



Vibrational Signals in Social Wasps: A Role in Caste Determination?

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SOCIAL INSECT COLONIES are characterized by specialization of their individual members whose diverse social activities are coordinated by means of cues and signals (Seeley 1995). It has long been recognized that the chemical mode dominates the signal channels used by social species (Wilson 1971). Mechanical signals, while probably less important than chemical signals, are also widely used and take a variety of forms, including stridulation, head-banging, piping, antennation, jerking, wing-buzzing, scraping, and drumming (Hill 2001; Hölldobler and Roces 2001).

Paper wasps (Vespidae) produce mechanical signals in a variety of contexts (Figure 11.1, Pratte and Jeanne 1984; Jeanne and Keeping 1995; Matsuura 1984). Mechanical signals are especially conspicuous in the independent-founding Polistinae belonging to the genera *Polistes*, *Mischocyttarus*, *Ropalidia*, and *Belonogaster*. Females produce these signals either by rapidly shaking the body while standing on the nest or by beating some part of the body against the nest or even a nestmate. Frequencies are typically in the range of 3–30 strikes/sec and may be of high enough amplitude to cause the nest itself to vibrate. In most cases they are issued in short bursts lasting a second or less, sometimes repeated regularly. Movements that strike the nest are often vigorous enough to produce sound audible to the human ear a meter or more from the nest (Keeping 1992; Pratte and Jeanne 1984). Because vespid wasps lack ears, these sounds are incidental and the energy must be perceived by colony members via vibration of the nest structure. The frequency and intensity at which they are produced, and the risk that the sounds produced may call

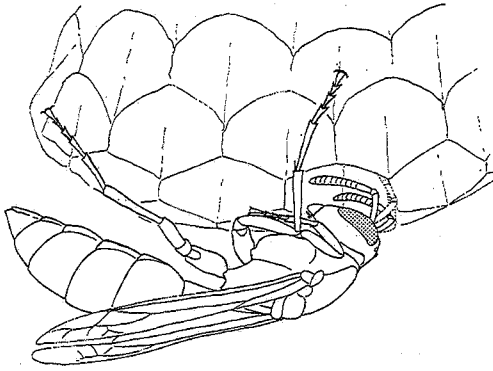


Figure 11.1. Antennal drumming by a *Polistes fuscatus* queen. The antennal flagella move in synchrony (see dotted outline of antennae) to strike the far rim of the larval cell over which she is poised. Drawn from a frame of 16-mm movie film. (Reproduced from Pratte and Jeanne 1984, with permission of the publisher.)

the attention of predators, suggest that these movements are costly to produce and that they are therefore likely to benefit their producers and can be assumed to be signals (Seeley 1995).

I have two aims in this chapter. The first is to review the occurrence of vibrational signals across the independent-founding wasps. The review is organized around the contexts in which the signals occur. Two contexts are recognized: brood care, particularly trophallactic contacts with larvae (feeding context), and non-brood care contexts (non-feeding context). Although some hornets and yellowjackets produce vibratory signals in similar contexts, because they are less well known the Vespinae are not considered here.

The second aim is to critically review hypotheses on the functions of vibratory signals in these wasps. Although several functions have been proposed, none is well supported, and the meaning of these signals remains mysterious. I propose a new hypothesis: that these vibrations are signals that bias caste development via biochemical changes and gene expression, either as stress inducers or as fertility indicators.

In this review I adopt the following terminology. If the vibration is produced by striking the nest with a part of the body, it is called *drumming*, modified by the body part used, if known (antennal drumming, gastral drumming). If it is not clear whether or not the nest is struck, and for

forms where the nest is not struck but is shaken, I use the term *vibration* preceded by a modifier describing the form of the movement (lateral vibration, longitudinal body vibration).

Feeding Context: Vibrational Signals Associated with Brood Care

Vibratory signals produced in close association with trophallactic visits to larvae occur in most of the better-studied species of independent-founding polistine wasps. The behavior has been most thoroughly studied in *Polistes*, but analogous behavior occurs in at least three of the four other genera.

