directional information to the separated individual. Fletcher's work provides the first experimental test of this hypothesis, and reveals additional complexity in the social communication of sawfly larval groups.

Resting clusters of spitfires are mostly quiet throughout the daylight hours. The first indication of an impending move is a wave of 'contractions', produced as each larva quickly twitches its body [17]. Individuals in resting groups are in physical contact, and contractions appear to influence the behavior of neighbors, resulting in a wave of movement that rapidly travels across the group. Group contractions initially occur at a rate of one every 15-30 minutes, increasing in frequency to a rate of one every few minutes prior to a group movement. Individuals spends a remarkable amount of time in this
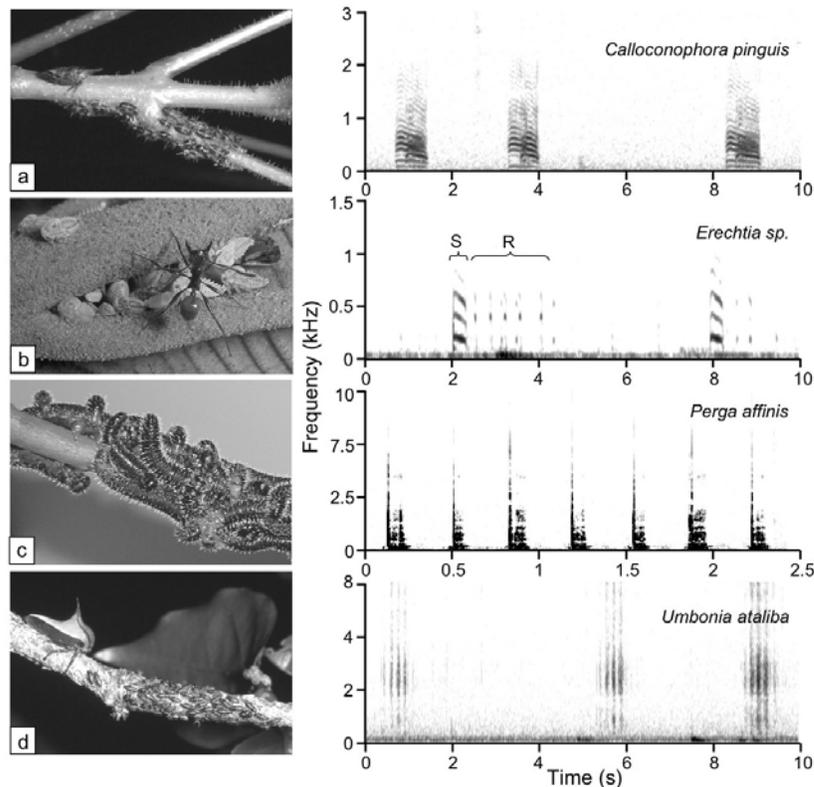
Figure 1. Vibrational signals of group-living treehoppers and sawflies. (a) Female and nymphs of *Calloconophora pinguis* on a new shoot, with synchronous signals produced by two nymphs at a new site; (b) ant-tended aggregation of *Erechtia* sp., with signals produced by searching nymph (S) and responses (R) from feeding nymphs at a nearby site; (c) processionary group of *Perga affinis* larvae, with series of taps from a lone larva (some echoes can be seen on the spectrogram); (d) Female and nymphs of *Umbonia ataliba*, with group signals produced by a small number of nymphs, each signaling once during a group display. Photo and recording in (c) by L Fletcher; others by RB Cocroft.

'pre-foraging' activity; in five colonies studied by Fletcher [17] groups didnot leave the resting site until they had engaged in 1.5 to 4 hours of periodic contractions.

