Chapter 18

Biotremology of Social Wasps: The Next Step to Understand Wasps' Social Life

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Abstract Vibrational communication, the use of the surface-borne component of mechanical waves, is widespread in arthropods, but its role is almost unknown for the majority of species. The preponderance of other communication modalities has often masked the occurrence of vibrational communication, even when observations suggested that substrate-borne waves were involved in the communication of the species. Social wasps are a good example of this knowledge gap: their social life has been considered to be based on chemical communication since the early 1970s and other modalities have been overlooked. Only recently, some attention has been paid to visual signals and vibrational communication is still largely neglected in this group. However, it has been confirmed that vibrations mediate crucial aspects of social life in some species. This chapter aims to provide an overview of our current, often scarce, incomplete, and disorganized knowledge on the production and use of substrate-borne waves in social wasps. Their putative and demonstrated functions in wasps' societies are then discussed. We hope to demonstrate that biotremology, the study of vibrational communication, represents a necessary next step toward a more complete understanding of social life of wasps.

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18.1 Introduction

People dislike social wasps, such as hornets and yellowjackets, for their disturbance and danger to human life; moreover, their ecological role and economic impact are underrated, and, as a consequence, the scientific effort to study these insects is low (Sumner et al. 2018). However, social wasps play a crucial role in regulating their ecosystem both as predators and as pollinators (Sumner et al. 2018; Thomson 2019). Thus, understanding their social life is crucial to increasing the awareness and conservation efforts for this group of insects.

By definition eusocial species live in colonies where two or more generations of adults overlap and show reproductive division of labor, that is the presence in the colony of non-reproductive individuals who cooperate in brood care and colony maintenance (workers) and of one or a few individuals who reproduce (the reproductives) (Wilson 1971). Eusociality has been documented in only three subfamilies in the family Vespidae: Stenogastrinae, Polistinae, and Vespinae (Hunt 2007). Their highly variable and plastic social structures differentiate them from other eusocial species, such as some ant species and honey bees. Their wide range of social organization, from the barely eusocial stenogastrines to the highly eusocial colonies of some of the swarm-founding polistines, has established them as a key group in which to study the evolution of sociality (Pardi 1996; O'Donnell 1998). This has held true since the early years of sociobiology in the 1940s, and they have been extensively studied ever since. Nevertheless, many critical aspects of their communication are yet to be understood.

Living in colonies poses a series of challenges to the members of the insects' societies, which are mainly related to the collaborative resource utilization, collective defensive actions, and the reproductive division of labor (Leonhardt et al. 2016). The latter adds an additional level of complexity to wasps' societies; in fact, Stenogastrinae and independent-founding Polistinae are considered primitively eusocial, that is most females can potentially mate and lay eggs, but only one of them, the dominant female, secures reproduction, while the others remain in the nest as workers (Jeanne 2003; Hunt 2007). Thus, the dominant individual must impose its dominance over the other females and maintains it throughout the colony cycle.

Intraspecific communication plays a pivotal role in overcoming all these challenges, and chemicals have been considered to govern wasp social life (Richard and Hunt 2013; Leonhardt et al. 2016). For instance, the chemical blend (mainly hydrocarbons) that covers the cuticle of these insects has been shown to distinguish both nestmates from alien individuals and the dominant female from subordinates (Bruschini et al. 2010); the alarm pheromone released by the venom gland recruits nestmates and coordinates a collective defense when the colony is threatened (Jeanne 1981; Fortunato et al. 2004; Bruschini et al. 2008).

As chemicals are extremely important in the social life of wasps, their study might have biased a comprehensive investigation of communication. Other modalities have been left in the shadow, as in the case of visual signals (Cervo et al. 2015) and vibrations. The mechanical modality is extremely suitable for communication in the colony life of wasps. First, all intracolony activities take place in the nest, which is made by the wasps themselves, who mix organic and inorganic material with their saliva and manipulate it into the nest structure. Both the structure (single or multiple combs, with or without envelope) and the materials of their nests have always been considered suitable for substrate-borne wave propagation (Schaudinischky and Ishay 1968). Secondly, behaviors that may induce vibrations in the nest's structure (i.e., vibrational behaviors) have been reported for several species in all three subfamilies, Stenogastrinae, Vespinae, and Polistinae (Jeanne and Suryanarayanan 2011; Turillazzi 2012) (Fig. 18.1). These behaviors have been identified with several names (e.g., oscillatory behavior, drumming, vibration, waving, wagging, scraping), and in some cases, a correlation to other social traits has been found, such as to the dominant or subordinate role in Polistinae and Vespinae, respectively (Ishay and Schwartz 1973; Jeanne 2009). Yet, just a few studies measured the substrate-borne waves associated with such behaviors, and in a minority of those, a functional hypothesis has been tested (Ishay 1975; Ishay and Nachsen 1975; Brennan 2007; Suryanarayanan et al. 2011; Pepiciello et al. 2018; Taylor and Jeanne 2018). Thus, for most of these behaviors a function has yet to be identified.

Despite social wasps being good candidates for the use of vibrational communication, biotremology is still a niche topic in this group. In this chapter, we give an overview of the current knowledge on the occurrence of substrate-borne waves and vibrational communication in all three subfamilies of social wasps. We take into consideration how wasps effectively transmit vibrations to the nest structure, how receivers on the nest perceive them, and the transmission properties of different nests. Then we discuss their functions, either putative or tested, and we classify vibrations induced by social wasps based on the context in which they are usually displayed. By the end of the chapter, we hope to convey the message that vibrational communication in wasps deserves a higher consideration than it has received so far.

18.2 How and Where: Mechanisms of Production, Perception, and Transmission of Vibrations in Wasps

18.2.1 Production of Vibrations

Insects have many mechanisms for transmitting vibrations to the substrate on which they are standing. Some of them do not require specialized structures or organs, but employ peculiar vibrational behaviors, such as tremulation, drumming, and scraping (Hill 2009).

There are several behaviors of social wasps that likely induce vibrations in the substrate, none of which require specialized structures. However, they have rarely been studied as vibrational signal mechanisms: descriptions are often incomplete and the measurement of the vibrations is lacking for most of the species. They have been

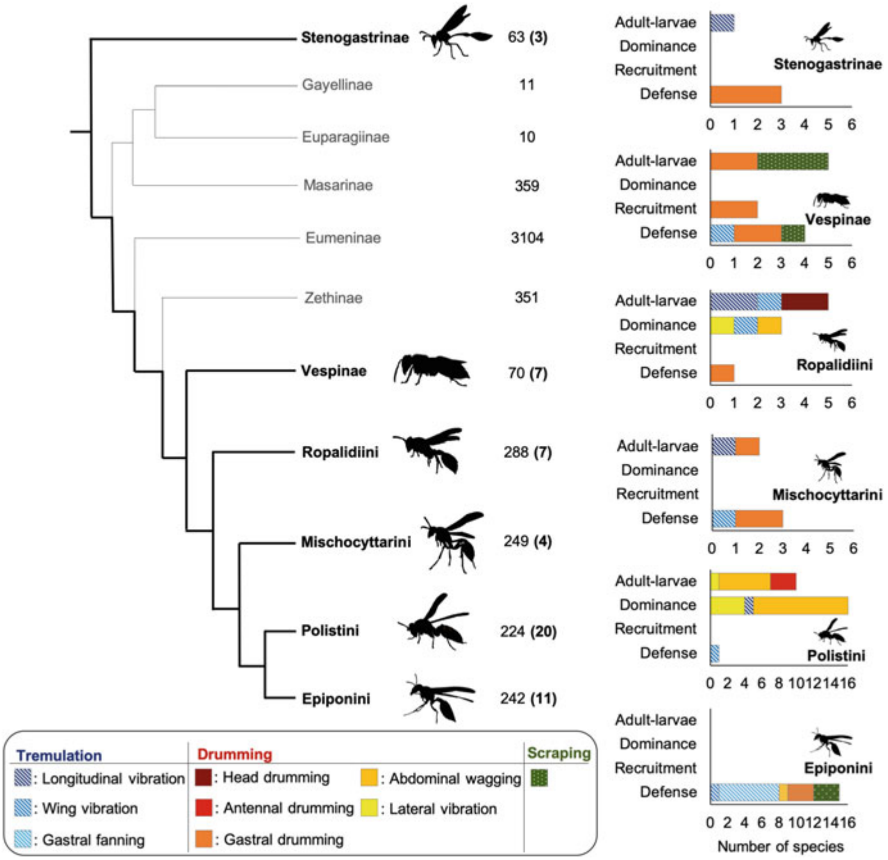

Fig. 18.1 Cladogram of social wasp taxa and presence of behaviors inducing vibrations in the nest. Groups containing solitary species are in gray. The subfamily Polistinae is divided into four tribes. The number next to the taxon name is the total number of species; the number in brackets is the number of species in which at least one vibrational behavior has been described. Histograms report the context in which the vibrational behavior has been observed or to which it has been associated. The cladogram has been drawn by the authors based on data from Hines et al. (2007) and Piekarski et al. (2018)

described merely based on the basis of the behavioral patterns associated with the production of vibrations as drumming, beating, rattling, body oscillations (waving, wagging, vibration), and scraping. Plus, the terminology used so far to describe these behaviors is inconsistent. To facilitate further studies of the biotremology of social wasps, we propose to categorize the behaviors that have been reported to induce substrate-borne waves by social wasps based on the mechanisms of the vibrations' production: tremulation, drumming, and scraping (Fig. 18.2).