Polistes

Pratte and Jeanne (1984) showed that antennal drumming (AD) in *P. fuscatus* is associated with the feeding of prey liquid to larvae (Figure 11.1). When a founding-stage queen returns to the nest with prey, she malaxates it for several minutes, imbibing the juices, then distributes the solid residue to the larger larvae. She then moves from cell to cell in the nest, pausing to drum her antennae on the rim of each without contacting the brood, before moving on to the next cell and repeating. The dorsal surfaces of the antennal flagella synchronously strike the rim of the cell at a rate of 25–32 beats per second; each drum lasts about one second. When the drumming is performed especially vigorously, the wasp's entire body moves rapidly forward and backward in synchrony with each strike of the antennae (see Pratte and Jeanne 1984, Figure 11.1, for an illustration). After several minutes of this, the queen enters each cell after drumming on it. If the cell contains a larva, she regurgitates a droplet of the prey liquid she has imbibed, touches it to the larva's mouthparts, and the larva ingests it. She repeats this sequence until each larva is visited and regurgitated to many times. Essentially the same behavior has been reported for *Polistes annularis*, *bellicosus*, *canadensis*, *carnifex*, *carolinus*, *erythrocephalus*, *exclamans*, *instabilis*, *jokahamae* (*fjadwigae*), *metricus*, and *versicolor* (Pratte and Jeanne 1984).

Although *P. dominulus* lacks AD, females perform a more or less vigorous side-to-side shaking of the abdomen (Brillet, Tian-Chansky, and Le Conte 1999) that is virtually identical in form to the lateral vibration (LV) described for other *Polistes* (Savoyard et al. 1998; see below). The intensity

of LV varies but may be strong enough to cause the entire body to shake, and sometimes the abdomen strikes the nest during vibration (Brennan 2007). Nearly 90% of the LVs were performed in the context of feeding larvae; the other 10% occurred in non-feeding contexts such as aggressive encounters with other adults (Brillet, Tian-Chansky, and Le Conte 1999; see below). Unlike *P. fuscatus*, a female *P. dominulus* performs LV as she begins to feed the solid bolus, continuing, but with reduced intensity, as she feeds the liquid. LVs are also sometimes performed during inspection of cells without feeding (Brillet et al. 1999).

Mischocyttarus

Females of the Neotropical wasp *Mischocyttarus drewseni* process and distribute solid food in the same way as *Polistes fuscatus* (Jeanne 1972). During the subsequent liquid-feeding phase, the female rapidly drums the gaster dorsoventrally (GD) against the nest for a fraction of a second prior to entering each cell. At the end of a round of feeding, the female occasionally performs a violent longitudinal body vibration (LBV) with its head inserted in an egg or larval cell, producing an audible rattle (Jeanne 1972). GD is also performed by *M. bimaculatus* and *M. mexicanus* (S. Suryanarayanan, pers. comm.).

Ropalidia

R. cincta females issue a vigorous wing buzz prior to entering a cell to feed solid food to the larva (Darchen 1976). After the solid is distributed, the females engage in trophallaxis with the larvae, again preceding each visit by a wing buzz. *R. marginata* females perform three kinds of body oscillations in the feeding context (S. Suryanarayanan, pers. comm.): a burst of wing-buzzing upon leaving a larval cell after feeding solid or liquid; a vigorous LBV, sometimes hitting the rim of the cell with the head or antennae; and a jerk of the body after exiting from a cell. While feeding liquid, *R. fasciata* females perform LBV with the head in the cell, the vibration lasting 10–30 seconds (Ito 1983). *R. revolutionalis* antennal drums like *Polistes fuscatus* (pers. obs.).

Belonogaster

In the first report of vibrational signaling in wasps, Roubaud (1916) described how, after feeding solid prey to the larvae, females of *B. juncea*

rustle or vibrate the wings before entering each larval cell. For the same species, Tindo, Francescato, and Dejean (1997) describe a dorso-ventral movement of the gaster. *B. petiolata* performs an LBV with the body head-down and nearly perpendicular to the nest surface, occasionally causing an audible rattle (Keeping 1992; M. G. Keeping, pers. comm.). Several females, including those not feeding larvae, may perform LBV simultaneously and synchronously.

Several facts argue against a role for these signals in dominance interactions among adults. First, solitary foundresses perform the behavior in the absence of other adults (Brillet, Tian-Chansky, and Le Conte 1999; Harding and Gamboa 1998; Pratte and Jeanne 1984). Second, even when other adults are present, the behavior is not directed at them (Harding and Gamboa 1998). Finally, other adults on the nest do not respond in any way to the vibrations (Brillet, Tian-Chansky, and Le Conte 1999). On the other hand, there is ample evidence that the signals are directed at the brood, and particularly the larvae. First, they are closely temporally associated with adult-larva contacts. Second, the behavior does not appear in a developing colony until after the hatching of the first larvae (Brennan 2007; Brillet, Tian-Chansky, and Le Conte 1999; Jeanne 1972; Pratte and Jeanne 1984; S. Suryanarayanan, pers. comm.). On balance, the evidence supports the conclusion that these signals are directed at the larvae and not the adults.