Eventually the spitfires begin to move. Movement is processionary, with individuals remaining in physical contact while moving. Groups move in short stages, with each burst of movement preceded by 2-3 group contractions, then tapping by a subset of the individuals. After a short move, the group becomes stationary again, until the next contractions and taps initiate another movement. Stationary periods allow stragglers to catch up. Individuals that have become separated from the group tap (Fig. 1c) and are answered by the group. Group taps elicit walking and searching by the

separated individuals, and group tap response correlates with the degree of the lone individual's persistence and effort. Fletcher concluded that individuals and groups probably receive mutual but asymmetric benefits if an individual finds and joins a group; i.e. the group may receive a small, incremental increase in benefits (e.g. thermoregulation, protection against dessication, and predator defense), while an individual is likely to perish if it remains solitary.

Once at the foraging site, the large group splinters into smaller groups on several nearby leaves. Short-range food recruitment apparently occurs at the foraging location, at least at the start of the feeding period: when only a few larvae are present on a leaf, they tap until they are joined by more individuals. Fletcher [17] speculates that tapping rates may vary between low- and high-quality leaves, as in *Hemichroa crocea* (above). It is unclear how spitfire groups decide where to forage, or where to rest during the day, though Fletcher [pers. comm.] indicates that groups may split at a branching location and exchange tapping signals before regrouping.

Food recruitment communication in tortoise beetles?

Recruitment to a feeding site using vibrational signals is likely to occur in group-living phytophagous beetles, especially in taxa like the cassidine Chrysomelidae, where group-living larvae are common. Anecdotal observations of two species reveal that both group movements and vibrational signals are present, but so far observations have been limited to the communication involved in group cohesion. In the chrysomelid *Polychalma multicava*, larvae have a nomadic foraging pattern similar to that of *Perga* sawflies: groups migrate from resting sites at the base of their host plant to feeding sites at the tips (D. Windsor pers. comm., as reported in Cocroft [6]). During travel, larvae stay in a compact group; if the group splits at a branching point, it re-forms after back-and-forth tapping of the substrate, as in the groups of larval sawflies studied by Fletcher (above). Pre-foraging communication and recruitment signaling at feeding sites seem likely to occur, but have not been investigated.

In another tortoise beetle (*Stolas* sp.), larvae feed in a dispersed group on several nearby leaves, as in larval sawflies. Greenfield [21] observed that, in response to disturbance of the plant stem, foraging individuals would begin "vibrating". These vibrations apparently led individuals to aggregate in a ring (cycloalexy), with heads pointing inwards. These larvae are "trash bearers", and in some species the shields carried above the body contain chemical defenses [22] that may be more effective when larvae are in a group.

General comments on food recuitment signaling

Recruitment to a feeding site by means of vibrational signals is probably widespread in the "other insect societies", but has only been studied in detail in a few species of sawflies and membracids, with suggestive observations from a few other taxa. Even among these few examples, however, there is a striking diversity of signals and signaling contexts. The communication systems that evolve to coordinate group decisions in nomadic foragers will vary depending on how much coordination there is among individuals when leaving the old site, during travel, and when arriving at the new site (Fig. 2). In the only two species studied in pre-foraging aggregations (*P. affinis* and *C. pinguis*), there are extended exchanges of tactile and vibrational signals, often taking place for an hour or more before the group starts moving. Why this process takes so long is unclear. In the treehopper nymphal groups, one interpretation of the 'running in place' behavior that begins once site quality declines is that individuals are assessing whether the decline is local (in which case moving to another site within the group will suffice), or global (in which case finding and moving to another site is necessary). One reason why the process takes so long may lie in a conflict of interests about leaving the group, since the first individual(s) to leave are likely to face increased predation risk. In sawfly larval groups, it is unclear why the daily pre-foraging signaling period can take up to four hours; perhaps here too there is a conflict of interest, if individuals have different optimal trade-offs between foraging needs and predation risk.

Communication during a move may be restricted to species with a group defense that requires them to stay in close contact. Such a defense occurs in spitfires and possibly in the two tortoise beetle larval groups. In contrast, in nymphal groups of *C. pinguis* there is no group defense, and nymphs leave the old site individually over a period of tens of minutes. Moving individuals walk in response to signals of the scout and new recruits at the feeding site, but decisions about when and where to move do not involve exchanging signals with other group members.