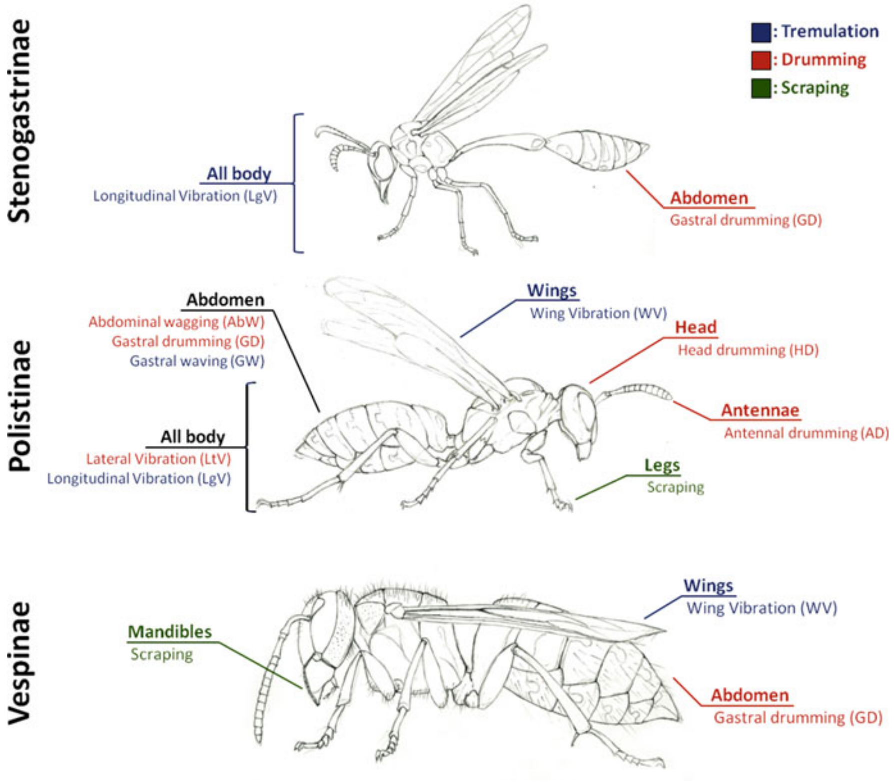

Fig. 18.2 Scheme of the behaviors inducing substrate-borne waves into the substrate for each subfamily of social wasps. Drawings by Marco Valerio Rossi Stacconi

18.2.1.1 Tremulation

Tremulation consists in a general shaking of the whole body or parts of it (i.e., wings and abdomen) while the wasp is standing or walking on the nest. The trembling of the body causes the nest to shake jointly with the wasp. An example of tremulation is the "longitudinal vibration" (LgV) of *Polistes metricus*, which consists in a backward and forward movement of the wasp along her longitudinal axis. A behavior similar to LgV has been reported in two other genera of Polistinae, *Belonogaster petiolata* (Keeping 1992), *Belonogaster juncea juncea* (Tindo et al. 1997), *Mischocyttarus drewseni* (reported as "pecking"; Jeanne 1972), and one species of Stenogastrinae, *Eustenogaster fraterna* (Francescato et al. 2002).

In some cases, wasps contract flight muscles while standing on the comb. As a result of the contractions, the wings are rapidly vibrated as if the individual is ready to fly away from the nest. The "wing vibration" (WV) has been observed in *Vespa orientalis* (Ishay and Sadeh 1982), *Ropalidia revolutionalis* (Ito 1987), *Ropalidia marginata* (Sen and Gadagkar 2006), *Polistes dominula* (formerly *P. gallicus* and

P. dominulus, Castro and Dvořák 2009; Bruschini et al. 2005), *Polybia occidentalis* (Jeanne 1981), and *Mischocyttarus cerberus* (Togni and Giannotti 2010).

In seven species of the Epiponini tribe, *Polybia occidentalis, P. dimidiata, P. dimorpha, Agelaia yepocapa*, *Apoica albomacula, Brachygastra augusti*, and *Synoeca septentrionalis*, workers have been reported to perform "gaster-flagging" (GF), which consists in waving the uplifted abdomen side to side while standing on the nest surface (Jeanne 1981; O'Donnell et al. 1997). In these species, the oscillating movement of the gaster may potentially induce vibrations in the nest, particularly when multiple individuals perform GF simultaneously, but vibrations of the nest surface have never been measured.

18.2.1.2 Drumming

Among all families of social wasps, drumming is the mechanism most widely used to induce vibrations into the nest. It consists of the wasps rhythmically striking the nest surface with parts of the body, such as the head, the abdomen, or the antennae.

Depending on the body part contacting the nest, the direction of the movement (parallel or perpendicular to the nest), and the intensity of the movement, the following five behaviors have been described: "head drumming" (HD), "antennal drumming" (AD), "gastral drumming" (GD), "abdominal wagging" (AbW), and "lateral vibration" (LtV). When inspecting cells containing larvae, adults have been documented to repeatedly beat the cell rim with either the head (HD) or the antennal flagella (AD). HD is peculiar to *Ropalidia revolutionalis* (Hook and Evans 1982) and *R. fasciata* (Ito 1983), whereas AD was described for the first time in *Polistes fuscatus* (F.) (Rau 1928; Pratte and Jeanne 1984), and it has been observed in *Polistes snelleni* (Yamane 1971) and *Polistes carnifex* (Corn 1972).

Among social wasps, striking the abdomen on the nest surface is more common than the head or its appendages. The GD consists of the wasp moving the abdomen perpendicularly to the nest to hit the comb, and it is performed by species of all the three subfamilies of social wasps. The part of the gaster used to hit the substrate varies depending on the species, from the distal tip of the abdomen to its ventral section. Among Vespinae, GD was originally named "awakening dance" (Ishay and Schwartz 1973). It is always performed on the back of the comb and has been reported in *Vespa orientalis* (Ishay and Schwartz 1973), *Vespula germanica* (Ishay and Brown 1975; Ishay and Nachsen 1975), *Vespula consobrina* (Akre et al. 1982)*, Vespula vulgaris*, and *Vespula maculifrons* (Ross 1982). Only one genus of Stenogastrinae, *Eustenogaster*, has been documented to perform behaviors inducing vibrations into the substrate. GD has been observed in three species: *E. calyptodoma* (Hansell 1987), *E. eximia* (Krombein 1991), and *E. fraterna* (Francescato et al. 2002). Among Polistinae, GD occurs in *Mischocyttarus labiatus* (Litte 1981), in *M. cerberus* (Togni and Giannotti 2010)*,* in *M. drewseni* (Jeanne 1972), in *Ropalidia opifex* (Fortunato et al. 2004)*,* in *Parachartergus colobopterus* (Jeanne and Keeping 1995), and in *Synoeca septentrionalis, Synoeca virginea*, and *Angiopolybia pallens* (West-Eberhard 1982). Two species of obligate social parasites among *Polistes*, *P. sulcifer* and *P. semenowi* perform GD after usurpation of the nest of congeneric host species (Cervo 1990; Zacchi et al. 1996).

Among the Polistini, the most common behavior inducing vibrations is AbW, which consists of the wasp swinging the gaster side to side while being stationary or walking on the face of the comb. Video and vibration recordings of AbW suggest that vibrations are induced by the wasp striking the nest surface with the ventral side of the gaster while wagging (see Sect. 18.2.1.4). The term "abdominal wagging" is actually incorrect, as it is the gaster to be moved (i.e., rearmost tagma, starting at the wasp "waist" or petiole), whereas "abdomen" includes the gaster and one or two anterior segments that in these Hymenoptera are fused with the thorax. AbW should thus be better called "gaster or gastral wagging." However, to assure continuity with previous literature and for a broader understanding also in a non-expert audience, we prefer to keep the term "abdominal wagging." This behavior has been described in several species of *Polistes*, including *P. dominula* (Heldmann 1936; Pardi 1942; Röseler and Röseler 1989; Brillet et al. 1999; Brennan 2007), *P. flavus, P. chinensis*, and *P. canadensis* (West-Eberhard 1969), *P. exclamans* (West-Eberhard 1969; Hermann et al. 1975), *P. versicolor* (de Souza and Prezoto 2012), *P. versicolor* var. *vulgaris* (Esch 1971), *P. carnifex* (Corn 1972), *P. annularis* (Hermann and Dirks 1975; Hughes et al. 1987), *P. metricus* (Gamboa et al. 1978; Gamboa and Dew 1981), *P. major* (West-Eberhard 1982), *P. instabilis* (Hughes and Strassmann 1988), *P. stigma* (Suzuki 1996), *P. fuscatus* (Harding and Gamboa 1998), *P. biglumis* and *P. atrimandibularis* (Mignini and Lorenzi 2015), *P. jokahamae* (Yoshimura et al. 2019), *P. gallicus*, *P. nimphus*, *P. semenowi*, and *P. sulcifer* (Cervo personal observation). However, AbW is also present in the ropalidiine *B. juncea* (Tindo et al. 1997), and the epiponine *Polybia atra* (Hase 1935).