The Non-feeding Context: Vibrations Not Associated with Brood Care

In *Polistes*, two forms of body oscillations occur outside the context of feeding larvae. The first is LV: the female shakes the gaster vigorously from side to side while standing or moving on the nest (Brillet, Tian-Chansky, and Le Conte 1999; Gamboa and Dew 1981; West-Eberhard 1969; see Savoyard et al. 1998, Figure 1, for an illustration). The posterior gastral sternites often brush the nest surface, producing a rustling or rattling sound audible a meter or more away (West-Eberhard 1969) and is sometimes vigorous enough to shake the entire comb (Savoyard et al. 1998). LV of essentially the same form has been reported for *Polistes annularis*, *bernardii*, *richardsi*, *chinensis*, *canadensis*, *dominulus*, *erythrocephalus*, *exclamans*, *flavus*, *metricus*, and *versicolor* (Brillet et al. 1999; Downing and Jeanne 1985; Esch 1971; Gamboa and Dew 1981; Hermann, Barron, and Dalton 1975; Ito 1995; Kasuya 1983; Strassmann 1981; West-Eberhard

1969). Mean frequencies are 15–21 strokes (i.e., half a cycle) per second and bursts last 0.3–0.7 seconds (Brillet, Tian-Chansky, and Le Conte 1999; Esch 1971; Savoyard et al. 1998). In *P. dominulus*, LV performed in this context is similar in form to LV performed in the feeding context (Brillet, Tian-Chansky, and Le Conte 1999). *Polistes*-like LVs have been reported for *Mischocyttarus angulatus* and *M. basimacula* (Ito 1993), but are absent in *M. drewseni* (Jeanne 1972). Dominant females of *Ropalidia cyathiformis* produce a rapid dorso-ventral or lateral movement of the gaster, or a single quick flap of the wings (Gadagkar and Joshi 1984). *Belonogaster juncea* shakes the gaster dorso-ventrally, sometimes causing the entire body to vibrate (Tindo, Francescato, and Dejean 1997).

The second form of body oscillation is similar in form to LV, but is a much slower abdominal movement. Described by Gamboa and Dew (1981) as “abdominal wagging” (AW), the female shakes her gaster horizontally at 3–7 oscillations per second as she walks over cells containing brood. It lasts 2–10 seconds and often produces a faint rustling sound (Gamboa and Dew 1981). It has been reported for *P. metricus*, *P. fuscatus*, and *P. stigma* (Gamboa and Dew 1981; Harding and Gamboa 1998; Suzuki 1996).

Whether LV and AW are qualitatively distinct in form is an open question. Some observations suggest they are points on a continuum (Brennan 2007). Vibrations intermediate in intensity between AW and LV have been observed in *P. metricus* (Gamboa and Dew 1981), and in *P. dominulus* LVs range continuously in intensity from extremely low (AW-like) to so vigorous that the entire body shakes (Brillet, Tian-Chansky, and Le Conte 1999).

Current Hypotheses on Function

Feeding-Context Vibrational Signals

One hypothesis is that vibrational signals in this context stimulate the larvae to release trophallactic salivary secretion (Darchen 1976; Keeping 1992; Roubaud 1916; Tindo, Francescato, and Dejean 1997). However, in species in which these trophallactic visits have been carefully observed, the direction of flow is to the larvae (Corn 1972; Ito 1983; Jeanne 1972; Röseler and Röseler 1989; Yamane 1971). In *P. fuscatus*, during a female's AD visits following distribution of solid food, she regurgitates a droplet then moves her head slowly into the cell until the droplet makes contact with the larva's mouthparts. The adult's mouthparts remain open and still,

while those of the larva quiver slightly, suggesting that the larva is imbibing the fluid. The adult's gaster telescopes slowly inward, indicating that liquid is being forced out of the crop. This has been confirmed for two species using dye-colored prey items (Jeanne 1972; Pratte and Jeanne 1984). The pattern in which the feeding of solid prey to larvae is followed by an extended round of repeated contacts for liquid trophallaxis with the larvae is widespread if not universal in these wasps. Parsimony therefore suggests that larvae are being fed similarly in those genera that have not yet been carefully studied, and that reports that the trophallactic contacts are solicitations of larval saliva are incorrect.