Long-range signaling about the location of a feeding site is so far known only from the treehopper *C. pinguis*. In the other treehopper species (*Erechtia*) and the two sawflies in which recruitment signaling occurs, it is a local process. It was initially surprising that nymphs of this *Erechtia* species did not produce recruitment signals after finding a new feeding site (Cocroft and Lin, unpublished data), given the behavior of related species such as *C. pinguis*. However, further observations revealed that individuals often moved singly, while other members of the group remained at the original site. Recruitment signals are thus only needed by actively searching individuals,
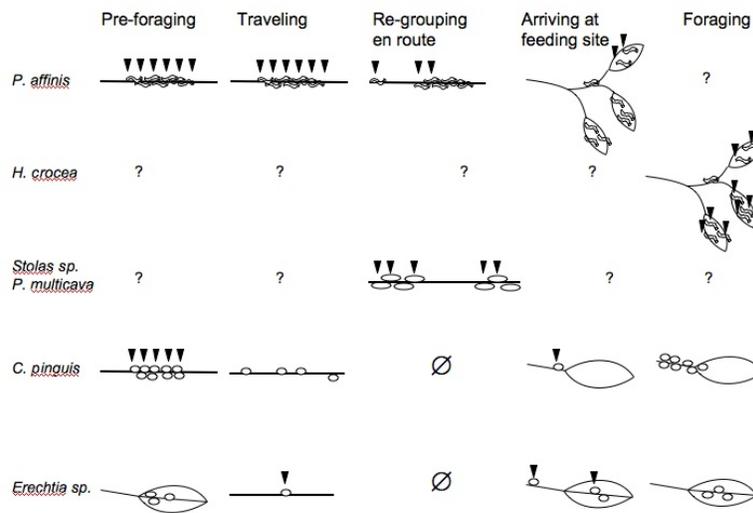
Figure 2. Schematic representation of the contexts in which vibrational signaling occurs in nomadically-foraging species (see text for details). A filled triangle (▼) near an individual indicates signal production, a question mark (?) indicates that no data are available, and the symbol (∅) indicates that signaling does not occur in that context.

whose signals elicit replies from nearby individuals at a feeding site. Whether searching sawfly larvae produce signals that elicit signals from feeding individuals is unknown. It is remarkable that in one sawfly species, *H. crocea*, signaling occurs throughout the feeding period. This would suggest that individuals are continuously moving from site to site within the feeding area, responding to higher signaling rates on nearby leaves. This continual signaling, like that of workers in the leafcutting ants [23], could result in a very efficient use of the food resource by the group as a whole.

Parental provisioning

In addition to the food-related signaling that takes place in nomadically-foraging larval groups, signaling to solicit food from a parent occurs in a range of species with maternal care. For a summary of social insect species with parental provisioning and the corresponding modality used by offspring for begging, we refer readers to the recent excellent review by Mas and Kölliker [7]). Currently, studies of vespid wasps provide the only documented examples of vibrational communication involved in parental provisioning. Recent work by Suryanarayanan and Jeanne [24] and Brennan [25] on *Polistes* spp. (Hymentoptera: Vespidae) has explored the function of

vibrational signals between queens and larvae during feeding. In other vespids (*Vespa orientalis*), larval scraping solicits feeding from workers [26].

Offspring signaling for parental provisioning is a nascent field of research for social insect taxa. Mas and Kölliker [7] point out that we have robust, testable evolutionary theory on parent-offspring conflict, but that most of our current information is from altricial birds, a group where offspring solicitation is obligate. We agree with Mas and Kölliker that the "other insect societies" include great variety both in parent-offspring communication and in degree of parental provisioning, which may be non-existent, facultative, or obligate. Accordingly, insects permit a wide range of experimental manipulations to tease apart the contributions of communication and parental provisioning to offspring survival. Mas and Kölliker point out that chemical communication is the most widely documented signaling modality in insects, but several of the taxa they list may be using multimodal communication, and for many taxa the signaling modality used to solicit parental resources is unknown. We suggest vibrational communication as a likely candidate in such cases.