A minority of species display a behavior similar in its movement to AbW, but that is generally described as more intense, the "lateral vibration" (LtV) of *P. metricus* (Gamboa and Dew 1981). In LtV the wasp shakes the entire body in a horizontal plane with respect to the nest's surface while stationary. This behavior has been described as very similar to AbW, but they can be distinguished by duration, frequency of body oscillation, and intensity (Gamboa and Dew 1981). In fact, the shaking of the nest is so intense that in some cases it can be distinctly seen moving and it produces an audible sound. Vibrations induced by LtV have never been recorded, and there is no video evidence that the abdomen touches the nest, but considering the similitude with AbW and the sound described, the mechanism of production of vibrations is likely to be drumming. A movement similar to the LtV of *P. metricus* has also been observed in *Polistes erythrocephalus* (West-Eberhard 1982), *P. canadensis* (West-Eberhard 1986), *P. fuscatus* (Savoyard et al. 1998), and *Ropalidia cyathiformis* (Gadagkar and Joshi 1984).

18.2.1.3 Scraping

Scraping the nest surface is another example of a mechanism to induce vibrations in the substrate that is made possible by the rigid exoskeleton. The individual scratches the nest with a part of the body and generates a signal that may consist of two components: substrate-borne waves and sound.

Guard wasps of *Asteloeca ujhelyii* are a subgroup of workers that usually stand on the outside of the nest defending it from intruders (Nascimento et al. 2005). While standing on the nest's envelope, some workers have been observed scraping the nest surface with the tarsal claws of their forelegs. Substrate-borne waves were recorded when a dissected wasp's leg was moved repeatedly along the surface of the nest envelope. Similarly, workers of *Synoeca virginea* (Overal 1982) and *S. septentrionalis* (O'Donnell et al. 1997) have been observed scraping their mandibles on the nest when attacked.

Larvae of social wasps have softer bodies compared to the adults and they are constrained inside a cell where their movements are restricted. Thus, they are not the perfect candidate to emit vibrations. However, larvae of *Vespa crabro* and *V. orientalis* have been reported to concurrently generate sounds and induce substrate-borne waves into the nest (Ishay and Landau 1972; Ishay and Schwartz 1973; Barenholz-Paniry and Ishay 1988). While contracting their soft bodies in an antero-posterior direction, the larvae scrape the interior wall of the cell with their sclerotized mandibles inducing the nest to vibrate. A similar behavior is also performed by larvae of *Vespa velutina* (Cervo, Cini, and Pepiciello personal observation).

18.2.1.4 Spectral and Temporal Features of Vibrations

Despite numerous descriptions of vibration-inducing behaviors that have been reported among social wasps, although with a confusing terminology (see Sect. 18.2.1), direct measurement of substrate-borne waves associated with such behaviors is scarce. Knowing the structure of a signal is a crucial aspect of the study of animal communication. First, because it gives us more information about how the signal is produced, thus clarifying terminology and classification, as in the case of the AbW. Second, because it helps to understand how the receiver actually perceives the signal, which is crucial to test the function with playback experiments. Vibrational signals are substrate-borne waves and their specific features can be described in terms of spectral (i.e., the frequency pattern, the energy distribution according to the frequency) and temporal parameters (i.e., duration of a signal, interval between signal emissions). In this regard, it must be noted that in earliest papers, the term "frequency" was referred to the frequency of oscillation describing the wasp's body movement (e.g., Gamboa and Dew 1981; Savoyard et al. 1998). Nowadays, it is consolidated to refer to the frequency as a parameter associated with the wave (i.e., substrate-borne vibrations) produced by behavior of the sender. The oscillation of the wasp may determine different parameters of the associated waves, depending on the mechanism of production. For instance, if the abdomen strikes the nest, as in the AbW, the oscillation would determine the interval between pulses (Fig. 18.3).

There are several instruments available to record substrate-borne vibrations and measure their parameters (see Chap. 8). Most devices need to be in contact with the

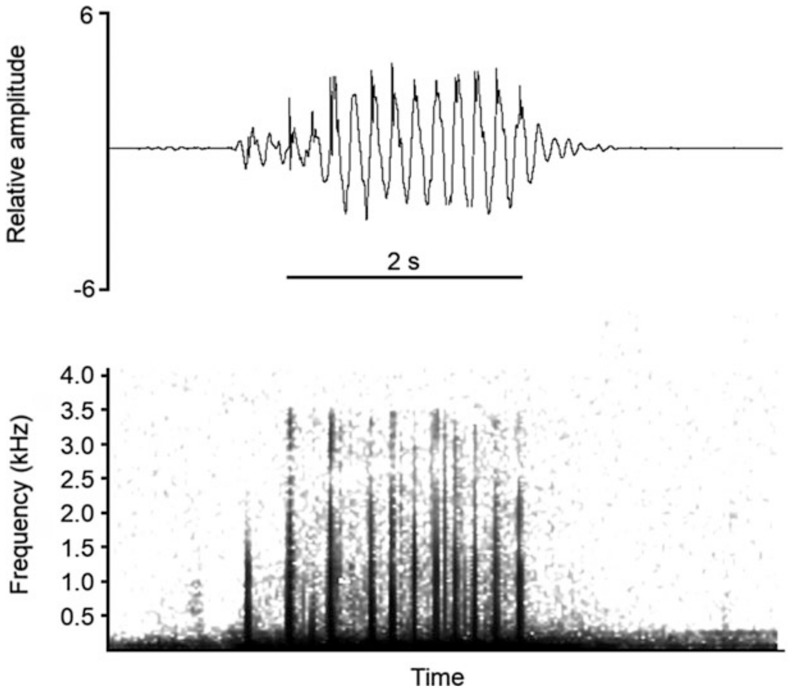

Fig. 18.3 Oscillogram (above) and spectrogram (below) of substrate-borne waves induced into the nest by abdominal wagging (AbW) of *P. dominula* and recorded by means of a laser vibrometer focused on the back side of the nest

substrate (e.g., accelerometer, piezo electric, cartridge), but some, such as the laser Doppler vibrometer, record the displacement of the substrate without adding any weight to it. One downside of contact instruments is that when coupled with the substrate, the weight of the device modifies the structure of the substrate itself and it may distort the original vibration, thus giving imperfect information. To date, laser Doppler vibrometers are considered to be one of the few methodologies capable of recording the displacement of the substrate without affecting the signals' structure. Another important parameter of vibrational signals is the intensity of vibrations. Most instruments listed earlier detect the relative amplitude of vibrations, but only calibrated instruments can measure the absolute amplitude. For this reason, usually an accelerometer or a laser vibrometer is needed to measure the acceleration (m/s^2) or the velocity (m/s) of the substrate's displacement, respectively.

