Insectes soc. 45 (1998) 215 – 230
0020-1812/98/020215-16 $ 1.50+0.20/0

Insectes Sociaux

Research article

The communicative meaning of body oscillations in the social wasp, *Polistes fuscatus* (Hymenoptera, Vespidae)

J.L. Savoyard, G.J. Gamboa*, D.L.D. Cummings and R.L. Foster[1]

Department of Biological Sciences, Oakland University, Rochester, MI 48309, USA
[1] *Department of Psychology, University of Puget Sound, Tacoma, WA 98416, USA*

Key words: *Polistes*, oscillatory behavior, adult-larval communication.

Summary

The oscillatory behavior of paper wasps, *Polistes fuscatus*, was examined in field observations (401.9 h) of 37 preworker (pre-emergence), multiple-foundress colonies. Additional field observations were conducted on 16 multiple-foundress colonies (96 h) both before and after worker emergence, and on 10 preworker colonies (40 h) before and after eggs had hatched into larvae. In addition, we observed 18 preworker, multiple-foundress colonies: six undisturbed controls (12 h), six larvae removed (12 h), and six larvae removed and replaced (12 h). Finally, we analysed video and audio sequences of oscillatory behaviors (lateral vibrations).

Higher ranked foundresses performed lateral vibrations (LVs) at a significantly greater rate than lower ranked foundresses. However, there was no significant association between rates of LVs and (1) aggression or (2) magnitude of differences in dominance indices among cofoundresses. There was also no significant temporal association between LVs and departures or returns. Lateral vibrations were commonly performed by foundresses that were alone on the nest. These results and others indicate that LVs do not function in adult-adult communication.

Lateral vibrations were significantly, temporally associated with high activity level, primarily cell inspection. Lateral vibrations were significantly, positively correlated with abdominal wagging and antennal drumming, both of which have been implicated in adult-larval communication. Foundresses of colonies containing eggs only (compared to colonies containing eggs and larvae) rarely displayed LVs. Removal of larvae significantly reduced the rates of LVs and the replacement of removed larvae caused a marked increase in the rates of LVs. Video analyses revealed that larvae retracted their head capsules in response to an LV. All of these data indicate that LVs involve adult-larval communication via substrate vibrations. Some indirect evidence suggests that LVs signal larvae to stop secreting saliva to adult wasps.

Introduction

Among the most conspicuous yet enigmatic behaviors displayed by paper wasps (*Polistes*) are body oscillations performed by adult females on the comb. These oscillations, which superficially resemble certain aspects of the honey bee waggle

---

* Author for correspondence.

dance, appear to be widespread among temperate *Polistes*. Body oscillations have been reported for *P. gallicus* (Pardi, 1942; Theraulaz et al., 1991); *P. stigma* (Suzuki, 1996); *P. versicolor* (Esch, 1971); *P. chinensis* (Morimoto, 1961); *P. fuscatus*, *P. canadensis*, *P. flavus*, *P. annularis*, and *P. exclamans* (West-Eberhard, 1969), and *P. metricus* (Gamboa et al., 1978). Body oscillations have also been reported for other genera of social wasps including *Belonogaster* (Keeping, 1992; Tindo and Dejean, 1996; Tindo et al., 1997); *Mischocyttarus* (Jeanne, 1972); *Dolichovespula* (Jeanne, 1977); *Vespa* (Ishay et al., 1974); and *Ropalidia* (Darchen, 1976; Gadagkar and Joshi, 1984).

In *P. metricus* (Gamboa and Dew, 1981) and *P. fuscatus* (Downing and Jeanne, 1985; Pratte and Jeanne, 1984), three distinct oscillatory behaviors have been reported. One oscillation, longitudinal vibration (Gamboa and Dew, 1981) or antennal drumming (Pratte and Jeanne, 1984), consists of a female positioning her head in the opening of a cell containing a larva and rapidly hitting the rim of the cell with her antennae. Sometimes the wasp's entire body moves rapidly forward and backward along its longitudinal axis during this behavior. Since we believe that "antennal drumming" more accurately describes this oscillation than "longitudinal vibration", we refer to this oscillation as antennal drumming in our paper. Antennal drumming is thought to be associated with adult-larval communication (Pratte and Jeanne, 1984).