Reports for several species that vibratory signaling occurs during the feeding of solid food and non-feeding inspections of brood cells (Darchen 1976; Brillet, Tian-Chiansky, and Le Conte 1999; Suryanarayanan, pers. comm.) also fail to support this hypothesis: females feeding solid material to larvae are unlikely to simultaneously solicit larval saliva to imbibe. Furthermore, males and newly eclosed adults of both sexes visit larvae and solicit trophallactic saliva (Jeanne 1972), but have never been reported to perform any kind of vibrational behavior. Thus, vibratory signals are not necessary to elicit larval saliva.

Taken together, these observations indicate that this hypothesis has little support and that vibrational signaling in this context does not function as a stimulus for the release of larval saliva.

An alternative hypothesis states that vibrational signaling in this context inhibits the release of salivary secretion by larvae. Pratte and Jeanne (1984) showed that larvae of *Polistes fuscatus* released significantly less saliva following AD than when not subjected to AD. They hypothesized that the inhibition prevents saliva from becoming mixed with and diluting the liquid food coming from the adult (Pratte and Jeanne 1984).

However, several observations raise doubts about this hypothesis as well. First, Pratte and Jeanne (1984) found AD in the feeding context to reduce trophallactic saliva release by less than 23% over controls, not a very strong inhibition. Second, vibrational signaling does not always accompany the feeding of liquid. Workers rarely perform it when feeding larvae, indicating that it is not a necessary signal in this context (Brillet, Tian-Chansky, and Le Conte 1999, Pratte and Jeanne 1984). Third, in *P. dominulus* LV is frequently performed during non-feeding inspection visits to brood cells (Brillet, Tian-Chansky, and Le Conte 1999). Finally, late in the colony cycle of *P. dominulus* feeding-context LVs are rare or

absent, yet larvae are fed liquid normally (Brillet, Lian-Chansky, and Le Conte 1999).

Non-Feeding-Context Vibrational Signals

Compared to feeding-context signals, it has been more difficult to determine whether non-feeding-context signals are directed at the adults or the larvae. Again, there are two hypotheses on function.

First, there is some evidence that LV is a form of aggression toward other *Polistes* adult females. This evidence follows several lines. In a number of species, LV is performed most frequently and/or energetically by queens, less frequently by high-ranking subordinates, and rarely by workers (Brillet, Tian-Chiansky, and Le Conte 1999; Downing and Jeanne 1985; Gamboa and Dew 1981; Ito 1995; Kasuya 1983; Savoyard et al. 1998; Strassmann 1981; Theraulaz et al. 1992; West-Eberhard 1969, 1986). Similarly, abdominal wagging in *Polistes* is more often performed by queens than by subordinate foundresses or workers (Gamboa and Dew 1981). Furthermore, dominance hierarchies based on frequency of performance of LV match those based on aggressive interactions (Hughes, Beck, and Strassman 1987; but see Savoyard et al. 1998) and LV is often temporally associated with aggressive encounters (Brillet, Tian-Chiansky, and Le Conte 1999; Ito 1993; Theraulaz et al. 1992; West-Eberhard 1969, 1986; but see Downing and Jeanne 1985). In particular, in some species LV is most conspicuous during the founding period or after queen disappearance, when there is reproductive competition among females (West-Eberhard 1969). Subordinates and dominants react differently to the behavior (Gamboa and Dew 1981; Ito 1993; Theraulaz et al. 1992). Performance of an LV is sometimes directed at another adult on the nest, especially newly emerged females, subordinates, and workers (Brillet, Tian-Chansky, and Le Conte 1999) which may avoid individuals engaging in LV or leave the nest in response (West-Eberhard 1986). Finally, LV performance frequency is positively correlated with ovary development (Ito 1995).

A second hypothesis is that vibratory signals in the non-feeding context regulate the release of larval trophallactic saliva. Indeed, there is some evidence that these signals are directed at the larvae. LV and AW in *Polistes* may be performed by a solitary foundress or by a co-foundress when she is alone on a nest containing larvae (Downing and Jeanne 1985; Savoyard et al. 1998). In some cases LV and AW in *Polistes* spp. occur rarely or not at

all until the larvae hatch (Downing and Jeanne 1985; Gamboa and Dew 1981; Savoyard et al. 1998). In *P. metricus*, the frequency of LV and the number of larvae in the nest are positively correlated (Gamboa and Dew 1981). The strongest evidence that LV is correlated with the presence of larvae comes from Savoyard et al.'s demonstration for *P. fuscatus* that removal of larvae from founding-stage, multiple-foundress nests significantly reduced the rate of lateral vibration. After the removed larvae were replaced, LV rate increased.

