

Intracolony vibroacoustic communication in social insects

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Abstract Vibrations and sounds, collectively called vibroacoustics, play significant roles in intracolony communication in termites, social wasps, ants, and social bees. Modalities of vibroacoustic signal production include stridulation, gross body movements, wing movements, high-frequency muscle contractions without wing movements, and scraping mandibles or tapping body parts on resonant substrates. Vibroacoustic signals are perceived primarily via Johnston's organs in the antennae and subgenual organs in the legs. Substrate vibrations predominate as vibroacoustic modalities, with only honey bees having been shown to be able to hear airborne sound. Vibroacoustic messages include alarm, recruitment, colony activation, larval provisioning cues, and food resource assessment. This review describes the modalities and their behavioral contexts rather than electrophysiological aspects, therefore placing emphasis on the adaptive roles of vibroacoustic communication. Although much vibroacoustics research has been done, numerous opportunities exist for continuations and new directions in vibroacoustics research.

Keywords Ants · *Apis* · Behavior · Johnston's organ · *Polistes* · Social bees · Social wasps · Subgenual organ · Stridulation · Substrate vibration · Termites · Waggle dance

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Introduction

Social life in insects requires communication between and among individuals on colony membership, group-level responses to environmental stimuli, and inter-individual interactions such as dominance. From an evolutionary perspective, communication in social insects might be thought of as part of a colony's "extended phenotype" sensu Dawkins (1982), and variation of the extended phenotype among colonies can have played a major role in the social insect evolution (Hölldobler, 1999). From an empirical perspective, social insect colonies can be understood to be group-level adaptive units with special systems of communication (Seeley, 1997). Therefore, to know and understand the modalities of intracolony communication and the roles they play is necessary for a full understanding of social insect biology.

While chemical communication by various means constitutes the primary category of intracolony communication modes in social insects (Richard and Hunt, 2013), there is another major category, 'vibroacoustic' communication, that incorporates communication modes that play significant roles in the lives of social insects. Social insects communicate via sight, sound, and jets of air as well as "knocking, stridulation, stroking, jerking, wagging, grasping, and antennation" (Hölldobler, 1999). Knocking, stridulation, jerking, wagging, sound, and jets of air all generate wavelike displacements of a medium that is disseminated from a point of origin. Sounds and jets of air are disseminated through air and the other vibrations through a substrate. Kirchner (1997) reviews acoustical communication in social insects and gives examples of sounds audible to humans that have been analyzed with regard to their electrophysiological characteristics. He notes, however, that sound has been shown to play a communication role only in

the recruitment dances of *Apis mellifera* (Michelsen et al., 1992). In all other instances, social insects “hear” only substrate vibrations. Because sounds and vibrations are often not easily demarcated from one another, they can be collectively encompassed by the term ‘vibroacoustic.’

Vibrational communication serves a great diversity of adaptive roles in animals (Hill, 2001, 2009). It is common and diverse in insects (Cocroft, 2011; Stewart, 1997; Virant-Doberlet and Čokl, 2004), and surprising adaptations are being found with increasing frequency as attention is given to vibrational communication. Male water striders use vibrational signals on the water surface to attract swimming predators and thereby intimidate females into accepting copulations (Han and Jablonski, 2010). A vibration signal of male treehoppers can competitively mask the courtship vibrations of other males (Legendre et al., 2012). Substrate-borne vibrations are the first step, as it were, in the courtship behavior of *Drosophila melanogaster* (Fabre et al., 2012).

Vibroacoustic communication occurs in social Hymenoptera and is widespread in Isoptera (Cocroft and Rodríguez, 2005). In some situations, such as alarm signaling in termites (Kirchner et al., 1994), substrate vibrations can disseminate information quickly, and vibrational behaviors are the major means of communication in *Polistes* paper wasps (Jeanne, 2009). In these and other cases among social insects, modalities of vibroacoustic communication are not a second-best substitute for chemical communication but instead have high adaptive value on their own merits. Accordingly, vibroacoustic communication is receiving increased attention for the important roles it plays in the lives of social insects (Casacci et al., 2013).

Studies of vibroacoustic communication in social insects often focus on a single taxon or communication modality, thereby inhibiting a broader view of the diversity and adaptive roles of vibroacoustic communication in social insects. Accordingly, the present review brings together literature on multiple vibroacoustic modalities of intracolony communication in termites, social wasps, ants, and social bees. Although each modality can be part of a multimodal signal (Hölldobler, 1999), the focus of this review is on the separate modalities themselves and exclusively on their use as communication modes within the hive or nest, omitting their possible uses outside the colony. The review emphasizes descriptions of the modalities and their behavioral contexts rather than electrophysiological aspects, thereby bringing attention to the adaptive roles of vibroacoustic communication. Emphasis is placed on recent literature, but earlier literature is included to cite taxon-specific studies or when the citation addresses a topic that has not been recently treated. Access to earlier literature can be found in Markl (1983), Gogala (1985), Hölldobler and Wilson (1990), and Kirchner (1997). Hrcir et al. (2006a) review literature with an exclusive focus on bees. The

present review is aimed at a general audience with knowledge of social insects rather than to specialists in social insect communication. The goal of the review is to foster wider knowledge and appreciation of the diversity, characteristics, and adaptive roles of vibroacoustic communication in the four major taxa of eusocial insects.

Means of generating vibroacoustic messages

Most vibroacoustic messages are generated by unspecialized morphological features that have little, if any, modification for adaptive roles in intracolony communication. In these cases, vibroacoustic modalities of communication can be thought of as exaptations sensu Gould and Vrba (1982) that have adaptive values that were not components of the adaptive evolution of the structures that produce the messages. Jerking and wagging the body while standing on the substrate require no special modifications. Wing vibrations can generate substrate vibrations. Wing muscle contractions without corresponding wing movements transmit vibrations via the substrate and via inter-individual contact. The sclerotized head capsules of termite soldiers generate vibrations when tapped against the substrate. Vibrations are generated as the mandibles of dry wood termites (Kalotermitidae) bite wood for feeding and extension of their gallery system. Each of these will be described and discussed in sections of the review in which they apply. A specialized morphological adaptation found in some ants that serves a vibratory communication function is the file and scraper stridulation structure. Vibrations generated by all of these means are often audible to humans; therefore, they are often described as sounds. Study methods applicable to sound analysis such as wave oscillation frequency and amplitude have been used in the study of social insect vibroacoustic communication.