To date, only the vibrations of *V. orientalis*, *V. germanica*, the AbW of *P. dominula*, and the AD of *P. fuscatus* have been measured with instruments capable of recording the substrate-borne component (Table 18.1). From these few studies, we know that vibrational signals of an adult hornet (GD) or paper wasp (AD and AbW) are characterized by a series of pulses with a broadband spectrum profile (Ishay 1975; Ishay and Nachsen 1975; Brennan 2007; Suryanarayanan et al. 2011) (Fig. 18.3). Most of the energy of GD is included in the frequency range of

Table 18.1 List of social wasps in which at least one behavior that may induce vibrations in the nest structure has been reported. The context of the behavior is reported when present in the literature. The vibration sensor and playback device are reported only for the species in which the vibrations transmitted to the nest have been recorded and /or tested with a playback experiment

Group	Species	Behavior	Context	References	Vibration sensor	Playback device
Stenogastrinae	*Eustenogaster calyptodoma*	GD	De	Hansell (1987)		
	Eustenogaster eximia	GD	De	Krombein (1991)		
	Eustenogaster fraterna	GD; LgV	De; A-L	Francescato et al. (2002)		
Vespinae	*Vespula consobrina*	GD	A-L	Akre et al. (1982)		
	Vespula germanica	GD	R	Ishay and Brown (1975), Ishay and Nachsen (1975), Taylor and Jeanne (2018)	Accelerometer	Speaker
	Vespula maculifrons	GD	De	Ross (1982)		
	Vespa crabro	S	A-L	Autrum and Schneider (1948), Ishay and Schwartz (1973)		
	Vespa orientalis	WV; GD; S	De; R; A-L	Schaudinischky and Ishay (1968), Ishay and Landau (1972), Ishay and Schwartz (1973), Ishay et al. (1974), Ishay (1975), Ishay and Sadeh (1982), Barenholz-Paniry and Ishay (1988)	Accelerometer; cartridge	“Home-made vibration transmitter”
	Vespa velutina	S	A-L	Cervo, Cini and Pepiciello pers. obs.		
	Vespula vulgaris	GD	De	Ross (1982)		
Ropalidiini	*Belonogaster juncea*	LgV; GD	Do; A-L	Tindo et al. (1997)		
	Belonogaster petiolata	LgV	A-L	Keeping (1992)		
		LtV	Do	Gadagkar and Joshi (1984)		

	Ropalidia cyathiformis					
	Ropalidia fasciata	HD	A-L	Jeanne (1975), Ito (1983), Ito (1986)		
	Ropalidia marginata	WV	A-L	Sen and Gadagkar (2006)		
	Ropalidia opifex	GD	De	Fortunato et al. (2004)		
	Ropalidia revolutionalis	WV; HD	Do; A-L	Ito (1987), Hook and Evans (1982)		
Mischocyttarini	*Mischocyttarus cassununga*			Santos et al. (2007)		
	Mischocyttarus cerberus	WV; GD	De	Togni and Giannotti (2010)		
	Mischocyttarus drewseni	GD	De	Jeanne (1972)		
	Mischocyttarus labiatus	GD	De	Litte (1981)		
Polistini	*Polistes annularis*	AbW	Do; A-L	Hermann and Dirks (1975), Hughes et al. (1987)		
	Polistes atrimandibularis	AbW	Do; A-L	Mignini and Lorenzi (2015)		
	Polistes biglumis	AbW	Do; A-L	Mignini and Lorenzi (2015)		
	Polistes canadensis	LtV	Do	West-Eberhard (1969), West-Eberhard (1986)		
	Polistes carnifex	AbW; AD	Do; A-L	Corn (1972)		
	Polistes chinensis	AbW	Do	West-Eberhard (1969)		

(continued)

Table 18.1 (continued)

Group	Species	Behavior	Context	References	Vibration sensor	Playback device
	Polistes dominula	WV; AbW	De; Do; A-L	Heldmann (1936), Pardi (1942), Röseler and Röseler (1989), Brillet et al. (1999), Bruschini et al. (2005), Jha et al. (2006), Brennan (2007), Pepiciello et al. (2018)	Accelerometer; laser vibrometer	Electrodynamic shaker
	Polistes erythrocephalus	LtV; AbW	Do			
	Polistes exclamans	AbW	Do	West-Eberhard (1969), Hermann et al. (1975)		
	Polistes flavus	AbW	Do	West-Eberhard (1969)		
	Polistes fuscatus	LtV; AbW; AD	Do; A-L	Rau (1928), Pratte and Jeanne (1984), Harding and Gamboa (1998), Savoyard et al. (1998), Suryanarayanan et al. (2011), Jandt et al. (2017)	Piezoelectric polyvinylidene fluoride foil	Solenoid; piezoelectric polyvinylidene fluoride foil
	Polistes instabilis	AbW	Do	Hughes and Strassmann (1988), Jha et al. (2006)		
	Polistes jokahamae	AbW	Do	Yoshimura et al. (2019)		
	Polistes major major	AbW	Do	West-Eberhard (1982)		
	Polistes metricus	LtV; LgV; AbW	Do; A-L	Gamboa et al. (1978), Gamboa and Dew (1981)		
	Polistes semenowi	GD		Zacchi et al. (1996)		
	Polistes snelleni	AD	A-L	Yamane (1971)		
	Polistes stigma	AbW	Do	Suzuki (1996)		
	Polistes sulcifer	GD		Cervo (1990, 2006)		

	Polistes versicolor	AbW		Esch (1971), de Souza and Prezoto (2012)		
Epiponini	*Asteloeca ujhelyii*	S	De	Nascimento et al. (2005)		
	Agelaia yepocapa	GF	De	O'Donnell et al. (1997)		
	Apoica albomacula	GF	De	O'Donnell et al. (1997)		
	Brachygastra augusti	GF	De	O'Donnell et al. (1997)		
	Parachartergus colobopterus	GD	De	Jeanne and Keeping (1995)		
	Polybia dimidiata	GF	De	O'Donnell et al. (1997)		
	Polybia occidentalis	WV; GF	De	Jeanne (1981)		
	Polybia dimorpha	GF	De	O'Donnell et al. (1997)		
	Polybia atra	AbW	De	Hase (1935)		
	Synoeca septentrionalis	GF; GD; S	De	West-Eberhard (1982), O'Donnell et al. (1997)		
	Synoeca virginea	GD; S	De	Overal (1982), West-Eberhard (1982)		

Behaviors: *LtV* Lateral vibration, *LgV* Longitudinal vibration, *WV* Wing vibration, *GF* Gastral fanning, *AbW* Abdominal wagging, *GD* Gastral drumming, *AD* Antennal drumming, *HD* Head drumming, *S* Scraping. Contexts: *De* Defense, *R* Recruitment, *Do* Dominance, *A-L* Adult–larvae

80–2000 Hz, with a dominant frequency of 500 Hz and 125 Hz in *V. germanica* and *V. orientalis*, respectively (Ishay 1975; Ishay and Nachsen 1975). In contrast, the dominant frequencies of AD and AbW are 16 Hz and 50 Hz, respectively (Suryanarayanan et al. 2011; Pepiciello et al. 2018).

Among arthropods, vibrational signals produced by individuals drumming on several different substrates are usually characterized by a broadband spectrum profile (Elias and Mason 2010). This mechanism theoretically generates a broadband signal that at the source contains all frequencies at equal intensities; the filtering properties of the substrate are responsible for the final spectrum profile of the signal (Hebets et al. 2008). Wasps' drumming vibrations are consistent with the vibrational signals of other arthropods. The differences in the dominant frequencies within different species performing GD, and between AbW and AD, may be due to the differences in nest structure, either of the material or the geometry, and the peculiar way each species strikes the surface.

Until recorded with an accelerometer, AbW was considered to transmit vibrations into the nest just by tremulation (i.e., without contact between the abdomen and the comb) (Brennan 2007). However, spectral analysis (Fig. 18.3) supports the hypothesis that an oscillatory behavior, such as AbW, can also be considered as a particular form of drumming, in that they both transmit similar broadband spectrum profiles in the nest structure when the body of the wasp comes in contact with the comb. Additionally, the simultaneous recording of AbW with an accelerometer and a video camera revealed that each pulse is induced by the beating of the abdomen on the nest (Brennan 2007). Sometimes, during the oscillation, the abdomen does not touch the nest; in these cases, the characteristic pulses of AbW are not picked up by the accelerometer.

As expected for broadband signals, the temporal features seem to be a better candidate to distinguish drumming behaviors among species and within a species, but associated in different contexts (Elias and Mason 2014). In Vespinae, the interval between pulses of GD is shorter in *V. germanica* than in *V. orientalis*, and in the latter, different rhythms distinguish scraping from GD, as well as GD performed by workers in different contexts, e.g., to stimulate the queen to resume her laying activity or to increase the activity of larvae and workers (Ishay et al. 1974; Ishay and Brown 1975).

The frequency profile of vibrations induced by scraping is similar to the spectrum profile of drumming. In the case of Vespinae larvae, most of the energy of the signals is in the range of 100–2000 Hz, and the temporal distinction of discrete pulses is determined by the rhythmic contraction of the larva inside the cell (Ishay and Landau 1972; Ishay and Schwartz 1973). The leg scraping of Polistinae guard wasps induces vibrations with a dominant frequency of 500 Hz, which is maintained even when the velocity of scraping varies (Nascimento et al. 2005).

Unfortunately, vibrations induced in the nest material by tremulation (LtV, LgV, and WV) have not been measured yet. But from what we know of other insects using this mechanism of production, we can expect these behaviors to induce substrate-borne waves with most of the energy concentrated in a narrow range of low frequencies (Hill 2009).

18.2.2 Perception of Vibrations

To communicate via substrate-borne waves, insects usually rely on mechanical receptors that detect particle motion perpendicular to the direction of propagation of waves (reviewed in Hill 2009; and Lakes-Harlan and Strauß 2014). Among social Hymenoptera, most of the knowledge of mechanical receptors comes from studies on *Apis mellifera*, but the few studies on solitary and social wasps unveiled the mechanism of perception of vibrations that is also found in Vespidae (Staudacher et al. 2005; Hunt and Richard 2013).