Based on patterns of occurrence, Harding and Gamboa (1998) hypothesized for *Polistes fuscatus* that AW stimulates release of larval saliva and LV inhibits it. Larvae released significantly less saliva immediately after an LV than 30 minutes after (Cummings, Gamboa, and Harding 1999). Noting that LVs cluster in the 2.5-minute interval prior to a foraging trip, Cummings et al. suggested that LV minimizes release of larval saliva during the foundress's absence when it might attract parasites and predators to the nest.

The case that non-feeding-context signals regulate release of larval saliva is less than compelling for several reasons. First, the experimental work with LV has shown only modest reductions (20–30%) in the amount of saliva yielded by larvae (Cummings et al. 1999), less than expected if the signal were an effective inhibitor. The reduced yield of saliva and the retraction of larvae in response to these signals (Cummings, Gamboa, and Harding 1999; Savoyard et al. 1998) could be generalized startle responses. Second, if these signals had to do simply with the mechanics of regulating flow of larval saliva, why should only the most dominant females use them? Third, there is no experimental evidence that AW stimulates release of larval saliva. Finally, why and how could AW and LV evolve to have opposite affects on the receiver, when they are so similar in form (Brillet, Tian-Chansky, and Le Conte 1999; Gamboa and Dew 1981)?

Although there is evidence that LV and AW are directed at larvae, the case against their being directed at adults as well is not compelling. There are reports of these signals being performed on multi-foundress nests containing only eggs (Hughes, Beck, and Strassman 1987; Strassmann 1981; Tindo, Francescato, and Dejean 1997), and LV is often closely associated with adult-adult aggression and/or is directed at other females. It is possible, therefore, that these signals have effects on both larvae and adults.

Vibrational Signals and Caste Determination

Do vibrational signals play a role in caste determination? Existing hypotheses on the function of these signals assume that the signals have releaser effects on behavior. I suggest that this is incorrect, and that they instead have a modulatory effect on growth, development, and reproductive physiology. This notion was first suggested by Brillet, Tian-Chansky, and Le Conte, whose observations of LV in *Polistes dominulus* led them to conclude that feeding-context signals can have little to do with the mechanics of adult-larva trophallaxis and to suggest instead that it somehow helps to prepare workers for their future status as dominated subordinates (Brillet, Tian-Chansky, and Le Conte 1999). They also suggested that vibrational signals performed in the non-feeding context maintain females in a subordinate, nonreproductive state.

I suggest that Brillet et al.'s hypothesis can be applied to all the independent-founding polistine wasps, that the various forms of vibrational signals performed in the feeding context are directed at the developing larvae, and that vibrations performed in the non-feeding context have effects on both the larvae and adults. Further, I hypothesize that all of these signals are part of the same functional continuum as physical attacks by dominant individuals on subordinates; that is, they act via the same pathways to have suppressive effects on reproductive physiology of the recipients. Finally, I argue that the signals initiate a cascade of biochemical events in the recipients, resulting in patterns of gene expression that reduce the reproductive potential of the recipient. The vibrations are transmitted through the nest carton to the adults standing on the nest as well as to the brood inside the cells, whereas dominance attacks transmit the signal directly onto the body of the recipient adult female.

The argument that vibrational signals directed at the larvae bias development toward worker-like adults rests on the assumption that some degree of pre-imaginal caste determination occurs in these wasps. The queen has an interest in producing early offspring that will behave as workers, and to this end she can exert influence on them both as larvae and as adults. Although most independent-founding polistines lack discrete morphological castes, there is evidence of behavioral, physiological, and morphological differences among adults that are traceable to the larval stage (Gadagkar et al. 1991; Hunt and Amdam 2005; reviewed by O'Donnell 1998). Eickwort (1969) found that females of *P. exclamans* on late-season

nests fall into two groups based on quantity and quality of fat body. Workers had fat body that was thin, patchy, opaque, and yellowish, while gynes had a continuous thick blanket of whitish, translucent fat body. Keeping (2002) has shown for *B. petiolata* that gynes are significantly larger, differ in body shape, and have significantly more fat than workers. In the only direct test of the null hypothesis that all adult females are reproductively capable, Gadagkar et al. (1991) showed that when eclosing females of *Ropalidia marginata* were isolated and fed *ad-libitum*, only about half were capable of initiating nests and laying eggs. Finally, analysis of storage proteins in adult *Polistes* showed differences between females emerging early and late in the colony cycle that could be linked to caste differentiation in the pre-imaginal stage (Hunt, Buck, and Wheeler 2003). It should be cautioned that pre-imaginal influences appear to have only a biasing effect on caste in most of these wasps, leaving considerable flexibility in the adult stage for social and environmental factors to influence caste (Gadagkar et al. 1991; Mead and Gabouriaux 1993).