Means of perceiving vibroacoustic messages

Insects perceive vibroacoustic signals via sensilla, which are sensory receptors innervated with one to several neurons. There are at least ten structural varieties of sensilla (Horridge, 1965). Trichoid (hair) sensilla are sensory hairs or setae that project outward from the cuticle and serve as receptors in several sensory modalities including tactile, auditory, gustatory, and olfactory (Horridge, 1965). Studies of the structure and functioning of hair sensilla in social insects include the termite *Hodotermopsis sjostedti* (Ishikawa et al., 2007); the ant genera *Diacamma* (Gronenberg and Peeters, 1993), *Myrmica* (Gronenberg et al., 1998), and *Odontomachus* (Gronenberg and Tautz, 1994; Ehmer and Gronenberg, 1997); the wasp *Paravespula* [*Vespula*] *germa-*

nica (Agmon et al., 2006); and the honey bee *Apis mellifera* (Scheiner et al., 2005).

Chordotonal organs, which are found in all members of class Insecta, are a category of mechanoreceptor sensilla that respond to stimuli ranging from gross motor movements to sound and convert these to neural impulses (Field and Matheson, 1998). Three major categories of chordotonal organ are the tympanal organ, Johnston's organ, and subgenual organ. Tympanal organs are absent in Hymenoptera (Hoy, 1998), and a report of a tympanal structure in the termite *Zootermopsis angusticollis* is questionable (Yack and Fullard, 1993), but significant roles in the lives of social insects are played by the Johnston's organ, which is found in all adult insects, and the subgenual organ, which is present in some but not all insect orders (Chapman, 1998). The Blattodea, including termites, and Hymenoptera, including wasps, ants and bees, have subgenual organs. The Johnston's organ (Fig. 1a) is neuro-sensitive to deflections of the antennal flagellum, air movement, and sound (Dreller and Kirchner, 1993; Yack, 2004; Nadrowski et al., 2011). Studies of the structure and functioning of the Johnston's organ in social insects include the termite *Z. angusticollis* (Howse, 1965), the wasps *A. pallipes*, *P. paulista*, and *M. cassununga* (Santos et al., 2007), the ant *Camponotus vagus* (Masson and Gabouriaux, 1973), and the honey bee *A. mellifera* (Dreller and Kirchner, 1993; Ai et al., 2007; Brockmann and Robinson, 2007; Tsujiuchi et al., 2007). The subgenual organ (Fig. 1b) is the primary receptor for substrate vibrations. Studies of the structure and functioning of the subgenual organ in social insects include the termite *Zootermopsis angusticollis* (Howse, 1962, 1965), the carpenter ant *Camponotus ligniperda* (Menzel and Tautz, 1994), the wasps *Agelais pallipes*, *Polybia paulista*, and *Mischocyttarus cassununga* (Santos et al., 2007), and the honey bee *Apis mellifera* (Rohrseitz and Kilpinen, 1997; Kilpinen and Storm, 1997).

Stridulation in ants: a morphologically specialized messaging modality

Stridulation is found in the ant subfamilies Nothomyrmecinae, Ponerinae, Ectatomminae, Pseudomyrmecinae, and Myrmicinae. The scraper (*plectrum*) is the upper posterior edge of the petiole or, in taxa with two petiolar segments, the postpetiole, and the file (*pars stridens*) is ventral to the scraper on the upper anterior surface of the first gastral segment. *Nothomyrmecia macrops* is an exception, with the stridulatory organ situated ventrally (Taylor, 1978). Stridulation is generated by movement of the file against the scraper. Anatomical studies of the stridulatory structure include *Ectatomma* and *Pachycondyla* (Pavan et al., 1997; Ferreira et al., 2010), *Messor* (Grasso

et al., 1998), *Aphaenogaster* (Schillinger and Baroni Urbani, 1985), and *Crematogaster* (Ruiz et al., 2006). The structure is present in males and gynes of *Pogonomyrmex* (Markl et al., 1977), *Myrmica* (Barbero et al., 2009), and *Crematogaster* (Ruiz et al., 2006), and it is probably also present in reproductives of other stridulating species. Vibrational characteristics of stridulation have been examined in *Leptogenys* (Chiu et al., 2011), *Ectatomma* and *Pachycondyla* (Pavan et al., 1997), *Myrmica* (DeVries and Crocroft, 1993), and *Aphaenogaster* (Schillinger and Baroni Urbani, 1985). Ferreira et al. (2010) document distinct differences in stridulation patterns among six to nine cryptic species in the *Pachycondyla apicalis* species complex. The capability to produce and interpret modulated stridulatory signals may be subject to positive natural selection in many of the contexts where it has evolved (Chiu et al., 2011).

Although humans and perhaps also vertebrate predators of foraging ants (Hölldobler et al., 1994) perceive stridulation as sound, stridulation transmits information among ants via substrate vibrations (Markl, 1967; Markl and Hölldobler, 1978; Baroni Urbani et al., 1988; Roces et al., 1993; Hölldobler and Wilson, 2009). The proposition that ants communicate via sound (Hickling and Brown, 2000) was based on a model of sound wave propagation and a speculation that sound is detected by a concentration of trichoid sensilla near the tip of the antenna. Roces and Tautz (2001) note that Hickling and Brown (2000) did not have a controlled experimental bioassay, no trichoid sensilla of sufficiently subtle sensitivity to detect sound have been shown for any ant, and the amplitude of stridulatory sound waves is below the sensitivity threshold for hearing. In a natural history observation, removal of the leading ant from a successful foraging raid by *Pachycondyla commutata* had no effect on other foragers if the leader was placed in a soundproof container, but if the leader was held above the foraging raid and allowed to stridulate, the other foragers dropped their prey and quickly dispersed beneath leaf litter, and some began to stridulate (Mill, 1984). Although seemingly a case of auditory communication, the possibility of chemical alarm communication was not controlled for. When developing *Myrmica scabrinodis* reach the state of having a sclerotized pupal cuticle, they possess a fully formed stridulatory organ. The pupae can stridulate, and adults direct their attention toward stridulating pupae (Casacci et al., 2013). Although the pupal stridulations were reported and quantified as acoustics, during playback experiments the speaker rested on the substrate where it would have generated vibrations. There is currently no substantive evidence to show that ants perceive airborne sound.