Social wasps have both external (i.e., hair sensilla) and internal (i.e., scolopidial sensilla) mechanical receptors (Hunt and Richard 2013). All of them are able to detect the displacement of the organ with respect to the environment and translate it into an electrical impulse that is processed by the nervous system. However, probably not all of them are involved in vibrational communication (Lakes-Harlan and Strauß 2014).

To perceive vibrational signals propagated through the nest, social wasps must be able to detect the displacement of the comb’s surface perpendicular to their legs. In order to do so, they likely rely on complex chordotonal organs, such as the subgenual organ in the proximal tibia and the Johnston’s organ in the antennal pedicel (Fig. 18.4). The detection of the substrate’s displacement requires the stimulus and the receptor to be coupled, meaning that the part of the body in which the receiving organ is located must be in contact with the vibrating surface, either directly or indirectly. Since the legs are always in contact with the substrate, the subgenual organ is considered the primary organ for perceiving the vibrations in many insects, and it is also likely the principal receiving mechanism in adult social wasps (Hunt and Richard 2013). The Johnston’s organ might play a role in the perception of substrate-borne waves as well, since the highly mobile antennae can easily come in contact with the substrate.

The sensitivity of the subgenual organ has been tested in *V. crabro* (Autrum and Schneider 1948), and its morphology has been described in three polistine species: *Agelaia pallipes, Polybia paulista,* and *Mischocyttarus cassununga* (Santos et al. 2007). In the latter study, the number of scolopidia in the subgenual organ is shown to be around 40. This is consistent with the number of scolopidia observed in other social Hymenoptera, such as ants (Howse 1964; Menzel and Tautz 1994) and honey bees (Kilpinen and Storm 1997). The sensitivity of the subgenual organ in *V. crabro* seems to be tuned to the substrate-borne waves produced by the species. In fact, most of the energy of the vibrations emitted by the larvae is around 160–200 Hz and the lower threshold of the subgenual organ is at about 80 Hz, while its sensitivity decreases rapidly until 1000 Hz (Ishay and Schwartz 1973).

The Johnston’s organ has been described in Polistinae, and it perceives the displacement of the flagellum with respect to the pedicel of the antenna (Santos et al. 2007). This means that during inspection of the nest or the brood, when the wasp inserts its head in the cell, the flagellum is very likely to touch the cell’s wall from which it could easily then perceive the vibrations.

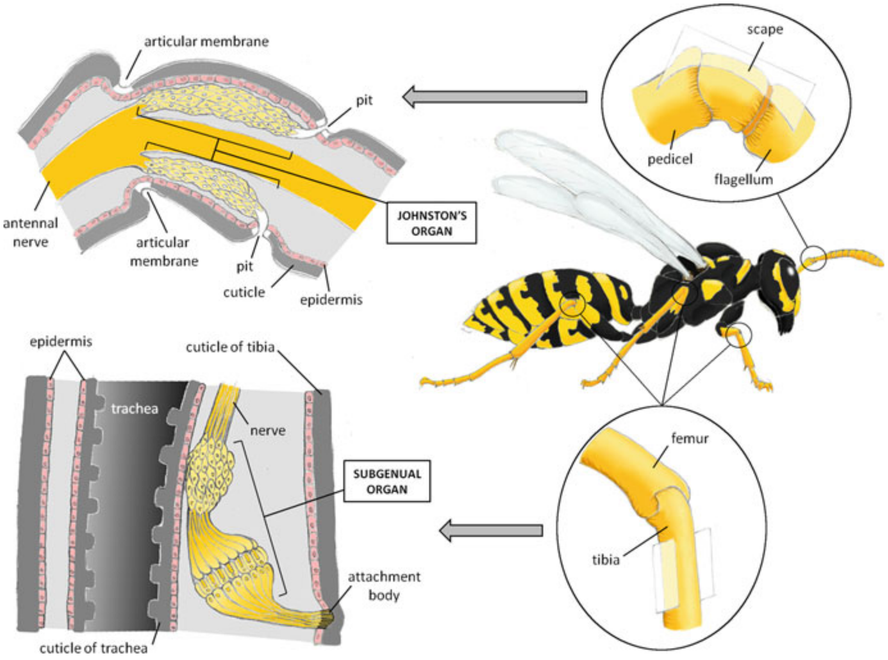

Fig. 18.4 Drawing of a wasp with highlighted locations of mechanoreceptors. Sections are of Johnston's organ and the subgenual organ. Drawings are adapted from Hunt and Richard (2013) and Santos et al. (2007). Drawings by Marco Valerio Rossi Stacconi

On the contrary, there is no evidence so far that social wasps perceive airborne vibrations (sounds). Tympanic organs, which are chordotonal organs specialized in the detection of sounds, are considered absent in all Hymenoptera (Hunt and Richard 2013). An "acoustic box," found in the center of the head of Vespinae (absent in Polistinae), has been hypothesized to be used for gravity and sound perception (Ishay and Shimony 1986). However, the function of this organ has yet to be tested. Even if the dedicated organs are not present, we cannot exclude the possibility that social wasps may be able to detect airborne vibrations. For instance, in *A. mellifera* several ingenious studies revealed that workers are not able to perceive the compressional waves of sounds, but they are sensitive to airflows associated with them (Michelsen 2014), even if the mechanism that enables the workers to perceive the airflow is still unknown.

18.2.3 Transmission of Vibrations

The substrate in which vibrational signals are induced has a key role in biotremology. The geometry and material of the substrate determine the type of waves that are transmitted by the insect and how they are filtered (Elias and Mason

2014). In social wasps, all behaviors involved in transmission of vibrations into the substrates are performed on the nest: on the combs or on the envelope enclosing them. Thus, understanding how substrate-borne waves propagate in the nest structure is crucial in the biotremology of social wasps.

The architecture of nests in social wasps is extremely variable, and it has been studied from an evolutionary point of view in relation to predatory and parasitic pressure (Jeanne 1975). The transmission properties of the nests have been poorly investigated, but the structural similarities with other social insects, and some peculiar characteristics, suggest that it may be a suitable substrate for propagation of vibrational signals. As in the hive of honey bees, the comb of social wasps is made of adjacent hexagonal cells. This structure creates a continuum in the substrates represented by the rim of the cells, which, at least in Vespinae, are thicker compared to the cell walls (Schaudinischky and Ishay 1968). In honey bees, this web made of cell rims enables a very good transmission of vibrations (Michelsen et al. 1986). Moreover, in most wasps' nests, the comb is free on all sides. In the honey bee's comb, the impedance of the comb is lower when the cells are open, and closer to the border of the comb, when it is free to move, as in wild combs that are attached just by one side. Likely for this reason, in commercial hives in which combs are framed, honey bees free the comb from the frame in the area where they usually perform the dances (Sandeman et al. 1996). In the nest of social wasps, the propagation of vibrations may be different compared to the honey bee's comb for the following four characteristics: (1) the comb is usually free on all sides, (2) the surface is striped with a rough pattern, (3) when more than one comb is present, these combs are interconnected, and (4) an external envelope encloses the comb (Fig. 18.5). The first two characteristics are shared by most social wasps, whereas the third and fourth are peculiar to Vespinae and only found in some species of Polistinae (Kojima 1982; Wenzel 1998; de Seixas Felizardo et al. 2018). With the exception of Stenogastrinae and some epiponines, most social wasps' nests are attached to the supporting structure through one or more thin stalks, the petioles (Fig. 18.5). The main function is to defend the nest from intruders, such as ants, but it enables the nest to be entirely suspended and free from restrictions. In this way, we can expect the outer side of the comb to amplify the vibrations as happens in the hive of honey bees when the comb is free from the frame (Schaudinischky and Ishay 1968; Sandeman et al. 1996).

The building material is made by mixing only organic (vegetable fiber) or mineral materials (mud) or a combination of the two with saliva (Ganor et al. 1986). This manufactured material is laid horizontally in the cells' walls in consecutive layers, creating a rough surface. Thus, the stiffness is parallel to the comb's face along the rim of the cells, facilitating the transmission of substrate-borne waves, and the walls are striped with irregularities that enable the production of vibrations by scraping of the surface (Schaudinischky and Ishay 1968).