Current Hypotheses on Mechanisms of Pre-imaginal Caste Determination

The current consensus is that differential nutrition during the larval stage is the cause of pre-imaginal caste determination in social vespids (Hunt 1994; O'Donnell 1998; Wheeler 1986, 2003). Well-fed female larvae develop into gynes, whereas the less well-fed become workers (Hunt and Amdam 2005). This has some support from food supplementation studies. Compared with controls, colonies given ample nutrients produce higher frequencies of female offspring with gyne-like traits, including larger size, more fat body, and enhanced cold tolerance (Hunt and Dove 2002; Karsai and Hunt 2002; Mead et al. 1994; Miyano 1998; Rossi and Hunt 1988). Conversely, underfeeding produces smaller offspring (Karsai and Hunt 2002). It has been also suggested that workers produced early in the colony cycle are the result of poor larval nutrition due to a high larva/worker (L/W) ratio, while the later-eclosing gynes benefit from improved nutrition due to a declining L/W ratio (Gadagkar et al. 1991; Reeve 1991; West-Eberhard 1969).

Hunt and Amdam (2005) recently developed a model for the origin of eusociality in *Polistes* that is based on the developmental pathways already in place in the presumed bivoltine, solitary ancestor. They postulate that

larvae diverge into one of two developmental pathways: worker-biased if they receive scanty food, gyne-biased if they receive abundant food. However, the quantity of nourishment received by larvae appears to be insufficient to account for observed patterns of development (Reeve 1991; West-Eberhard 1969) for at least two reasons. First, rate of larval development, generally positively correlated with resource availability in insects (Nijhout 2003), does not correlate well with caste. In *Polistes* and *Ropalidia*, larval development times are shortest for the first few (worker) offspring, rise rapidly to a maximum for later-eclosing workers, then gradually decline to intermediate durations for the remainder of the colony cycle, when gynes are produced (Kojima 1989; Kudo 2003; Mead et al. 1994; Miyano 1983, 1990, 1998; Strassmann and Orgren 1983). Thus, larval growth rate of workers spans the range of fastest to slowest in the life of the colony, while gynes have intermediate development rates. This pattern is also found in tropical *Mischocyttarus* (Jeanne 1972), so it cannot be temperature related. Interestingly, virtually all the difference in development time between the earliest and later workers is concentrated in the fifth instar (*Polistes chinensis*: Miyano 1990), just as in *Apis mellifera* (Wang 1965). This may be a manifestation of the greater accumulation of hexameric storage proteins being laid down in the last instar (Hunt, Buck, and Wheeler 2003), as predicted by the Hunt and Amdam model.

Second, the first-produced workers not only develop more rapidly than any subsequently produced females, but paradoxically they are also the smallest (Karsai and Hunt 2002; Miyano 1983; Turillazzi 1980; Turillazzi and Conte 1981). Although Mead et al. (1994) and Kudo (2003) concluded that the rapid growth of the first larvae in *Polistes* is due to more intensive feeding, this is contradicted by supplemental feeding of larvae, which leads to both more rapid larval development and growth to larger, not smaller, adults (Kudo 2003; Miyano 1998; Rossi and Hunt 1988; West-Eberhard 1969). In other words, the sizes to which offspring grow do not correlate well with their rates of development as larvae. Furthermore, the larger females produced later in the colony cycle sometimes include workers that do not differ measurably in size from gynes (Miyano 1983).

In summary, quantity of food received by a larva appears to be insufficient to explain the patterns of offspring size, rate of development, and caste. The evidence suggests that the effect of nutrition must be modulated by at least one additional source of environmental input (Miyano

1983, 1990; Miyano and Hasegawa 1998; Reeve 1991). I suggest that the missing factor is the vibrational stimuli produced so prominently by these wasps.