Vibrational communication and predator-prey interactions

Group-living insects communicate not only about food, but also about predators. Antipredator communication probably occurs in "larval societies" such as the *Stolas* beetle larvae that vibrated and aggregated when their branch was disturbed (discussed above [21]). However, it has been best studied in species with maternal care.

Antipredator signaling and parental care

Maternal defense has been documented in several species of treehoppers (Hemiptera: Membracidae) (see Lin [27] for a review). In many species, treehopper families (i.e. mother and nymphs) occur in groups on plant stems and are mainly sedentary through juvenile development. Cocroft [28] found that the aggregated offspring of *Umbonia crassicornis* and *U. spinosa* produce synchronous, vibrational signals that elicit defensive behaviors from their mother (e.g. kicking, wing-buzzing, and signaling). Maternal defense is effective at deterring predators: in three studies of predation on *Umbonia* nymphs by vespid wasps, females drove away the wasp in $\geq 90\%$ of attacks [28-30]. In contrast, when wasps attacked aggregations from which the female was absent, they succeeded in removing a nymph in over 75% of attacks.

The group signals of *Umbonia* nymphs (Fig. 1d) are produced as a wave of signaling behavior sweeps through the group, initiated by the individuals nearest to the predator. The transmission of signaling behavior probably occurs through tactile cues, as with the wave of contractions that travels through a group of spitfires (and as with the sawfly larvae, individual *Umbonia* nymphs signal only once during each wave). Nymphs not only produce a short, pulsed vibrational signal, but also rock from side to side, and this rocking often brings an individual into contact with one or more neighbors.

Umbonia nymphs signal during predator encounters, whereas parent females signal after encounters end [31]. The functions of female signals are unknown. We hypothesize that female signals inhibit nymphal signaling, but they may also influence predator behavior. Signaling between female parents and predators may also occur in other species. Female burrower bugs (*Adomerus triguttulus)* drive away ants while guarding eggs, and respond to ants and light touching with forceps with abdominal vibration [32]. As in *U. crassicornis*, it is unknown whether *A. triguttulus* female vibrations are directed to predators, offspring, or both.

The defensive behavior of female *Umbonia* is effective only at close range, requiring the female to make contact with the predator. Information about the predator's location is thus very important to successful defense. What sources of information does the female have about where the predator is, once it has made contact with the brood? For large, active predators such as vespid wasps, visual cues are likely the main source once the female is alerted to the predator's presence. For smaller predators such as pentatomid bugs or syrphid fly larvae, the predator will be shielded from view by intervening nymphs. Furthermore, predators both large and small will be out of visual range if they are on the opposite side of the stem from the female.

In light of the importance for the defending mother of finding the predator, Ramaswamy and Cocroft (in press) investigated whether the collective signals of the nymphs provide localization cues to the defending mother. Predator attacks occur almost entirely on the two ends of these cylindrical aggregations [30], so the primary task of the female is to decide which end of the aggregation to approach. There were indeed localization cues in the synchronous vibrational signals of nymphs evoked by simulated predator attack (light contact with a watercolor brush). Nymphs closer to the predator were more likely to participate in a group signal than those farther away; and more individuals contributed to the signal when the predator attacked the far end of the aggregation from the mother's usual resting place at the base. Current research is investigating the female's ability to extract information about predator location from the group signaling behavior of nymphs.

Anti-predator protection through communication with mutualists

Insects can obtain protection from predators not just from conspecifics, but also from heterospecific mutualists. Indeed, the food-for-protection mutualism between ants and honeydew-producing insect herbivores is so widespread, and so influential in the structuring of arthropod communities, that it has been called a "keystone interaction" [33]. Ant-hemipteran interactions are especially common in the tropics, occurring on over 60% of trees surveyed in an Amazonian forest [34]. Given the importance of the interaction for both parties – ant attendance often has a dramatic effect on survivorship of honeydew-producing insects, and a hemipteran colony can be an important resource for an ant colony – we can expect mechanisms that allow each partner to maximize the benefits and reduce the costs of the mutualism.