In the species in which several combs constitute the nest, the transmission of vibrations from one comb to the others can be ensured by thin interconnecting columns made of the same material as the combs, or by the external envelope that, in some species, connects all the combs along their sides (Schaudinischky and Ishay 1968; Jeanne 1975). In a minority of species, multiple combs that are not attached to

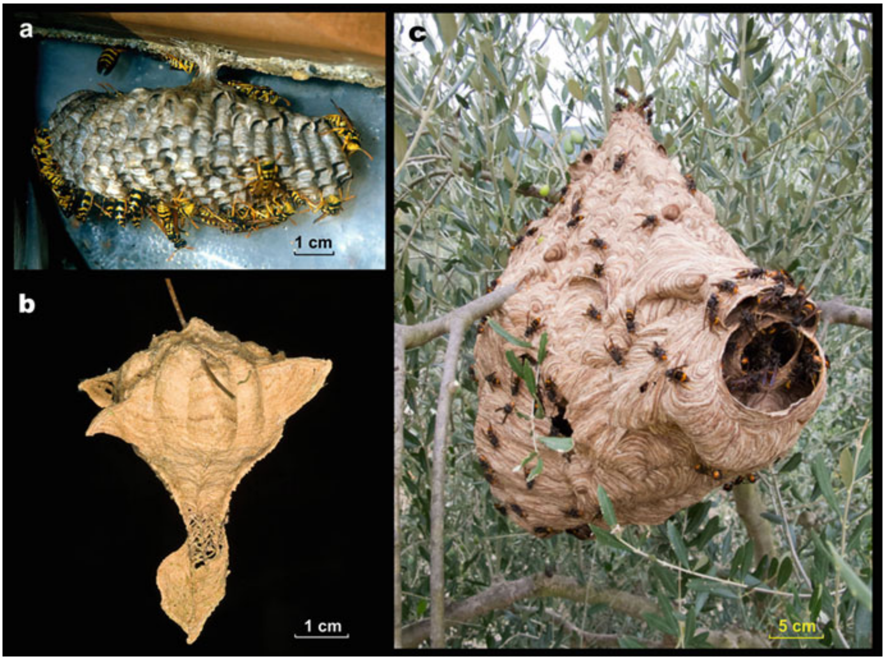

Fig. 18.5 Three examples of social wasps' nests and features that may enhance vibrational communication: (**a**) nest of *Polistes nimpha*, (**b**) nest of *Eustenogaster fraterna*, and (**c**) nest of *Vespa velutina*. In (**a**) the comb is free on all sides, in (**b**) and (**c**) the nest is enclosed in an envelope, in all three nests the surface is striped with a rough pattern. Photographs by Rita Cervo (**a** and **c**) and David Baracchi (**b**), with permission

one another can be part of the same colony (i.e., satellite nests), such as in the case of *R. fasciata* that performs HD (Jeanne 1975; Ito 1983, 1986). Vibrations are mainly transmitted when substrates are contiguous, but low frequencies can be transmitted also to substrates separated by an air gap up to 10 cm (Eriksson et al. 2011; Gordon et al. 2019). Thus, in species with satellite nests, vibrations can be transmitted to colony members present on either the same or close combs.

The external envelope may provide two additional advantages to vibration transmission, improving the use of vibrations as signals for communicative purposes. The envelope isolates the nest from airborne noises and provides a continuous substrate that encloses the entire colony and that may facilitate the exchange of information among all colony members (Schaudinischky and Ishay 1968). Moreover, in some Stenogastrinae, which lack the petiole, the envelope is the main surface to transmit and amplify substrate-borne waves (Hansell 1987; Turillazzi 2012).

Since all the colony activities and nestmate interactions take place on the nest, we expect wasps to take advantage of this self-made substrate and that the signals should match its transmission properties (Elias and Mason 2014). It is likely that wasps' mechanisms of vibration production evolved to match the transmission properties of the substrate. In hornets, the absorption coefficient of the comb is complementary to the spectrum profile of all three observed vibrational behaviors, i.e., the scraping of the larvae and the two drumming behaviors performed by workers (the "awakening dance" and the "dance facing the queen") (Ishay 1975). But this is likely to be a consequence of the production mechanisms, drumming and scraping, which induce broadband vibrations into the substrate (Hebets et al. 2008). Further understanding can be found by investigating other mechanisms of production, such as tremulation, which may induce vibrations with a narrower frequency profile into the substrate.

18.3 Why? Functions of Vibrational Signals in Social Wasps

Over the years, many, and sometimes contrasting, hypotheses on the function of vibrations in wasps' societies have been proposed. Most of the contradictions emerged as the hypotheses were based on correlative studies. In the last decade, some hypotheses have been tested using the playback of previously recorded vibrations, which have provided a clearer understanding of the communicative role of vibrations in social wasps. Nevertheless, the function of most vibrational behaviors in social wasps is yet to be determined, because of the abundance of the behaviors that induce vibrations and the variety of contexts in which they occur. With the aim of providing an overview of the functions that vibrations have in wasps' societies, we discuss the vibrational behaviors associated with the following four challenges faced by social wasps: defense, recruitment, dominance, and larvae–adult communication (Fig. 18.1). For each category, we address the proposed hypotheses, correlated evidence, and, when available, direct testing of functions.

18.3.1 Defense

When a colony is threatened by a predator, the members present on the nest use warning behaviors to both warn the intruder before a direct attack and coordinate a collective response (Starr 1990). Predators, either invertebrates or vertebrates, are warned by the visual and acoustic components, whereas the release of an alarm pheromone is used to recruit other members of the colony toward the attacker (Jeanne 1981; Fortunato et al. 2004). However, most warning behaviors also have a vibrational component, such as with wing vibrations, which are widespread in Polistinae and Vespinae (Ishay and Sadeh 1982; Bruschini et al. 2005; Togni and Giannotti 2010), leg scraping (Nascimento et al. 2005), abdomen drumming (Litte 1981; Ross 1982; West-Eberhard 1982; Hansell 1987; Krombein 1991; Jeanne and Keeping 1995; Francescato et al. 2002; Fortunato et al. 2004; Togni and Giannotti 2010), and mandible scraping (Barenholz-Paniry and Ishay 1988).

Vibrations are rapidly transmitted throughout the nest; thus, they can warn all nestmates standing on the nest of the imminent danger, regardless of their position or activity within the colony. In the termite *Macrotermes natalensis*, substrate-borne waves have been shown to give information on the direction from which the threat is coming and to be used for coordination of group defense (Hager and Kirchner 2014). When a predator attacks a colony, soldiers drum their heads on the walls of the nest, producing a vibrational alarm signal. In response to the alarm signal, workers retreated into the nest, whereas more soldiers were recruited toward the surface where the predator would be found. Termites make use of tropotactic directional vibration sensing to orient to the source of vibrations.

There is evidence in all three subfamilies of social wasps that vibrations can function as a defense-related signal. Among Stenogastrinae, females of *Eustenogaster* spp. often usurp a pre-occupied nest, so the resident female guards the entrance of the nest by standing next to the opening on the inside of the envelope (Hansell 1987; Francescato et al. 2002). Whenever an alien female approaches or lands on the nest, the resident female performs GD to warn the alien female that the nest is occupied. The alien performs GD too after landing on the nest, but if it does not leave the nest after perceiving the GD from the resident female, the confrontation can escalate into a fight. Interestingly, among Polistinae, *Parachartergus colobopterus* seems to have lost the alarm pheromone and replaced it with a form of GD, the gaster tapping (Jeanne and Keeping 1995). Similarly, the leg scraping of *Asteloeca ujhelyii* workers has been hypothesized to inform nest mates about the approach of a wasp to the nest entrance (Nascimento et al. 2005). In hornets, when a colony of *V. orientalis* is threatened, larvae scrape the walls of the cells and workers perform WV; immediately after the onset of WV, every activity on the nest stops (Ishay and Sadeh 1982; Barenholz-Paniry and Ishay 1988). Also among Polistinae WV is correlated with the defense of the colony; however, in this subfamily the vibrational component of WV is not sufficient to elicit a defense response from the colony members. Instead, WV is associated with the release of the alarm pheromone; therefore, in Polistinae, vibrations induced by WV seem to be a by-product of a pheromonal release (Jeanne 1981).

Nevertheless, in order to assess the role of vibrations in coordinating defense strategies in social wasps, experimental tests that quantify the response of colony members to the vibrational component of warning behaviors are needed.

18.3.2 Activation and Recruitment of Nestmates

In social wasps, the work is regulated among members of the colony. The hypothesis that vibrations regulate the activity in the nest was formulated for the first time in the 1970s, based on the observation of workers of *V. orientalis* performing GD (originally named “dance of awakening”) (Ishay and Schwartz 1973). When workers’ GD vibrations were played back into the nest, the activity in the nest increased: larvae began to scrape their cell walls and workers either resumed attending larvae or attempted foraging flights (Ishay et al. 1974).

Recently, it has been confirmed that in *V. germanica* substrate-borne waves act as a recruitment signal. The playback of the sole vibrational component of GD led to increased movement in the nest, trophallaxis, and worker departures from the nest (Taylor and Jeanne 2018).