The Mechanical-Switch Hypothesis: Possible Mode of Action

I postulate that vibrational signals performed in the context of larval feeding have developmental effects. How environmental signals induce gene expression leading to the development of castes in most eusocial Hymenoptera is not fully understood, but current evidence suggests that differences in food quality trigger changes in levels of neurohormones, juvenile hormone (JH), insulin, and ecdysone, which in turn may act as token stimuli that mediate the gene-expression differences leading to caste-specific developmental pathways (Nijhout 2003; Wheeler 2003). The vibrational signals transmitted through the nest to the larvae (Brennan 2007) early in the colony's development induce biochemical changes in the developing larvae that may ultimately trigger changes in gene expression, causing those larvae to develop worker traits. Vibration, when coupled with differences in quantity of nutrition received by the larvae, could give rise to the observed differences in development rates, sizes, and caste-specific traits. Thus, they may be modulator or inducer signals (Hölldobler 1999) in that they modify the developmental response of the larva to the amount of food it receives, or modulate the reproductive physiology of an adult female. This may explain why behavioral responses to these signals by larvae and adults are typically absent.

There is good evidence that various kinds of stressors, including mechanical, affect levels of biogenic amines in insects. *Tribolium castaneum* larvae subjected to tumbling in vials at 40 revolutions per minute for three days experienced a 191% increase in whole-body octopamine level over that of controls (Hirashima, Uenoi, and Eto 1992). Vibration stimulated pupation in *T. freemani* larvae housed in crowded conditions, suggesting that octopamine is involved in larval programming (Hirashima et al. 1995). Cockroaches, locusts, and crickets show elevated octopamine concentration in response to mechanical and other forms of stress (Davenport and Evans 1984; Orchard, Loughton, and Webb 1981; Woodring, Meier, and Rose 1988). Male *Drosophila virilis* show a significant elevation in dopamine concentration following shaking for 60 minutes (Rauschenbach et al. 1993). And worker honey bees subjected to dorso-ventral vibration by

other workers experienced significant elevations in JH titer 15 to 30 minutes later (Schneider, Lewis, and Huang 2004).

Changes in biogenic amine levels in turn influence levels of hormones, including juvenile hormone, known to be involved in queen-worker caste differentiation during the larval stage (Rachinsky and Hartfelder 1990; Rachinsky et al. 1990). Octopamine and serotonin stimulate release of JH by the corpora allata in honey bee larvae, suggesting a role for biogenic amines in the regulation of caste determination in *Apis* (Rachinsky 1994). There is also direct evidence that stress can cause developmental change. Subjecting *Tribolium castaneum* larvae to mechanical stress caused a 54% reduction in larval growth to 54% of that of controls (Hirashima, Uenoi, and Eto 1992), and vibration at 100 Hz for two days reduced weight gain to 55% that of controls (Hirashima et al. 1993). Exposure of mice to low magnitude, 90-Hz vibration for 15 minutes per day over 15 weeks inhibited adipogenesis by 27% (Rubin et al. 2007).

These studies suggest that repeated vibration may be as effective an environmental signal as food quality in triggering a cascade of events linking biogenic amines, through hormones, to patterns of gene expression and development, and thus may play a role in caste determination in independent-founding social wasps.

In *Apis*, *Vespa*, and *Vespula*, the third larval instar (of five) is the critical stage at which queen- and worker-destined larvae begin to diverge developmentally (Ishay 1975; Evans and Wheeler 1999). In *A. mellifera* this is caused by a "nutritional switch" (Wheeler 1986) that leads to differences in gene expression in the two developing castes (Evans and Wheeler 1999; Hepperle and Hartfelder 2001). In *Polistes dominulus* the onset of feeding-context LV signals coincides with the eclosion of third-instar larvae (Brillet, Tian-Chansky, and Le Conte 1999). In *P. fuscatus*, although Pratte and Jeanne (1984) reported that AD in lab colonies appeared with the first-instar larvae, in field colonies it begins with the third (S. Suryanarayanan, pers. comm.). Given the reasonable assumption that in these wasps, as in *Apis* and the vespines, the third is the instar at which developmental paths diverge, this pattern supports the hypothesis that feeding-context signals bias development of larvae into workers. It also suggests that third-instar larvae issue some cue or signal that releases feeding-context signals, as found in *Apis mellifera* (Brillet, Tian-Chansky, and Le Conte 1999).

Brillet et al.'s longitudinal study of vibrational signals in *Polistes*

dominulus showed that feeding-context LVs were most frequent when worker-destined larvae were being reared. LVs performed in the non-feeding context, on the other hand, increased sharply at about the time the first workers emerged (week five) and remained high through week 10, the end of Brillet et al.'s study. This pattern supports the hypothesis that these signals function in part to suppress reproductive maturation in adult worker offspring.