Among vertebrate mutualists, mechanisms for negotiating interactions among parties include communication. Perhaps the most famous example is the communication between avian honeyguides and their human mutualists. The resource in question is a beehive, and information about the hive's location (possessed by the honeyguide) is exchanged for access (provided by humans) to the honey and wax it contains. The vocal signals and flight behavior of honeyguides reveal the distance and direction to the beehive, and its human followers provide auditory feedback to indicate their approach [35]. We can likewise expect sophisticated communicative interactions among insect mutualists, which typically share communication modalities (chemical and vibrational) and belong to lineages with a history of ecological interactions extending over tens of millions of years [36].

Here we use the framework of Kostan [37] for classifying the nature of communication between mutualists. She describes four 'stages', differing in the degree to which the mutualism has shaped the evolution of receivers and signalers. In the first two stages, there has been evolution of receiver mechanisms in one or both species to exploit incidental information provided by communication among members of the other species. This use of incidental information is analogous to predator eavesdropping on prey signals [38,39]. In the second two stages, there has been evolution of signaling behavior (in one or both parties) whose evolved function (*sensu* Otte [40]) is to influence the behavior of mutualists.

Eavesdropping interactions (Kostan's stages 1 and 2) between group-living treehoppers and their ant mutualists are almost inevitable. Both taxa use vibrational signals in social communication, and the frequency range and

amplitude of their signals overlap. In various studies where ants were exposed to broad-band substrate vibrations, the ants have investigated the source of the vibration [41-43]. Because the social signals of treehopper nymphs falls within the perceptual range of their mutualist ants (Cocroft & Lin unpublished data), and because many treehopper signals are similar to those known to attract the attention of at least some ants, ants are likely to respond to treehopper intraspecific communication. Treehoppers, in turn, will perceive the vibrational signals exchanged among tending ants, which might provide information about the number of ants present or whether the ants are fending off a predator.

In treehoppers with ant-tended nymphs, exclusion experiments and correlational studies have consistently shown that ant attendance dramatically increases nymphal survivorship [44-49]. Accordingly, there is likely to be strong selection favoring treehopper behavior that attracts mutualist ants, as in the riodinid and lycaenid caterpillars [41]. One such behavior was found in the Brazilian *Guayaquila xiphias*, which flicks honeydew onto the ground around the host plant; ants that encountered honeydew droplets on the ground climbed onto the host plant and began tending nymphs [50]. Whether nymphs of *G. xiphias* or other species use vibrational signals to attract ants is unknown, though Cocroft [6] reported anecdotal observations of ant-tended membracid nymphs in Panama (*Tomogonia vittatapennis*) whose behavior is a good candidate for ant attraction. When tending ants were removed, *T. vittatapennis* nymphs dragged the base of the anal tube on the substrate, waved its long, contrastingly-marked anal tube over the body, and produced a long series of vibrational clicks (Cocroft, unpublished data).

Maternal care is frequent in ant-tended treehoppers [27, 51], and McEvoy [44] proposed that maternal attendance of early-instar nymphs may function to attract ants rather than to defend nymphs directly. This hypothesis was supported by a study of Billick et al. [52] on the North American *Publilia modesta*: ant attendance increased nymphal survivorship but maternal attendance did not. If the major function of maternal care in such species is indeed to initiate contact with ant mutualists that will tend offspring [53], then vibrational signals provide a potential (and as yet unexplored) mechanism.