In some Polistinae, vibrations are correlated with an increase in general activity of colony members. For instance, LtV is related to an increase in activity and, in particular, of other vibrational behaviors in colonies of *P. fuscatus* (Savoyard et al. 1998). In *P. dominula* and *P. instabilis*, the activity on the nest increases after AbW (Jha et al. 2006). However, this response has yet to be demonstrated to be caused by vibrational stimuli alone.

18.3.3 Dominance

Social structure varies widely across wasp taxa. In Vespinae, reproductive females and workers are clearly distinct, both morphologically and physiologically, whereas in Stenogastrinae and Polistinae there is a more flexible division of labor and all females can potentially lay eggs (Hunt 2007). Among Polistinae, since potentially all females can reproduce, a linear dominance is established; the dominant individual assumes the role of queen and lays eggs, while all other females are subordinates with a lower-ranking position and act as workers (i.e., non-reproductive females that help in maintaining the colony) (Pardi 1948). This structure is established and maintained by means of dominance interactions, which are more aggressive at the beginning of the colony cycle and ritualized once the dominant individual has established its role (Pardi 1948; Jandt et al. 2014). At this stage, the dominant female diverges from the subordinates both in terms of behavior and physiological features; she performs "dominance behaviors" toward subordinates and workers (Pardi 1942) and develops a unique profile of cuticular hydrocarbons (Dapporto et al. 2007). Over the years, many tremulatory and drumming behaviors have been reported to be part of the suite of "dominant behaviors." In particular, LtV, LgV, and AbW are usually performed more frequently by the dominant female, and they have been associated with adult–adult aggressive interactions in several species (Ropalidiini: Gadagkar and Joshi 1984; Ito 1987; Tindo et al. 1997; Polistini: West-Eberhard 1969, 1982, 1986; Corn 1972; Gamboa and Dew 1981; Hughes et al. 1987; Hughes and Strassmann 1988; Suzuki 1996; Savoyard et al. 1998; Brillet et al. 1999; Mignini and Lorenzi 2015). Even in non-aggressive species such as *P. jokahamae,* only the queen performs AbW in association with higher oviposition frequency (Yoshimura et al. 2019).

All "dominance behaviors" are considered to be involved in the maintenance of the reproductive monopoly by the dominant female (Pardi 1948; Jandt et al. 2014). The vibrational component of these behaviors has been hypothesized to be one of the mechanisms by which the dominant individual achieves and maintains the monopoly, both by communicating to the subordinates of the presence on the nest of an active dominant female (direct influence) and by inducing a physiological change in the subordinates to ensure their non-reproductive status (indirect influence) (Jeanne 2009). Whether vibrations have either a direct or indirect influence on subordinates and workers has yet to be tested. The direct influence is difficult to test, because during dominant interactions visual, chemical, and vibrational signals occur together in signaling status, and it is difficult to disentangle the relative role of each of them on fertility, as well as experimentally decouple fertility from dominance. However, the indirect effect of mechanical stimulation has been demonstrated on larval physiology (see Sect. 18.3.4 for details) (Suryanarayanan et al. 2011). Thus, it is possible that vibrational signals associated with "dominance behaviors" also affect the reproduction of workers (Jeanne 2009).

An interesting insight into the role of vibrational stimuli in dominance can be found by studying obligate social parasites and their hosts. Three species of the *Polistes* genus are obligate social parasites. They lack the worker caste and need to usurp a colony from a closely related species to obtain parental care for their brood and thus reproduce (Cervo 2006). The female parasite usurps a nest and eventually replaces the dominant female (which can either stay on the nest as a subordinate or abandon the colony) and begins laying eggs. Workers of the usurped colony then rear the brood of the parasite. The parasite is able to integrate herself into the social structure of the host by performing "dominance behaviors" and modifying her own chemical profile to match that of the host colony (Lorenzi 2006). However, at least in one species, the control over the reproduction of the host is limited (Cini et al. 2014). It is possible that one or more components of the "dominant behaviors" of social parasites may differ from its host. Social parasitism has proven to be a useful tool to reveal mechanisms and evolution of insect societies that are still unknown (Cini et al. 2019), and it may be the case also for vibrations associated with "dominant behaviors." In fact, all three species of obligate social parasites perform AbW in the days following the usurpation of the nest, and *P. semenowi* and *P. sulcifer* also display GD (Cervo 2006; Mignini and Lorenzi 2015). A recent study on the host–parasite model *P. biglumis*–*P. atrimandibularis* supports the use of AbW in the host, *P. biglumis,* as an indication of dominant status (Mignini and Lorenzi 2015). Interestingly, when the parasite *P. atrimandibularis* took the dominant role on the nest, the parasite performed AbW at a rate similar to the dominant female before the intrusion, whereas the subdued female performed AbW less frequently than in non-parasitized colonies. Unfortunately, the AbW and associated vibrations were not measured in this study or in any other host–parasite system to date. The comparison between the host and the parasite vibrations could unveil to what extent dominance is expressed by the vibrational component of "dominant behaviors."

18.3.4 Adult–Larvae Communication

Adults are not the only members of a wasp colony. The immature brood of eggs, larvae, and pupae are often present in the nest, which literally surrounds them within the cell walls. Interactions between larvae and adults can be crucial in social wasps; they often exchange saliva (trophallaxis), which provides essential nutrients to the adults in Vespinae (Ishay and Ikan 1968), and larvae rely on the adults to be fed. Therefore, communication between larvae and adults in the colony is fundamental. The exchange of vibrations is bidirectional: from larvae to adults and from adults to larvae.

Larvae use vibrations to communicate their feeding status to workers and to warn them of an approaching threat. The "hunger signal" of *V. orientalis* larvae is one of the first wasp vibrational signals for which the function has been identified and tested with a playback experiment (Ishay et al. 1974). Ishay and collaborators demonstrated that the scraping of the mandibles on the cell's wall generated by starved larvae attracts workers to the vibrations' source. The attraction was clearly related to feeding. In fact, workers brought food and droplets of saliva to the cell in which the shaker emitting the playback was positioned. Scraping is also performed by larvae of *V. crabro* and *V. velutina*, in which it likely has the same function as in *V. orientalis*. However, it has never been recorded in species of *Vespula* (*V. germanica:* Schaudinischky and Ishay 1968; Ishay and Brown 1975; *V. pensylvanica* and *V. atropilosa:* Akre et al. 1976), and it is not reported in any Stenogastrinae and Polistinae species. In *V. orientalis*, when the colony is disturbed by any threat, larvae scrape the walls of the cells using a different rhythm from that of the "hunger signal." Such behavior has been hypothesized to transmit the alarm inside the nest (Barenholz-Paniry and Ishay 1988).

Adults also use vibrational stimuli to communicate to larvae. For instance, in Vespinae, GD triggers larvae to emit the "hunger signal" (Ishay et al. 1974). In Polistinae, several correlative data showed that larvae may be one of the recipients of adults' vibrational signals: (1) AbW appears when larvae reach at least the third instar, (2) AbW and LtV are performed also in the absence of other adults on the nest, and (3) LtV, AbW, and AD are performed while adults are feeding the larvae (Brillet et al. 1999; Brennan 2007).

A proposed function of vibrations induced by LtV and AbW was that they signal the larvae when to release or withhold their saliva during feeding interactions (Harding and Gamboa 1998; Savoyard et al. 1998). This hypothesis has been recently rejected in *P. dominula*, in which a playback experiment demonstrated that AbW does not have any direct effect on the larvae's release or withholding of saliva (Pepiciello et al. 2018). However, the study showed that AbW elicits an increase in larval movements, which likely attracts the attention and care of the adults, thus providing the first direct demonstration of an adult–larvae vibrational signal in *P. dominula*.

Another function of signals directed at larvae is caste determination, as explained by the "mechanical switch hypothesis" (Jeanne 2009). For many years, the nourishment level of larvae has been considered the only mechanism determining the physiological differences between workers and reproductive females in Polistinae (i.e., low nourishment levels would determine a worker phenotype) (Judd et al. 2015). The "mechanical switch hypothesis" predicts that vibrational stimuli modulate the biochemical pathways that direct the larval development toward a worker phenotype, so that vibrations would have a modulatory effect on the nourishment level and an indirect effect on caste determination (Jeanne 2009). The correlation between the beginning of vibrational behavior occurrence and third instar larvae in the nest supports this hypothesis, as the third instar is the stage at which developmental paths diverge (Jeanne 2009). To date, the "mechanical switch hypothesis" has been verified only for vibrations induced by AD in *P. fuscatus* (Suryanarayanan et al. 2011). In this study, the females emerging from the nests that were subjected to a vibrational playback similar to AD had a more pronounced "worker" phenotype (i.e., low percentage of fat stores) compared to the females that emerged from control nests (i.e., more gyne-like levels of fat stores). Additionally, a novel transcriptional experiment demonstrated that either vibrations or nourishment level alone can influence the gene expression in *P. fuscatus* offspring, but their interaction defines the caste of colony members (Jandt et al. 2017). The validity of the "mechanical switch hypothesis" has yet to be tested for other *Polistes* species and their vibrations.