Stridulation occurs more frequently in species that nest in soil rather than in plants, rotten logs, leaf litter, or other materials that would be poor vibration transmitters (Markl, 1973; Spangler, 1974). A low frequency component of the stridulation output is emphasized underground (Masters

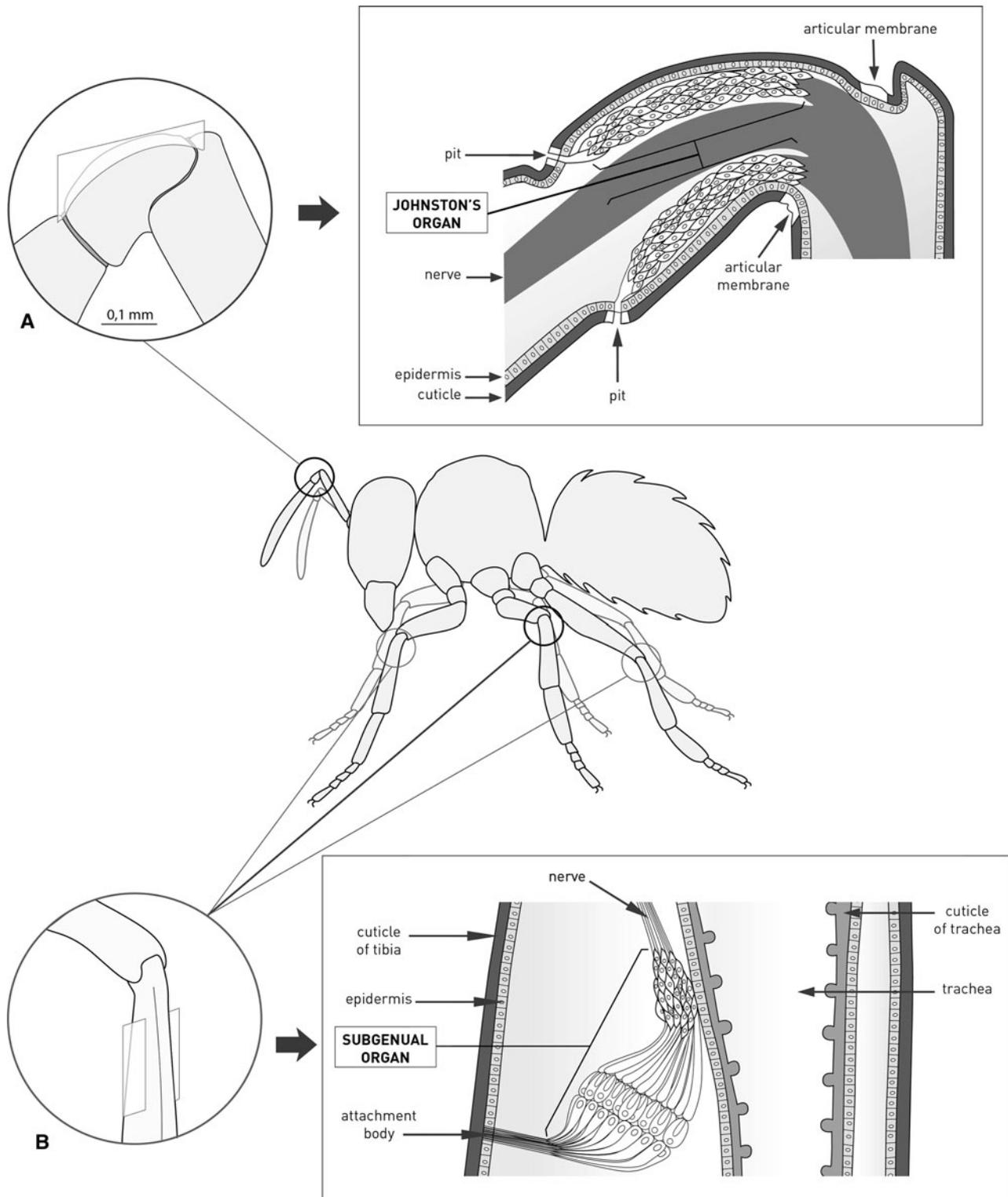


Fig. 1 The Johnston's organ (a) and subgenual organ (b) are the primary receptors for vibroacoustic signals. Located within the pedicel of the antenna, the Johnston's organ is connected at its distal end to a ring of pits in the articular membrane between the pedicel and first segment of the flagellum. Movement of the antennal flagellum in response to vibrations and sounds (in honey bees) is sensed by the Johnston's organ and translated into nerve impulses that are transmit-

ted to the central nervous system. Subgenual organs are located in the proximal portion of the tibia on all legs. Substrate vibrations received via the legs are sensed by the subgenual organs where they are translated into nerve impulses that are transmitted to the central nervous system. For detailed descriptions of these sensory organs see the references cited in the text

et al., 1983). Markl (1967) proposed that underground stridulation in *Atta cephalotes* recruits nestmate workers from distances of up to 8 cm to undertake nest excavation, perhaps to rescue stridulating nestmates trapped by nest cave-ins. Using an experimental design that replicates cave-in conditions in laboratory colonies of *Solenopsis invicta*, Rauth and Vinson (2006) recorded a six-fold increase in stridulation over baseline levels during excavation and mound construction. *Myrmica sabuleti*, *M. scabrinodis*, and *M. schencki* have differences between worker and queen stridulations, and some nest parasite caterpillars can mimic queen stridulations more than those of workers and thereby receive increased attention from workers (Barbero et al., 2009). In a similar ant-parasite system, Travassos and Pierce (2000) specify that they use the terms “sounds” and “calls” for simplicity when describing substrate-borne vibrations. Species differ in sound level and distance at which stridulations are perceptible (Markl, 1965; Spangler, 1967). Perception at different distances in a single soil type when dry vs. moist suggests a role for differences in substrate properties (Spangler, 1974).