The first experimental demonstration of communicative interactions between treehoppers and ants was provided by an elegant study of the North American *Publilia concava* [43]. Female *P. concava* guard egg clutches and nymphs, and multiple females with clutches can often be found on the same host plant. Morales et al. [43] showed that females guarding nymphs produced signals in the presence of a predator. The authors introduced either a predatory coccinellid beetle or a mutualist *Formica* ant onto plants

containing a single female with nymphal offspring. Females produced series of short, broad-band signals when approached and contacted by the predator, but not when approached by an ant. The authors then tested the response of mutualist ants to membracid signals, in one of the first vibrational playback experiments ever conducted in the field. The number of patrolling ants increased in response to playback of maternal signals, but not to playback of male advertisement signals. Alarm signaling by female *P. concava*, then, has probably evolved at least in part because of its effect on mutualists. It is worth noting that these signals likely have social functions as well (e.g., to communicate with offspring or other females tending brood on the same plant), so further research will be required to determine the extent to which ants are eavesdropping on membracid-to-membracid communication (Kostan's stage 1), vs. membracids signaling to attract ants (Kostan's stage 3).

Larvae and pupae of many species of riodinid and lycaenid caterpillars have mutualistic relationships with ants, which provide protection against predators and harvest secretions from specialized glands [54]. DeVries [41] discovered that larvae produce vibrational signals that attract mutualist ants, and that larval vibrational signaling is widespread in the Riodinidae and Lycaenidae [55]. In some lycaenids, larvae and pupae occur in aggregations [56], and Travassos and Pierce [57] tested both an ant-attraction hypothesis and a conspecific-attraction hypothesis for the function of larval signaling. Only the ant-attraction hypothesis was supported in that study, but the potential role of vibrational signals in larval social behavior deserves further exploration.

Vibrational signaling to predators?

Among the potential receivers of signals produced in the presence of a predator is, of course, the predator itself [58]. Masters [59] investigated whether insect stridulations deter attacking invertebrate (spiders) and vertebrate (mice) predators. Insects producing defense stridulations experienced shorter attacks from both spiders and mice than did silenced insects. Although the three insect species Masters used in the experiment are known for producing airborne signals through stridulating, it is likely that the vibrational component of these signals also plays a role. To mimic vibrations that are transferred through a stridulating insect's cuticle, Masters included a treatment where a vibration probe was presented to spiders. Spiders ended attacks more rapidly with vibrating probes than with silent probes. Masters suggests that such signals may function to startle predators or to alert predators that further defenses (e.g., stings or other chemical defenses) are forthcoming. In some group-living species (e.g., sawflies; Hograefe [16]),

disturbance vibrations are produced by multiple individuals, and such group displays might be especially effective at disconcerting predators. Another possible example of a group disturbance display was observed in a chemically-defended phasmid in Florida, USA; in a large aggregation of male-female pairs, multiple males drummed their feet on their palmetto substrate, producing an audible signal [60]. The context of this group signaling, however, is unclear.

Tupelo leafminers (*Antispila nysaefoliella*) often occur at high densities, with multiple individuals per host plant leaf. Larvae produce two types of vibrational signals, and one of the signal types is produced most often in the presence of searching parasitoid wasps [61]. Because parasitoid wasps are likely to be a strong selective agent on leafminers and because miner larvae can detect characteristic vibrations produced by searching wasps [62], the leafminer's vibrational signals probably have a defensive function.

Group living and predator eavesdropping

We have described a number of communication systems that have likely evolved in response to the threat of predation, with signaling occurring between parents and offspring, among offspring within a brood, between insects and their ant mutualists, and between insects and their predators. Predators can also locate prey by eavesdropping on signals [38,39], and this cost of communication may be especially high in group-living species. Consider, for example, the vibrational beacon produced by a group of *H. crocea* sawfly larvae that continually produce scraping signals while feeding. In addition to the signals of group-living species, other activities such as locomotion during daily migrations between resting and feeding sites can also produce vibrational cues detectable by predators. These potential risks of social life have not been assessed for group-living insects, but here we suggest that predation risk is likely to be an important cost of vibrational communication and group movement.

Predators may gain detailed information about the identity and location of the organism producing the vibration, from both signals and incidental vibrations (e.g. from chewing or walking). Pfannenstiel and Hunt [63] found that a predatory pentatomid (*Podisus maculiventris*) orients to substrate vibrations produced by both real and recorded feeding caterpillars (*Plathypena scabra*), a common prey item. The authors suggest that for walking invertebrate predators in complex plant habitats, vibrational cues provide important information for foraging decisions, as vibrations may propagate farther than predators can see and faster than odor plumes can travel.