A second kind of oscillation, abdominal wagging, consists of a female wagging her abdomen from side to side against the face of the comb as she walks over cells. The pivotal point of the oscillation appears to be the petiole. The frequency of abdominal wagging is variable (approximately 2–7 oscillations/s) as is its duration (~2 s to >15 s; Gamboa and Dew, 1981). Abdominal wagging has also been implicated in adult-larval communication (Gamboa and Dew, 1981; Downing and Jeanne, 1985).

A third kind of oscillation, lateral vibration (LV), is the most vigorous and audible of the three oscillations. Lateral vibrations consist of a female rapidly moving her abdomen from side to side against the nest surface producing a short (<1 s) but loud burst of sound. Unlike abdominal wagging, females are stationary while executing LVs (Gamboa and Dew, 1981). Lateral vibrations have been hypothesized to function in adult-adult dominance interactions (Gamboa and Dew, 1981) and in adult-larval communication (Downing and Jeanne, 1985).

Since LVs are the most conspicuous yet least understood of the three kinds of oscillations, we focused our study on LVs. We utilized high resolution video tapings and highly sensitive audio recordings to provide visual and audio analyses of LVs. We also examined the context of the performance of LVs and experimentally manipulated colonies in order to understand the communicative meaning of LVs.

Methods

Field observations

We conducted field observations in 1989, 1991, and 1994 of 37 multiple-foundress colonies of *P. fuscatus* nesting in plywood nestboxes near Rochester, Michigan.

Of the 37 colonies, 26, 7, and 4 had two, three, and four foundresses, respectively. Foundresses were marked for individual identification in early to mid-May, approximately 2–3 weeks prior to the beginning of behavioral observations. Colonies were surveyed periodically shortly after sunrise to record brood contents and the identity and number of females at the nest.

Behavioral observations were conducted at three different times during the preworker (pre-emergence) stage of the colony cycle: (1) in late May and early June (mean date 2 June) as soon as the membership in foundress associations stabilized, (2) in mid-June (mean date 18 June), and (3) in late June and early July (mean date 28 June) during the week preceding the emergence of the colonies' first workers. Field observations were conducted between 10 and 17 h when ambient air temperatures were ≥21 °C. Each colony was scheduled to be observed for 4 h in each of the three sets of observations for a total of 12 h. However, observations were sometimes shortened by rain or other factors. We completed 401.9 h of observation, with a mean of 10.9 h per colony.

Activity states, interactions, departures, and returns as well as their associated times were recorded on a microcassette audio recorder throughout an observation for all foundresses at a nest. Activity states included cell inspection, walking, cell construction, chewing or exchange of pulp or prey, pedicel maintenance, egg laying, fanning, autogrooming, and immobility. Following Reeve and Gamboa (1983), active behaviors were cell inspection (including adult-larval food/liquid exchange), walking, cell construction, prey or pulp exchange, chewing of pulp or prey, and pedicel maintenance. Inactive behaviors were immobility, egg-laying, fanning, and autogrooming. Interactions included chasing, falling fights, grappling, biting, lunging, brief (≤2 s) unilateral and mutual antennation, long (>2 s) unilateral and mutual antennation, standing on body of another wasp, division of pulp and prey, and solicitation. We also recorded items foraged (prey, wood pulp, or nothing visible in mandibles) and oscillatory movements (antennal drumming, abdominal wagging, and LVs).

For each foundress we calculated a dominance index, which consisted of the proportion of observation time a given foundress spent on its nest plus the proportion of its interactions that it initiated, divided by 2. The dominance index can range from 0 to 1. We considered the foundress with the highest dominance index in each colony to be the queen. The queen's identity was confirmed on the basis of egg laying and dominant-subordinate postures. For each observation we also calculated a tolerance value as described by Gamboa et al. (1991). The tolerance value has been used extensively to estimate tolerance in *Polistes* (e.g., Gamboa et al., 1986, 1991; Pfennig, 1990; Bura and Gamboa, 1994). The tolerance value, an estimate of spatial tolerance, is based on the 10 interaction types described above, excluding solicitation and division of pulp and prey. Larger values indicating greater tolerance. For a more complete discussion of the tolerance value see Gamboa et al. (1986, 1991).