Gross motor movements that generate vibroacoustic messages

Whole-body movements

Termites

Some termites perform a behavior called jerking, in which there are pronounced backward and forward movements of the whole body without the body touching the substrate (Hertel et al., 2011). Workers and soldiers of *Reticulitermes*, *Coptotermes*, and *Incisitermes* perform the jerking behavior in response to disturbance. If the disturbance continues, soldiers of *Coptotermes* combine the jerking with ejecting fluid from the frontal gland, and soldiers of soil-inhabiting species begin drumming their heads (Hertel et al., 2011). Worker and minor soldier *Macrotermes subhyalinus* respond to *M. bellicosus* invading their nest by running hectically and bumping into nestmates by laterally jerking the body. The alarm behavior spreads as increasing numbers of termites are contacted (Kettler and Leuthold, 1995). When exposed to spores of a fungal pathogen, worker *Zootermopsis angusticollis* produce a vibratory motor display in which the entire body of the termite lunges in an anterior–posterior motion while the legs flex dorsoventrally (Rosengaus et al., 1999). These vibrations induce nestmates to move away from rather than toward a spore-exposed individual, while the spore-exposed individual remains in place and signals to nestmates at a rate dependent on the concentration of spores encountered.

Wasps

Hornets and yellowjackets (Vespidae: Vespinae) and paper wasps (Vespidae: Polistinae) live in nests constructed of paper consisting of wood fibers mixed with saliva that is shaped into sturdy hexagonal cells. The construction is highly favorable to the transmission of vibratory signals. At least nine genera of social wasps that live in paper nests, including at least eleven species of *Polistes*, perform body oscillation behaviors (references in Brennan, 2007). The behaviors are conspicuous when performed on the un-enveloped nests of *Polistes*, *Mischocyttarus*, *Belonogaster*, and *Ropalidia*, but they have been well-studied only in *Polistes* (Jeanne, 2009). In *Polistes* there are three types of body oscillation behaviors: antennal drumming, abdominal wagging, and lateral vibrations. All three are performed primarily at early stages of the colony cycle by queens, co-foundresses in co-foundress colonies, and by early-emerging offspring (Suryanarayanan et al., 2011a; Jeanne, 2009). All three are believed to be signals to larvae (Harding and Gamboa, 1998; Savoyard et al., 1998; Brillet et al., 1999; Cummings et al., 1999). The sequence is invariant: antennal drumming precedes feeding liquid food to larvae, abdominal wagging precedes drinking saliva from larvae, and lateral vibrations precede departure from the nest (Gamboa and Dew, 1981; Pratte and Jeanne, 1984; Downing and Jeanne, 1985; Harding and Gamboa, 1998; Savoyard et al., 1998; Cummings et al., 1999; cf. Jeanne, 2009).

Antennal drumming in *Polistes* consists of an adult rapidly moving her body forward and rearward while rapidly vibrating (trilling) her antennae against the inner wall of a nest cell that she is facing, a behavior that could signal larvae to anticipate being fed with liquid food (Pratte and Jeanne, 1984; Suryanarayanan et al., 2011a). Vegetable die and radiotracer experiments confirm that passage of larval saliva to the provisioning adult does not occur at the same time (Pratte and Jeanne, 1984; Suryanarayanan and Jeanne, 2008). Antennal drumming begins in *Polistes* colonies only with the appearance of third-instar larvae, although removal of such larvae from a nest does not lead to cessation of the behavior following its first performances during colony development (Suryanarayanan and Jeanne, 2008). Antennal drumming may play a role in biasing larvae that develop early in the colony cycle toward worker phenotypes (Suryanarayanan et al., 2011a) by activating expression levels of some genes and peptides/proteins that differ quantitatively from expression of the same genes and peptides/proteins in larvae that develop later in the colony cycle (Hunt et al., 2007, 2010; Toth et al., 2007). Experiments with a mechanical device to vibrate gynec-producing nests at a natural vibration frequency of antennal drumming (Suryanarayanan et al., 2011b) led to low body fat, which is a worker phenotype characteristic (Eickwort, 1969; Hunt et al., 2007; Toth et al., 2009), relative to higher body fat levels, which is a gyne characteristic, in offspring emerging

from control nests vibrated with white noise. From an evolutionary perspective, this indicates that antennal drumming could be a mechanism of “maternal manipulation” (Alexander, 1974) that can initiate the divergence of two developmental pathways that subsequently provide the framework for caste differentiation (Hunt and Amdam, 2005; Hunt, 2012).

Abdominal wagging in *Polistes* is a slow side-to-side movement of a queen’s gaster as she walks over brood cells, with bouts of abdominal wagging alternating with bouts of cell inspection (Brennan, 2007). As with antennal drumming, abdominal wagging is initiated with the appearance of the earliest third-instar larva (Brillet et al., 1999). Abdominal wagging occurs in most *Polistes* species, but it is the only vibrational behavior observed in *Polistes dominulus*. Abdominal wagging in *P. dominulus*, as described in more detail by Brennan (2007), combines elements of the separate behaviors of abdominal wagging and lateral vibrations of other *Polistes* species. When performing the behavior the *P. dominulus* wasp stands with head, forelegs, and antennae extended while facing a larva-containing cell. The thorax is elevated while standing on the mid- and hind legs, and the apex of the gaster is pressed against the nest carton and oscillated from side to side. Vigorous bouts of the behavior can shake the entire nest. The wasp usually inspects the nest cell it was facing when the behavior stops, or the behavior alternates with bouts of cell inspection (Brillet et al., 1999; Brennan, 2007), which are probably trophallaxis behaviors. Detailed mechanical aspects of the behavior based on accelerometer readings are given by (Brennan, 2007).

Lateral vibrations in *Polistes* consist of short bursts of a queen’s vigorous side-to-side vibrations while standing in place on the brood cells. They occur more frequently on single foundress than on multiple foundress nests of *Polistes metricus* (Cummings et al., 1999) and, like antennal drumming, only on nests that contain third instar or larger larvae (Savoyard et al., 1998; Suryanarayanan and Jeanne, 2008). Cummings et al. (1999) describe several aspects of the behavior in *P. metricus*. Cell inspections are more frequent in the 2 min preceding lateral vibrations than afterward, and foundresses performing the behavior typically become inactive afterward. Departures from the nest are more frequent within 2.5 min following lateral vibration than in a similar period preceding it, and the frequency of performing the behavior prior to departure is significantly higher if that departure will result in the nest being unattended. Larvae surrendered significantly less saliva following lateral vibration than did non-vibrated controls. Savoyard et al. (1998) observed that larvae appear to retract or shift their head capsule into their nest cell in response to lateral vibrations, and Cummings et al. (1999; cf. Jeanne, 2009) interpret the lateral vibrations as a signal to larvae to withhold saliva. Similar retraction of the head capsule by larvae of *Mischocyttarus immarginatus* and *M. mexicanus cubicola* was interpreted as a selfish behavior by larvae that refused to

surrender saliva to soliciting adults (Hunt, 1988). An untested alternative hypothesis is that larvae performing the behavior have little saliva to surrender. As is the case with antennal drumming, lateral vibrations by queens of *P. dominulus* and other paper wasp species could bias which will become workers vs. future foundresses (Brillet et al., 1999).