It is important to keep in mind the ecological diversity of insects that have access to incidental vibrations and vibrational signals. Whereas *P. maculiventris* eavesdrops on incidental vibrations of potential prey, parasitoids eavesdrop on courting pentatomids [64]. Brown stinkbugs *(Euschistus heros)* engage in vibrational duets when courting mates, and *Telenomus podisi* (Hymenoptera: Scelionidae) orient to the songs, particularly to female *E. heros* signals. *Telenomus* is an egg parasitoid. The authors suggest that *T. podisi* uses female *E. heros* signals to find areas likely to have eggs, and that once in such an area, chemical and/or visual cues may play a more important role.

Spiders use vibratory cues in predation, attending to both incidental vibrations and communication signals of their prey [65,66]. Roberts et al. [67] showed that combining seismic signals with visual signals in courting wolf spiders (*Schizocosa ocreata*) increased the response speed for a natural predator, also a spider (*Phidippus clarus*; Salticidae). Multimodal signaling in many taxa where one modality is vibrational may act similarly, increasing the overall detectability of prey.

Studies by Meyhöfer et al. [68,69] were prompted by observations that a parasitoid wasp, *Sympiesis sericeicornis* (Hymenoptera: Eulophidae), is very successful when hunting for its hosts, a species of leafminer (*Phyllonorycter malella* (Lepidoptera: Gracillariidae)). After landing on a leaf with multiple mines, the parasitoid does *not* probe to determine which mines are empty versus occupied. Somehow the wasp visits every potential host but seldom wastes time on empty mines. The authors showed that vibrations produced by a leafminer provide reliable information on both the life stage and the current activity of an individual [68]. A review by Meyhöfer and Casas [70] suggests that parasitoid wasps from at least three different families use the information in leafminer vibrations. Djemai et al. [71] confirmed this for *Sympiesis sericeicornis*, which increased their foraging time and oviposition effort in response to synthetic vibrations alone. The authors here note that *S. sericeicornis* parasitizes up to 72 species, most of which reside in mines or similar leaf microhabitats. Leaves may contain multiple leafminers [61], suggesting a complex vibrational environment where hosts presumably detect other hosts' vibrations, parasitoids detect host vibrations, and hosts detect parasitoid vibrations (see next section).

Predator detection in group-living species

The incidental vibrations generated by a walking predator may provide sufficient cues for potential prey to adopt defensive strategies. From the leafminer-parasitoid relationship described above, Djemai et al. [62] showed

that miners responded evasively to synthetic vibrations typical of foraging *S. sericeicornis.*

How much information about the predator is available to prey through incidental vibrations? Castellanos and Barbosa [72] calculated average peak frequencies for substrate vibrations generated by invertebrate predators (*Polistes fuscatus* and *Podisus maculiventris*), vertebrate predators (*Parus bicolor*) and walking herbivores **(***Orgyia leucostigma, Oncometopia orbona* and *Acanalonia conicai***)**. The authors played these frequencies back to caterpillars (*Semiothisa aemulataria*). Defensive behavior for geometrid larvae includes dropping and hanging from the plant by silk they have produced. Hanging increases larvae survival during predator attacks. Larvae discriminated between the playbacks of walking invertebrate predators, walking herbivores, and vertebrate predators, only dropping and hanging in response to walking invertebrate predators. Moreover, larvae dropped three times as far from the branch in response to playbacks of a flying invertebrate predator (*P. fuscatus*) as they did for the walking invertebrate predator (*P. maculiventris*). This differential response resulted in larvae hanging well outside the search radius of wasps and outside the reach of walking *P. maculiventris*, but without unnecessary silk production.