Although several studies have found little evidence that adults are the target of vibrational signals in this context (Downing and Jeanne 1985; Gamboa and Dew 1981; Savoyard et al. 1998) or that adults respond to the signals (Brillet, Tian-Chiansky, and Le Conte 1999; Esch 1971; Gamboa and Dew 1981; Savoyard et al. 1998), others link vibrational signals to physical dominance attacks. In *Mischocyttarus drewseni*, dominance attacks involving chewing on the body of a subordinate female were often accompanied by a rapid longitudinal body vibration (LBV), with the head of the dominant striking the subordinate (Jeanne 1972). On other occasions the dominant, while still facing a subordinate it had just dominated, drummed the gaster (GD) vigorously against the nest surface. Both LBV and GD are also used in the feeding context (see above), suggesting similar function whether directed at larvae or adults and supporting the notion that non-feeding-context signals are directed at both larvae and adults. Brillet et al. (1999) have linked non-feeding-context LVs to aggressiveness in *P. dominulus*, noting that they were often directed at newly eclosed workers. Although LV is apparently absent in *Ropalidia fasciata* (Ito 1983), the dominant female often mounts the back of a newly returned forager and solicits fluid from it, sometimes while vibrating the body violently enough to cause the forager's body to shake (Ito 1993).

If the mechanical-switch hypothesis is correct, vibrational signals in the non-feeding context may well affect development of both larvae and adults and need neither be directed at nor elicit a behavioral response by individuals of either to have their effect.

Conclusions

Vibrational signals in the independent-founding polistines, notwithstanding their conspicuousness and frequency of occurrence, have proven remarkably resistant to functional analysis. Part of the difficulty may be traced to our reluctance to think of functions other than releasers of

behavioral responses in larvae and/or adults. The difficulty may also be due in part to the narrow focus to date on one or a few related species in attempts to understand function. The comparative review presented here suggests not only that these signals are widespread and variable across taxa, but highlights differences in details of temporal pattern, form, and association with other social behavior on the nest that do not fit current hypotheses based on releaser functions. The broader perspective taken here suggests instead that these movements may have become ritualized to have inducer, or modulatory, functions relating to development of caste differences. The hypothesis proposes in broad outline how vibrational signals may have developmental consequences for larvae and adults.

In socially complex Hymenoptera such as honey bees and many ants, the production of workers and gynes is ultimately regulated by queen pheromones. Proximate control is provided by environmental stimuli in the form of different chemical signals issued, respectively, to worker- and queen-destined larvae. Recent research, especially on bees and ants, has begun to piece together the biochemical pathways that bring about the differential gene expression leading to caste differentiation and to specialization within the worker caste (Evans and Wheeler 1999; Toth and Robinson 2007; Wheeler 2003). What is proposed here is that the biochemical machinery of the pathway is in place in even the most primitively eusocial species. The onset of vibrational signaling in the feeding context in *Polistes* coincides with the appearance of third-instar larvae in the nest (Brillet, Tian-Chansky, and Le Conte 1999), which suggests that it is the third larval instar that is sensitive to an environmental trigger, as in more complex bees and wasps. In the simple societies of the independent-founding wasps chemical triggers may be absent. Instead, vibrational signals may represent an alternative, albeit cruder, mechanism for biasing the development of the first offspring toward worker-like behavior and suppressing their reproductive function as adults.

In making the case for the effect of vibrational signals on the development of larvae, I have adopted the language of "parental manipulation" to describe how these signals manipulate the development of the larvae, possibly against their own interests. Inasmuch as the larvae are completely subject to the control of the adults on the nest in terms of how they are fed and otherwise treated, this seems a reasonable interpretation. Nevertheless, it is equally possible to interpret these vibrations as fertility signals that indicate the presence of a viable egglayer and that larvae and adults

respond by adopting a developmental pathway that is likely to maximize their inclusive fitness under those conditions (Peeters and Liebig, this volume). Just as the weight of evidence supports such an assessment hypothesis for adult-adult interactions among social insects (Liebig, Monnin, and Turillazzi 2005; Peeters and Liebig, this volume; West-Eberhard 2003), it may well turn out to be the case for adult-brood interactions as well.

In adopting the comparative approach in this chapter I have made the simplifying assumption that the functions of vibrational signals are the same across the independent-founding polistine genera. There is the risk that this glosses over what may be real differences in function among species and genera. On the other hand, focusing on the differences can point the way to fruitful lines of research. A particularly interesting avenue for further study is whether these wasps all use vibrational signals in the same way or whether some will be shown to have pheromonal regulators of caste. The differences and anomalous cases among the species and genera reviewed here will provide the footholds and leverage necessary to tease apart the details of the function or functions of these conspicuous, yet puzzling, signals.

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