Neotropical swarm-founding wasps (Epiponini) perform two body oscillation behaviors, the parasite alarm and the buzzing run. The parasite alarm, which is also found in independent-founding wasps such as *Polistes*, is a jerky movement performed in response to the presence of ectoparasitoid flies and moths or endoparasitoid wasps. The behavior is sometimes followed by nest abandonment (West Eberhard, 1969; Strassmann, 1981). The buzzing run is a frantic jerky running by one or more wasps on the nest (Jeanne, 1975; Forsyth, 1981; West-Eberhard, 1982). Buzzing runs are performed by workers and occur most frequently in large colonies prior to swarm emigration (Forsyth, 1981; West-Eberhard, 1982; Ezenwa et al., 1998).

Ants

Whole-body movements that convey information are less common in ants than in termites, wasps, and bees. Lower attine ants perform a “jigging” behavior in which an ant lifts its forelegs from the substrate and oscillates the body and forelegs vertically (Weber, 1957, 1972) or horizontally (Kweskin, 2004). The behavior may be performed as an alarm response to stimuli such as a puff of air or sudden light (Weber, 1972, Weber 1957) or to collembola invading the colony (Kweskin, 2004). In a laboratory colony of *Acropyga epedana*, workers meeting in tunnels “jerked” their bodies horizontally forward 3–6 times, lightly touching the other ant (LaPolla et al., 2002). In *Camponotus socius*, two types of body oscillation behaviors occur during recruitment of one nestmate by another. During recruitment to food there is a lateral wagging of the body, whereas a forward and back jerking of the body is recruitment to emigration that also retains alates that may be departing the nest prematurely (Hölldobler and Maschwitz, 1965; Hölldobler, 1971).

Honey bees

During *Apis* honey bee forager recruitment dances, a dancing bee waggles her gaster and vibrates her wings and in doing so simultaneously generates substrate-borne vibrations, near-field sounds, and jets of air (Michelsen et al., 1986a; Dreller and Kirchner, 1993; Michelsen, 2003; Hrncir et al., 2006a), all of which can transmit information from the dancer to follower bees. Waggles enhance the transmission of thoracic vibrations to the substrate (Tautz et al., 1996), with maximum signal transfer when the thorax is fully laterally

displaced during a waggle (Storm 1998 in Hrncir et al., 2006a). Varied postures of bee's legs perceive both horizontal and vertical components of the substrate vibrations (Sandeman et al., 1996; Rohrseitz and Kilpinen, 1997), and substrate vibrations are translated into neural impulses via the subgenual organ (Kilpinen and Storm, 1997). Waggle dances occur more frequently on open cells in honeycomb than on capped cells, and dances on open cells more strongly attract inactive potential foragers, indicating that substrate properties are a component of signal transmission (Tautz, 1996). Even though substrate vibrations during waggle dancing transmit information from the dancing bee to bees attending the dance, the substrate vibrations may not provide specific information about the velocity and direction of the dancer during the waggle run (Nieh and Tautz, 2000).

Upon returning to the nest, some forager honey bees will perform a rather jerky, non-rhythmic behavior, the “tremble dance,” in which they have a strong side to side and sometimes front to back shaking of the whole body as they walk with constant changes of direction across the comb (Seeley, 1992). The tremble dance appears to have approximately the same frequency as the waggle dance, but it does not include a directional component. Rather than recruiting new foragers, the tremble dance apparently serves to inhibit new foraging flights by diminishing the number of waggle-dancing bees (Nieh, 1993) and recruiting in-nest workers to increase nectar processing (Seeley, 1992; Seeley et al., 1996).

Stingless bees

Stingless bee foragers, after returning to the nest following a successful foraging trip, engage in “jostling” in which they contact nestmates during zig-zag (“agitated”) running (Nieh and Roubik, 1998; Hrncir et al., 2000). The number of jostles correlates positively with the number of foragers recruited but not with the distance or direction of the food source (Hrncir et al., 2000; Schmidt et al., 2008).

Bumble bees

Bombus terrestris foragers, after returning to the nest following a successful foraging trip, engage in irregular “excited” runs through the nest during which they bump into and climb over workers. These runs often last several minutes and are the longest following discovery of food. No extended interactions with other bees occur, and most contacts appear to be accidental touching or pushing. It seems that no signal is dependent on direct contact. Instead, information could be transferred from forager to worker bumble bees via deposition of foraged nectar into honeypots and perhaps also by a pheromone. The combination of the running, nectar deposition, and possible pheromone results

in increased “excitement” in the colony (Dornhaus and Chittka, 2001).