It cannot be excluded that the "mechanical switch hypothesis" may be valid also for species of other subfamilies, in which the hypothesis has not yet been tested, but vibrations are known to be associated with the feeding of larvae, such as LgV in *E. fraterna* (Francescato et al. 2002) and GD in *V. consobrina* (Akre et al. 1982). Both these species have a primitive social structure similar to Polistinae, in which workers and reproductive females do not differ morphologically. Taking into consideration just Vespinae and Polistinae, it has been hypothesized that vibrations were the rudimentary mechanism for caste biasing in the common ancestor of these two subfamilies, and for this reason, vibrational behaviors associated with brood attendance have been observed only in species with primitive caste differentiation (Jeanne and Suryanarayanan 2011). According to this evolutionary hypothesis, such a rudimentary mechanism would have been replaced by ritualized behaviors in less derived taxa, such as Polistinae, and by more specialized mechanisms, such as pheromones and differences in food quality, in the more derived species of Vespinae. However, this evolutionary model neglects the occurrence of similar vibrations in at least one species of Stenogastrinae. Additionally, according to the most recent molecular studies, sociality evolved twice in social wasps, once in Stenogastrinae and once in Vespinae + Polistinae (Piekarski et al. 2018). So, testing the "mechanical switch hypothesis" also in Stenogastrinae could have an important role in further understanding the evolution of sociality in wasps.

18.4 Perspectives

This chapter highlights that the use of substrate-borne waves is widespread and central to the integration of social life in the wasps. Vibrational communication occurs in all three subfamilies of Vespidae, and in at least two of them, it has been demonstrated to play a crucial role in the organization and maintenance of sociality. In both Vespinae and Polistinae, vibrations mediate adult–brood communication in both directions. Additionally, in Vespinae vibrations are a signal for the recruitment of nestmates, and in Polistinae, vibrations modulate the effect of nourishment on caste determination. Because the number of studies testing the role of vibrations in wasps is so low, much low-hanging fruit remains to be picked. The development of informed, competing hypotheses on function, followed up by well-designed experiments to test them, will yield rapid gains in understanding. We suggest that further work, in particular in the four areas discussed in this section, will bring a better understanding of the social life of wasps and of biotremology of social insects in general.

18.4.1 Measurement of the Surface-Borne Component of Vibrational Behaviors

More than 50 species have been reported to perform vibrational behaviors, but the vibrations associated with these behaviors have been measured in only four of them. Moreover, for one mechanism of production, tremulation, no attempt has yet been made to measure the surface-borne component (Ishay 1975; Ishay and Nachsen 1975; Brennan 2007; Suryanarayanan et al. 2011). The description of spectral and temporal features of substrate-borne waves is essential to being able to compare different behaviors in the same species and across species. This lack of knowledge is probably the main cause of confusion and redundancy in the terminology used so far to describe vibrational behaviors of wasps. Furthermore, any investigation on the communicative role of vibrations requires a functional test, for which a description of the temporal and spectral features of the signal is essential.

Some aspects of the life of social wasps are still poorly investigated and have not yet been associated with the production of substrate-borne waves. Yet, it is possible that some vibrational behaviors have yet to be described. For instance, males in social insects are often neglected, despite the importance and complexity of mating behaviors (e.g., males can establish leks, perform impressive sexual displays, and have alternative mating tactics) (Beani et al. 2014). In many polistine species, males have been observed to scrape either the substrate or the female with the abdomen, legs, or mandibles before and during mating; these behaviors have always been hypothesized to be associated with the release of pheromones (Turillazzi and Cervo 1982; Beani and Calloni 1991a, b; Beani 1996; Ayasse et al. 2001). However, the role of male pheromones has not been demonstrated in social wasps, whereas visual cues have been found to play a role in identification of genders and female choice, at least in Polistinae (Ayasse et al. 2001; Izzo and Tibbetts 2012; Cappa et al. 2016). It is possible that vibrations also mediate male territoriality or male–female interaction.

18.4.2 Mechanisms of Perception and Propagation into the Substrate

The knowledge on both the mechanisms of perception and propagation of vibrations into the nest comes from a minority of species or from the comparison with closely related species. Even though it has been shown that wasps' nests are a suitable substrate for the propagation of vibrations (Schaudinischky and Ishay 1968), it should be recognized that any substrate filters substrate-borne waves, affecting their spectral features in particular (Elias and Mason 2014). Thus, a better understanding of both the material and the structure of the substrate is needed to identify the key characteristics of the putative signal that may convey information. Similarly, understanding the mechanism by which receivers perceive a stimulus can be useful to identify what communication modality is mainly used by an animal. For instance, the inability of honey bees to perceive compressional waves excluded sounds from the possible communication modalities of the species (Michelsen 2014). Mechanoreceptors of social wasps have been poorly investigated. On one hand, the mechanism of perception still needs to be identified, as in the case of larvae. They lack legs and their antennae are too short to easily come in contact with the nest; it is possible that they rely on hair sensilla to perceive vibrations, but it has never been verified. On the other hand, physiological studies on the sensitivity of known mechanoreceptors in wasps are needed to identify the spectral and temporal features of vibrations that may play a major role in communication.

A better understanding of how vibrations are transmitted in the nest structure and perceived by the receivers will also clarify how social insects avoid interference caused by other individuals signaling or moving on the nest (i.e., biotic noise). In social wasps, from a few tens to hundreds of individuals can be present simultaneously in a colony, depending on the species. Additionally, most vibrational behaviors (i.e., drumming and scraping) induce vibrations in the nest surface that have a spectrum similar to that induced by any generic wasp's movement, such as walking. Thus, social wasps must have evolved behavioral and/or physiological strategies to avoid biotic noise (Virant-Doberlet et al. 2014). Vespinae are known to use two behavioral strategies that decrease noise interference: they avoid signals when other substrate-borne waves are induced into the nest (either abiotic or biotic) and they synchronize signaling (Ishay et al. 1974; Ishay and Brown 1975; Barenholz-Paniry and Ishay 1988). Additionally, it is possible that the temporal component of the signals (the total length and the interval between pulses) increases their detectability with respect to incidental vibrations. However, other strategies to reduce noise interference have yet to be investigated.

18.4.3 Playback Tests to Assess the Communicative Function of the Surface-Borne Component

To switch from correlational evidence to a direct test of signal function, all components of a signal should be decoupled and singularly tested on the receivers to quantify their behavioral changes. Such changes can be easily recognized and measured when the signal modifies the behavior of the receiver, as in the case of releaser pheromones, but it may be more difficult when the signal acts on the physiology of the receiver, as for primer pheromones (Richard and Hunt 2013). In social wasps, playback tests enabled the verification of the role of vibrational stimuli in recruitment and adult–brood communication in some species, and gave opportunities for similar tests in other species (Ishay et al. 1974; Suryanarayanan et al. 2011; Jandt et al. 2017; Pepiciello et al. 2018; Taylor and Jeanne 2018). Furthermore, these studies highlighted the findings that substrate-borne waves can act both in a direct and indirect way on the receivers' behavior, similarly to the primer and releaser mechanisms known for pheromones.

Two contexts in which vibrational behaviors are displayed—defense and dominance—have yet to be verified as relying on vibrational communication. Even though, in both contexts, wasps use chemical and visual communication, animal communication is usually complex and often involves multicomponent signals (Higham and Hebets 2013; Richard and Hunt 2013; Cervo et al. 2015). Thus, it is likely that vibrational stimuli modulate the effect of chemicals. For instance, in ants, the vibrational component of stridulation modulates the communicative function of the pheromone released during stridulation (Kirchner 1997). Playback tests of specific functional hypotheses are probably the sole means available to disentangle the overlap of different communication modalities and the role of each one.

18.4.4 Mechanism of Action of Vibrations on Insect Physiology

Mechanical stimuli are known to affect the physiology of insects: for instance, mechanical stress modifies the biogenic-amine levels, larval growth, and tissue damage in the red flour beetle, and substrate-borne waves modify the quantity of the juvenile hormone in honey bee workers (Hirashima et al. 1993; Schneider et al. 2004; Jinham et al. 2012). However, the mechanisms of action present at the molecular level are still unknown. The study of the effect of mechanical stimuli on a wasp's transcriptome and phenotype opens the way to further investigate the causal relation of this phenomenon (Jandt et al. 2017).

Caste determination is crucial in the evolution of sociality and thus of social wasps, and it may be modulated by vibrations not only in the tribe Polistini but also in other subfamilies as proposed by Jeanne and Suryanarayanan (2011). Social wasps are a suitable model to further investigate the processes associating vibrations, physiology, and social behavior.

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