Dropping from a branch as a means of escape is not restricted to lepidopteran larvae. Aphids will also drop from a branch to escape predation. Dropping is costly for aphids, which face dessication and predation by predators on the ground. Roitberg and Myers [73] and Clegg and Barlow [74] showed that pairing a vibrational stimulus with alarm pheromone dramatically increased the percentage of pea aphids that dropped from a branch, compared with response to alarm pheromone or the vibrational stimulus alone. Some aphid predators, such as coccinellid larvae, will prey on an aphid aggregation multiple times [75] or on multiple aphids during one visit. Roitberg and Meyers suggest that the vibration and alarm pheromone act synergistically to simulate a nearby, struggling aphid. In other words, aphids may wait to take the high risks associated with dropping from a branch until predation seems certain.

The ability to discriminate among predator types based on vibrational cues may be widespread in insects. Losey and Denno [76] found that aphids dropped from a branch in responses to vibrations produced by some predators, but not others. The coccinellid *Coccinella septempunctata* elicited the most dropping responses from aphids and is also much heavier and more active than the other three predator species (*Orius insidiosus*, *Nabis americoferus* and *Geocoris punctipes)* included in this experiment. The authors are careful to note the difference in behavioral response by the aphids may be due to the amount of alarm pheromone produced by the aphids, the

substrate vibrations produced by the predator acting as a cue for the aphids, or an interaction between both factors.

Concluding remarks

Group living occurs in a large diversity of insect species in more than a dozen orders [5]. "Reciprocal communication of a cooperative nature" is the defining feature of sociality [77], and we are confident that some form of communication occurs in each of these insect groups. In spite of the centrality of communication to social behavior, however, there have been very few experimental studies of communication in the "other insects societies." Where social communication has been studied, it often occurs through chemical signals [10], but it is increasingly clear that there is a world of vibrational signaling among group-living insects, a world that is only beginning to come to light.

Vibrational communication provides a unique set of constraints and opportunities [2, 78] and some of these are illustrated by the examples we discuss above. For example, insect vibration receptors are in the legs, and as a result, a walking insect will be less able to detect and localize a vibration than an insect with all of its legs in contact with the substrate. This simple constraint shapes any communicative interaction that requires one individual to find another, and is revealed in the episodic movement of receivers responding to signals. For treehopper nymphs responding to a scout at a new feeding site, periods of listening for a signal alternate with short bouts of walking. For defending female treehoppers responding to the group signals of their nymphs, approaching the predator is a slow process, because when the female cannot see the predator she needs to stop and wait every few seconds, to update her information with the next offspring signal. For sawflies traveling from a resting to a feeding site, regular pauses allow stragglers to be detected by their colony mates, as they signal their need to rejoin the group.

Insects homing in on the vibrational signals of colony mates not only have to pause and detect the signals; they also have to locate them. Mechanisms of vibration localization are unknown for very small species, for which the time and amplitude delays between vibration receptors in fore- and hind-legs are vanishingly small [79, 80]. Social interactions such as food recruitment in very small insects are thus dependent on the presence of reliable mechanisms for determining the direction of propagation of a substrate vibration. With so little known about either social communication or localization mechanisms in group-living insects, we currently have no insight into how the ability to locate other group members may depend on

size, or how this potential constraint may influence the evolution of social interactions.

Perhaps the most striking pattern to emerge from our survey of social communication is the diversity of signals and signaling contexts even among closely related species. Why do some nymphs of some treehoppers advertise a newly found feeding site, while nymphs of close relatives do not? Why do larvae of some sawflies signal continuously while they are feeding, while larvae of other species do not? In addition to differences among close relatives, there are similarities among distant relatives. The long bouts of pre-foraging communication in treehopper nymphs and sawfly larvae surely represent convergent adaptations, although we do not yet know enough about the dynamics of information sharing in these social groups to understand why they behave as they do. Clearly the diversity of ecology and communication in the "other insect societies" provide exceptional opportunities for comparative study of the evolution of communication. As yet, however, no group has been sufficiently well studied to allow us to exploit this opportunity.

Acknowledgements

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