Vibration signal in honey bees

The “vibration signal” of honey bees is a tactile behavior that has been known by many other names (names and references in Schneider and Lewis, 2004). It occurs in *A. mellifera* under different circumstances than the waggle dance and is one of the most commonly performed honey bee behaviors (Schneider, 1987; Schneider and Lewis, 2004). Despite the similarity of names, the vibration signal does not generate substrate vibrations nor does it generate high-frequency vibrations by flight muscle contractions while the body remains stationary, thereby making it easily confused with the term ‘vibration signal’ as it used for stingless bees. During the honey bee vibration signal, workers “shake” other workers, queens, or queen cells by vibrating their bodies dorsoventrally for 1 or 2 s. A worker performing the vibration signal on another bee will grasp that bee with all six legs or only with the forelegs, or it will only “rest its head against the bodies” of bees being vibrated (Allen, 1959). The behavior functions as modulatory communication that is performed in a variety of contexts and has primer effects that shift the probability of engaging in other behavioral acts (Lewis et al., 2002; Schneider and Lewis, 2004). A worker performing the vibration signals on workers will move throughout the colony selecting fewer than half of other workers encountered as targets of vibration (Lewis et al., 2002). Inactivity of a recipient worker is the only significant criterion for choice of targets by a vibrating worker, leading Schneider and Lewis (2004) to conclude that the “message” of the vibration signal is an increase in activity, “with the specific response of a recipient being idiosyncratic and arising from an interaction of her age, physiological condition, genetically influenced response thresholds, work history and the other stimuli impinging on her at the time the signal is received.” Vibration signals modulate behaviors that primarily affect foraging-dependent tasks, swarming, and queen behavior during swarming and queen replacement (Schneider, 1991; Lewis and Schneider, 2000; Donahoe et al., 2003; Schneider and Lewis, 2004). The tendency to produce each signal, the ontogeny of signal performance, and the persistence with which individual workers perform the signals throughout their lifetimes all vary within and between patrines (Duong and Schneider, 2008).

Younger bees perform vibrations primarily in the context of orientation flights near the hive, and older bees perform vibrations primarily in the context of foraging (Painter-Kurt and Schneider, 1998). Workers receiving the vibrations show increased movement through the nest, increased frequency of cell inspection, and increased rates of trophallaxis

with non-vibrating workers, all of which potentially increase workers' perceptions of colony needs and can thereby increase organization of work in colonies (Cao et al., 2007).

The vibration signal may play a central role in the regulation of queen behavior during swarming and supersedure (Painter-Kurt and Schneider, 1998). Queens are directly vibrated throughout the two to three week pre-swarming period (Fletcher, 1978a, b), with rates increasing significantly in the final 2 or 3 days prior to liftoff, causing increased activity in the queen (Pierce et al., 2007). Vibration of workers in a swarm produces a general activation prior to swarm liftoff (Visscher et al., 1999; Lewis and Schneider, 2000). Vibrations that take place on queen cells during supersedure do not correlate with either queen emergence or queen success, and early- and late-emerging queens are vibrated at similar levels; however, virgin queens that are vibrated at higher rates survive longer, perform more bouts of piping [described below], eliminate more rivals, and are more likely to become the queens of new colonies (Schneider et al., 2001).

Workers also perform vibration signals on drones, which are more likely to be vibrated when they are sexually immature (Boucher and Schneider, 2009; Stout et al., 2011). Vibrated and non-vibrated drones do not differ in a number of characteristics, including total body weight, abdomen weight, abdomen-to-body weight ratio, total protein concentration, and hemolymph juvenile hormone (JH) titers (Slone et al., 2012). Vibrated drones do, however, have lower thorax weight and thorax-to-body ratios (Slone et al., 2012). These drones respond to the vibration signal by increasing movement and by interacting more with workers, which contributes to an increase in the proportions of time that they receive trophallaxis and grooming. Considering that vibrated drones have lower thorax weight and lower thorax-to-body ratios, and that trophallaxis supplies nutrients necessary for sexual maturation, the vibration signal could enhance development and mating performance in less-developed drones, thereby contributing to the production of greater numbers of competitive males (Slone et al., 2012). However, there is no evidence that the vibration signal is associated with the occurrence of drone flight (Boucher and Schneider, 2009).

Drumming

Substrate-borne vibrations called drumming can be generated by tapping sclerotized body parts against a resonant substrate. Drumming occurs in many termites and in a few wasps and ants, but not in bees.

Termites

Drumming occurs in soil-inhabiting termites but not in the drywood termite family Kalotermitidae (Hertel et al., 2011).

It is most frequently performed by soldiers, which can tap the substrate with their sclerotized head capsules, and it is widely considered to be an alarm signal (Howse, 1964; Kirchner et al., 1994; Connétable et al., 1999; Röhrig et al., 1999; Hertel et al., 2011). Physical properties of termite drumming and its use as an alarm signal are described by Howse (1964), Stuart (1963) and Kirchner et al. (1994).

Wasps

Workers of the Oriental hornet, *Vespa orientalis*, may gather into a circle facing a stationary queen, and one to four wasps in that circle may make a tapping sound by striking their gasters against the nest comb. This apparently induces the queen to begin moving (Ishay and Schwarz, 1965, Ishay and Schwartz 1973).

Ants

Among ants, drumming is widespread in arboreal species of *Camponotus* and *Polyrhachis* (Kirchner, 1997). *C. herculeaneum* workers generate vibrations by tapping the nest substrate with both the head and apex of the gaster (Fuchs, 1976a,b). The nest consists of lamellae of about 50–500 cm² derived from gnawing out the soft wood of a tree's annual growth rings, leaving the harder part of the rings. Fuchs (1976b) describes various aspects of this vibration signal and behavioral responses to it. Highest acceleration amplitudes of the drumming signal take place on the thinnest lamellae (about 1 mm thick), and the ants can perceive the drumming signal over an average distance of 10–30 cm and over 90 cm at the maximum. At high sine wave intensities and frequencies, "run"-reactions occur, whereas at lower ranges "stop"-reactions are more common. The signal shortens the time with which ants move from light nest regions to darkened ones, and if ants of other species intrude into a nest, the intruders are attacked more often.

Scraping

Termites

In the drywood termite *Cryptotermes domesticus* (Kalotermitidae), substrate vibration is generated by workers' mandibles chewing on wood. Such vibrations attract nest-mate workers (Evans et al., 2007). In a more sophisticated response to the vibrations, the termites assess size of the wood in which they are feeding (Evans et al., 2005, 2007). Termites in an experimental wood block 160 mm in length produce a signal at 2.8 kHz, whereas termites in a 20-mm block produce a higher frequency signal at 7.2 kHz (Evans et al., 2005). Discernment of the wood available for feeding

has the important colony-level consequence that a higher percentage of workers molt into neotenic reproductives in smaller pieces of wood (Lenz, 1994; Evans et al., 2005). In addition to assessing wood size, *Cryptotermes secundus*, which has colonies of a few hundred individuals, can “eavesdrop” on the vibrations of the dampwood termite *Copotermes acinaciformis* (Rhinotermitidae), which can have colonies of millions of individuals, and the *Cryptotermes* respond in ways that avoid confrontation (Evans et al., 2009).

