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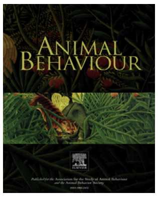

Special Issue: Communicative Complexity

Acoustic communication within ant societies and its mimicry by mutualistic and socially parasitic myrmecophiles

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This review focuses on the main acoustic adaptations that have evolved to enhance social communication in ants. We also describe how other invertebrates mimic these acoustic signals in order to coexist with ants in the case of mutualistic myrmecophiles, or, in the case of social parasites, corrupt them in order to infiltrate ant societies and exploit their resources. New data suggest that the strength of each ant–myrmecophile interaction leads to distinctive sound profiles and may be a better predictor of the similarity of sound between different myrmecophilous species than their phylogenetic distance. Finally, we discuss the evolutionary significance of vibrations produced by specialized myrmecophiles in the context of ant multimodal communication involving the use of chemical and acoustic signals in combination and identify future challenges for research including how new technology might allow a better understanding of the study systems.

Efficient communication to coordinate the actions of up to a million specialized nestmates is fundamental to the success of social insects, especially ants. Various modes of signalling have been identified, including the release of semiochemicals, visual behavioural displays involving movement or posture, tactile interactions, and the comparatively poorly studied use of acoustic signals (Hölldobler & Wilson, 1990, 2009). As hotspots of resources in their environment, ants fiercely defend their colonies using a wide range of weapons (e.g. gland secretions, mandibles, sting), which are deployed in the manner of coordinated attacks by legions of intercommunicating workers. Nevertheless, ant nests are also magnets for other organisms that have evolved means to overcome the hostility of the host ants. Thus, an estimated ca. 10 000 invertebrate species live as obligate social parasites of ants, able to penetrate and exploit the resources within host colonies in order to complete their life cycle (Thomas, Schönrogge, & Elmes, 2005). The large majority of these adaptations evolved in many separate lines, especially among Coleoptera, Diptera, Lepidoptera and other Hymenoptera, from a 10 times greater number of commensals or mutualists (Fiedler, 1998; Hölldobler & Wilson, 1990; Nash & Boomsma, 2008; Pierce et al., 2002; Thomas, Schönrogge et al., 2005). All these myrmecophiles show morphological, behavioural, chemical or acoustic adaptations to interact with ants (Cottrell, 1984; Donisthorpe, 1927; Hinton, 1951; Lenoir, D'Ettorre, Errard, & Hefetz, 2001; Malicky, 1969; Wasmann, 1913; Wheeler, 1910; Witek, Barbero, & Marko, 2014). Armour, stealth and the secretion of attractive food rewards are frequently sufficient for unspecific or facultative myrmecophiles to access the enemy-free spaces of ants. However, the subversion of the ants' chemical and/or acoustic signalling is generally required to enable true social parasites (sensu Nash & Boomsma, 2008) to live for long periods as undetected intruders in close contact with their hosts.

A key element of successful cohabitation in ant nests is to circumvent the host's ability to differentiate between nestmates and intruders. Nestmate recognition is a dynamic process, primarily based on the detection of distinctive species- or colony-specific cocktails of cuticular hydrocarbons (CHC) covering the surface of all individuals (Hölldobler & Wilson, 1990; Howard, 1993; vander Meer & Morel, 1998; Winston, 1992). Social interactions such as allogrooming ensure an exchange between the CHC mixtures among nestmates and give rise to a shared CHC gestalt odour (vander Meer & Morel, 1998). The role that chemical

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communication and nestmate recognition have in maintaining the cohesion of ant societies and those of other social insects has been subject to extensive study, with excellent recent reviews, for example by Martin and Drijfhout (2009) and van Wilgenburg, Symonds, and Elgar (2011): The deployment of chemical communication by obligate social parasites to subvert host recognition systems is equally well reviewed (e.g. Lenoir et al., 2001; von Thienen, Metzler, Choe, & Witte, 2014).

In contrast, the function, origin and role of acoustic signals in ants and their corruption by social parasites are much less well studied. In this review, we therefore focus on the state of the art concerning acoustic signalling in ants, and then consider the acoustic signalling of obligate and facultative myrmecophiles. In both cases we emphasize the insights that have resulted from recent technological advances that allow unalarmed ants and their guests to be recorded and to receive broadcasts of their acoustic signals under seminatural conditions (Barbero, Thomas, Bonelli, Balletto, & Schönrogge, 2009; Riva, Barbero, Bonelli, Balletto, Casacci, 2016).

We first examine ant sound-producing organs and convergent adaptations that allow organisms other than ants to mimic and subvert ant–ant communications, focusing on advances in knowledge since the reviews by Hölldobler and Wilson (1990), Fiedler (1998), Pierce et al. (2002), Thomas, Schönrogge et al. (2005) and Nash and Boomsma (2008), or covered cursorily by Witek et al. (2014). We then review recent insights into the ant acoustic signals themselves and their corruption by social parasites. This includes both the morphological adaptations to produce acoustic signals, the behavioural responses to them, and thus the impact on ant–social parasite/guest interactions. Much of this builds on the pioneering work of Markl (1965, 1967), DeVries (1991a, 1991b), Hölldobler, Braun, Gronenberg, Kirchner, and Peeters (1994) and Kirchner (1997). Finally, we present new data relating the intimacy of interactions of lycaenid butterfly larvae to phylogeny and the similarity of acoustic signalling.