Wasps

Adults of the swarm-founding wasp *Asteloeca ujhelyii* sitting near nest entrances produce a sound by scratching the nest envelope with their forelegs (Nascimento et al., 2005). Large (late instar) larvae of the Oriental hornet can rotate and move vertically within their nest cells, and as they do so they can scrape their mandibles against their nest cell walls and produce vibration and sound (Schaudinischky and Ishay, 1968). Starvation experiments and sounds played by small microphones placed within nest cells from which larvae had been removed (Ishay et al., 1974) suggest that the scraping vibrations are apparently interpreted by workers as hunger signals (Schaudinischky and Ishay, 1968).

Ants

Dolichoderus thorasicus produces vibration and sound by scraping the substrate with its mandibles (W. Rohe in Kirchner, 1997). *Aphaenogaster carolinensis* generates vibrations by a high-power strike against a substrate with its mandibles followed by dragging the mandibles across the surface (Menzel and Marquess, 2008). A photographed strike/drag had duration of about 0.06 s, but both the drag duration and number of drags in a single bout are highly variable. The behavior was documented in laboratory trials in which a single ant responded to the presence of single conspecifics or another species of *Aphaenogaster*, and it has not been studied in natural conditions.

Fine motor vibroacoustic communication in bees

Honey bees

Piping is a high-pitched “sound” produced by a honey bee while pressing its thorax against the substrate or another bee and activating its wing muscles without vibrating its wings (Pastor and Seeley, 2005). Piping sounds are generated by rhythmic oscillating contractions of the flight muscles (Hrncir et al., 2006a), presumably at higher frequencies than during flight (King et al., 1996). The highest frequency of

piping vibrations is generated when the wings are fully folded (Schneider 1975 in Hrncir et al., 2006a), and the fundamental frequency of piping sounds can be modulated by opening and closing the wings along with the signal (Seeley and Tautz, 2001). Piping by workers exists in three distinct varieties, each of which is performed in particular circumstances (references in Hrncir et al., 2006a): “wings-apart piping” (in hives), “wings-together piping” (in swarms), and the brief piping signal comprised of brief “beeps” or “short squeaks” (Kirchner, 1993), which is performed primarily around waggle dancing bees (Seeley, 1992; Kirchner, 1993; Seeley and Tautz, 2001).

Wings-apart piping is known from both queenright and queenless colonies (Ohtani and Kamada, 1980; Pratt et al., 1996). In queenright colonies, wings-apart piping is performed by only a small number of bees at one time. The piping bees had been engaged in foraging, and the greater number of piping bees on good weather days led Pratt et al. (1996) to infer that piping in queenright colonies, which “sounds reminiscent of the bleating of sheep,” is associated with foraging. Wings-together piping, the sound of which is “reminiscent of the revving of a racing car’s engine,” is performed primarily by nest scouts that scramble through a swarm cluster about 1 h before swarm liftoff, stimulating the non-scouts to warm themselves to a flight-ready temperature (Seeley and Tautz, 2001). Prior to this the queen is piped for several days and increasingly in the final 2–4 h prior to liftoff (Pierce et al., 2007).

In queenless colonies the piping is of two kinds, a high-frequency sound produced by guard bees at a colony entrance and a lower frequency sound produced by egg-laying workers (Ohtani and Kamada, 1980). Workers that pipe after egg laying are attacked by other workers (Ohtani and Kamada, 1980).

The brief piping signal, which can be produced by waggle dancers, dance followers, and tremble dancers (Nieh, 1993) and which has been known as the “begging signal” (Michelsen et al., 1986a) or “stop signal” (Kirchner, 1993; Nieh, 1993), causes waggle dancers to leave the dance floor, and it rarely elicits trophallaxis (Nieh, 1993). Because it can induce dancing bees to stop dancing (Nieh, 1993; Pastor and Seeley, 2005), it can thereby slow forager recruitment in response to an imbalance caused by forager bees bringing nectar at a rate exceeding the capacity of receiver bees to process it.

After a primary swarm of honey bees has departed the hive with the old queen, new queens within the hive produce piping of two sorts, “tooting” by young queens that have emerged from the cells in which they were reared and “quacking” by other young queens still within their cells (von Frisch, 1967; Bruinsma et al., 1981; Michelsen et al., 1986b). As is the case in worker piping, queen piping is produced by activating the wing muscles without wing

movements while pressing the thorax against a substrate (Simpson, 1964; Kirchner, 1993), and the piping is broadcast within the nest as vibrations of the combs (Hölldobler, 1977; Michelsen et al., 1986b). A chorus of synchronized quacking follows each tooting by an emerged young queen if more than one young queen is still present in their cells (Michelsen et al., 1986b). Quacking queens attract workers that cluster around the queen cells and seem to chase the first-emerged, tooting young queen away, and workers also feed quacking queens through a small slit in their cells (Kirchner, 1993). Once the tooting queen has departed with a colony's second swarm, one or more quacking queens emerge from their cells and become tooters. In time, one of these tooters kills all the other young queens (Kirchner, 1993). When a tooting queen is present, workers can delay the emergence of quacking queens from their cells by sealing slits in the queen cocoon or pressing their heads against partially opened cocoons (Bruinsma et al., 1981; Grooters, 1987).

Stingless bees

Stingless bees transmit information from foragers to in-hive food receivers via pulses of thoracic vibrations (Nieh, 2004; Hrnčir et al., 2004a, b; Hrnčir et al., 2006b; Hrnčir et al., 2008a; Barth et al., 2008). Vibrations occur primarily during trophallaxis, with the forager vibrating the receiver; 80 % of the bees receiving trophallaxis stay within 5 mm of the forager (Barth et al., 2008). As is the case with honey bees, these vibrations have been referred to as sounds (Aguilar and Briceño, 2002; Hrnčir et al., 2008b). The vibrations play a role in new forager recruitment and have been found to be positively correlated with the quality and distance of the food source (Nieh and Roubik, 1998; Aguilar and Briceño, 2002; Nieh et al., 2003; Hrnčir et al., 2004b), but Barth et al. (2008) disagree with other authors that the signals contain distance information.

Perspectives

Vibroacoustic modalities of communication have less diversity and subtlety than modalities of chemical communication, yet they are no less important in intracolony communication. In some cases they can play roles in situations in which chemical communication would be inadequate or could not serve the function served by the vibroacoustic signal. Examples described here include head banging in termites as part of an alarm response that can disseminate through the gallery system more rapidly than alarm pheromone, and perception of resource size via vibrations produced as drywood termites eat wood, which is an adaptation that could not be served by chemicals at all.

Behaviors such as body oscillations in paper wasps and the vibration signal in honey bees have considerable signal strength that cannot be ignored by the targets of those behaviors.

In the present review we have devoted exclusive focus to the presence, diversity, and adaptive roles that vibroacoustic communication can play in the lives of social insects. In a companion review (Richard and Hunt, 2013), we place chemical communication at the focus of attention. Although each of these can transmit intracolony information independently of the other, it is probably most often the case that vibroacoustic and chemical communication operate in synchrony and synergy as components of a multimodal signal. A truly comprehensive review of intracolony communication in social insects should therefore focus on multimodal communication (Hölldobler, 1999). Partan and Marler (1999, 2005) and Partan (2004) distinguish redundant signal components of a multimodal signal, in which each component carries the same message, from nonredundant signal components that may play different functional roles and provide increased signal content. Partan and Marler (2005) provide an overview of multimodal communication and discuss issues in the classification of multimodal communication. To review social insect communication in the context of the Partan and Marler classification system could identify suites of communication modalities that are repeated across taxa, thus enabling a clearer view of the adaptive roles of multimodal communication. In addition, such a review of social insect multimodal communication might reveal insights on the possible evolutionary pathways of single communication modalities and their integration into multimodal signals. As a guide for future empirical research on multimodal signaling, Hebets and Papaj (2005) put forward a framework of testable hypotheses. They make three points: that complex signals form functional units upon which selection can act, that selection pressure acting on both signal content and efficacy may account for complex signal function, and that individual components of signals need not be independent and can interact in a functional way. The most complex signal in social insects, the waggle dance of honey bees, probably meets these three criteria.

Natural history studies will, and should, continue to be the principal gateway to discovery and study of vibroacoustic behaviors and the contexts in which they occur. All of the topics reviewed here are founded on behavior observations. Manipulation experiments and 'natural experiments' are low cost gateways to new and expanded knowledge. Signal generation, propagation, and perception are more focused research areas that can be pursued in finer detail, but here, too, carefully planned experiments can add usefully to our knowledge. This approach is exemplified by the diverse studies of honey bee vibroacoustic communication and also

on the studies of drywood termites and their assessment of wood available for feeding. The studies that used sophisticated equipment to quantify termites' chewing vibrations in wood blocks of different sizes (Evans et al., 2005, 2007) were predicated on the results of a carefully designed, low-tech, low-cost experiment (Lenz, 1994).

Vibroacoustic studies in non-social insects are revealing increasing numbers of surprising, sophisticated, and adaptively significant findings. Among social insects, the apparent maternal manipulation via antennal drumming in *Polistes* is a surprising and sophisticated vibroacoustic behavior of considerable evolutionary significance. What other surprising and adaptively significant roles of vibroacoustic communication remain to be discovered if distinctive behaviors, including ones not now known to incorporate a vibroacoustic component, are pursued from new perspectives using new investigative methods? There could be many.

An area with considerable scope for new investigation is the role of vibroacoustics as modulators of other aspects of insect social life. In an example described here, the vibration signal of honey bees modulates a diversity of behavioral responses within the hive and prior to swarming in bees that are recipients of the signal. Stridulation in ants does not elicit a specific behavioral response, but instead it changes other behavioral activities to a greater or lesser degree (Markl and Hölldobler, 1978). Antennal drumming in paper wasps plays a significant evolutionary role by modulating larval development.

Sound and substrate vibration are inseparable when produced, but it would be of interest to use experimental methods to dissect them as carriers of information as has been done in honey bees. Another basic challenge would be to disentangle signal from noise in multimodal messaging. In relation to this, ecological selection pressures on vibroacoustic communication systems have been under-researched, and considerable opportunity exists for learning how vibroacoustic communication is influenced by the nature of the substrate, sources of environmental noise, interference from competitors, and eavesdropping by predators and parasitoids (Cocroft and Rodríguez, 2005). Vibroacoustic communication may be more widespread and more flexible between both adult and immature social insects than is generally recognized (Casacci et al., 2013).

An area with opportunity for future research can be drawn from Hölldobler's insight that communication can be considered to be part of an insect colony's "extended phenotype." How does signal variation among colonies of a species correlate with adaptive criteria such as colony growth, colony survival, and colony reproduction, and how have these affected the course of evolution? To date, among-colony comparisons of the topics treated here are virtually nonexistent.

A research area of considerable interest would be to pursue an evolutionary understanding of vibroacoustic communication itself. Given that vibroacoustic messages

are often exaptations of structures and behaviors selected in other contexts, what has been the evolutionary feedback from vibroacoustics on those structures and behaviors? Similar adaptive roles of vibroacoustic communication have evolved independently in diverse lineages of social insects, thereby raising the question of the degree to which the evolutionary pathways leading to the similar adaptive roles have themselves been similar. For example, stridulation structures and behaviors in ants evolved more than once; what shared alleles and/or developmental pathways underlie these independent evolutions? In Hymenoptera, the ability to perceive substrate vibrations in the context of prey location occurs in the basal ectoparasitoid family Orussidae and in derived endoparasitoids (Meyhöfer and Casas, 1999; Vilhelmsen et al., 2001). Given that communication among individuals is essential for social life, did the existence of this sensory capability in solitary taxa that were ancestral to social lineages play a role in the origin of sociality? Frameworks for pursuing these and other evolutionary questions include experimental studies, the comparative method (Harvey and Pagel, 1991), and phylogenetic methods. Success in pursuit of these goals will necessitate documentation and assessment of vibroacoustic communication in more species and in more contexts than have been studied to date. The increasing sophistication of affordable sound equipment could play important roles in this regard (Casacci et al., 2013).

In this review, we have given an overview of vibroacoustic communication intended to add to the knowledge base of social insect biologists and to show that vibroacoustic modalities are diverse, sophisticated, and play important roles in the lives of social insects. At the same time, and despite the many fine studies reported here, we hope that we have shown that the field is wide open for new research. We suggest that future studies involving vibroacoustic signal manipulation could be particularly informative.

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