ACOUSTIC SIGNALLING IN ANTS

The use of acoustics, whether through receiving pressure waves through the air (i.e. sounds stricto sensu) or substrate vibrations, is a common means of communication in insects, whose functions include defence, displays of aggression, territorial signalling and mate attraction (Bennet-Clark, 1998; Gerhardt & Huber, 2002). Its advantage as a signal over chemical volatiles lies in instantaneous reception that pinpoints a distant, but exact, location to the receiver, for example in social insects to attract help (Markl, 1965, 1967; Roces, Tautz, & Hölldobler, 1993). The physics, use and effects of substrate-borne vibrations of ants and other insects are comprehensively reviewed by Hill (2009). A simple form involves ‘drumming’, where the substrate is tapped by part of the exoskeleton to produce vibrations. Drumming is employed by many ant taxa, but at least four of the 11 subfamilies also stridulate by rasping a ‘plectrum’ across a ‘file’ (pars stridens), both chitinous organs being located on opposite segments of the anterior abdomen (see Fig. 1, k–o, u–y; Barbero, Thomas et al., 2009; Golden & Hill, 2016; Ruiz, Martinez, Martinez, & Hernandez, 2006). Although these stridulations produce airborne (as well as substrate-borne) pressure waves that are audible to the human ear, it remains uncertain whether ants can perceive sound as pressure waves through the air (Hickling & Brown, 2000, 2001; Roces & Tautz, 2001). In contrast, there is no controversy about the ants' ability to perceive substrate vibrations and two types of sensor have been proposed to receive substrate vibrations: campaniform sensilla measuring the tension in the exoskeleton and the subgenual organ, a spherical arrangement of sensory cells in the tibia, as described from *Camponotus ligniperda* (Gronenberg, 1996; Menzel & Tautz, 1994).

Most studies that measure insect acoustics have used accelerometers, moving coil or particle velocity microphones, often with phase inversion focusing on the vibrational part of the signal rather than pressure waves through the air. Hereafter in this review we use the term ‘sound’ in its broadest sense, as we do the terms calls, vibrations, vibroacoustics and stridulations.

Early studies suggested that acoustic signals were a minor means of communication among ants, largely confined to activities outside the nest and mainly signalling alarm or calls for rescue, for instance when parts of nests collapse (Markl, 1965, 1967). Owing to a perceived preponderance of stridulation organs among soil-nesting ant species, Markl (1973) hypothesized that stridulation evolved initially as a burial/rescue signal when volatile chemicals would be ineffective, whereas substrate-borne vibrations would at least travel short distances. However, this is not supported by Golden and Hill (2016), who showed that stridulation organs have evolved independently multiple times in ants. In addition, whereas Markl (1973) suggested that they would probably become vestigial over time in arboreal ant species, owing to the rarity of burial by soil, there was instead a strong positive association between the presence of functional stridulation organs and the possession of an arboreal lifestyle (Golden & Hill, 2016).

Nestmate recruitment is the most frequently reported function for ant–ant acoustic signalling. For example, outside the nest, *Atta cephalotes* uses vibratory signals to attract foraging workers towards newly found food sources (Roces & Hölldobler, 1995). The same authors also observed that in the presence of parasitic phorid flies, foragers used acoustics to recruit minor workers for defence, thus also employing vibrations as alarm signals (Roces & Hölldobler, 1995, 1996). Finally, although created by a scraper and file organ located on the first gastric tergite and the postpetiole, Tautz, Roces, and Hölldobler (1995) observed that vibrations travelled the length of the body to the mandibles, aiding the cutting of soft young leaf tissue by stiffening it. Behavioural experiments, however, suggest that this is a secondary effect and that communication is the main function for these vibrations (Roces & Hölldobler, 1996).

It has recently become clear that acoustic signals are also used to transmit more abstract information, including a species' identity or an individual's caste and status (Barbero, Thomas et al., 2009; Casacci et al., 2013; Ferreira, Cros, Fresneau, & Rybak, 2014). For example, modern molecular analyses revealed the Neotropical ponerine ant species *Pachycondyla apicalis* to be a species complex of five cryptic lineages. The stridulations of three largely sympatric lineages are also distinctive, suggesting that morphological characters on the pars stridens differ in length, width and ridge gap in each lineage (Ferreira et al., 2014; Wild, 2005). By contrast, two allopatric lineages had very similar acoustics, suggesting disruptive selection on this trait where sympatric overlap is high.

Acoustic patterns also signal caste and hierarchical status in at least two genera of Myrmicinae ants: *Myrmica* (Barbero, Thomas et al., 2009) and *Pheidole* (Di Giulio et al., 2015). In both taxa, the queens produce distinctive stridulations which, when played back to kin workers, elicit additional ‘royal’ protective behaviours compared with responses to worker signals (Barbero, Bonelli, Thomas, Balletto, & Schönrogge, 2009; Barbero & Casacci, 2015; Barbero, Thomas et al., 2009; Casacci et al., 2013; Ferreira, Poteaux, Delabie, Fresneau, & Rybak, 2010). In addition, in *Pheidole pallidula* the soldier and minor worker castes also make distinctive vibroacoustic signals (Di Giulio et al., 2015). Unlike *Pachycondyla* species, little interspecific variation was detected in either the queen or worker sounds made by closely related

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