We also observed 16 multiple-foundress colonies (range of 2–6 foundresses) in 1995. We observed each colony for 3 h during the week preceding worker emergence and 3 h approximately 7–10 days after the emergence of the first workers (96 h). During these observations we recorded departures, returns, interactions between foundresses, and the frequency and location of LVs in both preworker and postworker colonies. Queens were determined on the basis of their dominance index.

In addition, in 1996 we conducted observations of undisturbed colonies and observations of manipulated colonies. For undisturbed colonies, we observed 10 multiple-foundress colonies for two hours when each colony contained only eggs (mid- to late May; mean date 29 May) and the same colony again for two hours when the colony contained eggs and larvae (mid-June; mean date 22 June) for a total of 40 h. During these observations we recorded the numbers of LVs and the identities of the foundresses performing LVs.

For manipulated colonies, we observed (1) six undisturbed colonies (natural controls), (2) another six colonies in which all larvae had been removed (treatment), and (3) six other colonies in which all larvae had been removed and replaced in their original comb (disturbance controls). All 18 colonies were two-foundress colonies. For undisturbed colonies, treatments, and disturbance controls, nestboxes containing colonies were cooled in ice chests for approximately one hour. Foundresses were then removed from their combs with clean tweezers and placed in small glass vials laid on top of ice in ice chests. For treatments and disturbance controls, larvae were aspirated from their cells with a 10 ml pipette and either replaced in their original comb (disturbance control) or destroyed (treatment). Although we attempted to remove all larvae from each comb, it is possible that a few small larvae, i.e., first instar larvae, escaped removal. After the removal or replacement of larvae, we replaced foundresses from all 18 colonies on their original combs and returned nestboxes containing foundresses and their combs to their original location in the field. After a reacclimation period of two hours, we completed two hours of behavioral observations on each of six disturbance controls, six treatment colonies, and six undisturbed colonies for a total of 36 h. During observations we recorded the numbers of LVs and the identities of the foundresses performing the LVs. Observations were conducted between 10 and 17 h when ambient air temperatures were ≥21°C in late June and early July just prior to the emergence of the first workers.

Audio and visual analysis of LVs

We videotaped three multiple-foundress colonies of *P. fuscatus* in nestboxes for a total of 16 h in July and August of 1996. A video camera (Sony TR910 high resolution 8 mm) was positioned on a tripod approximately 0.9 m directly beneath the nestbox so that the field of view consisted of the face of the comb and the dorsal surface of the wasps on the comb. The video was filmed at 30 frames per second with a 15X optical telephoto that provided a field of view of ~ 7 cm. We selected for analysis 8 LVs from our 16 h of video taping that we felt were our most illustrative sequences of LVs. Four of these LVs were performed by foundresses and four were performed by workers.

We analyzed LVs by viewing them at 1/5 normal speed and frame by frame. From the video analysis, we determined the (1) duration, (2) number, (3) frequency, and (4) amplitude of the oscillations for each LV. We considered one oscillation to be the swing of the abdomen from one extreme to the other. The amplitude of the oscillation was the angle between the longitudinal axis of the wasp prior to the LV and the maximum deflection of the abdomen. In several LVs we were unable to determine the amplitude of the oscillations because of the plane of the wasp performing the LV. Fortuitously, these sequences provided us a lateral view of the wasp, which allowed us to view the dorso-ventral movement of the wings and gaster prior to an LV.

The built-in microphone of the Sony TR910 camcorder was bypassed with an ultra miniature tie clip microphone that was placed inside the nestbox within 5 cm of the comb. The omni-directional tie clip microphone had a frequency response of 70–16,000 Hz and a sensitivity of 65 dB (±3 dB). We copied the audio from 13 video-taped LVs onto analog audiocassette tapes. The audio was then digitized at 11.25 kHz with a 16 bit sample size. The resulting sound files were analyzed on a PC computer using Syrinx, a spectral analysis program under development at the University of Washington. Each LV was displayed as a spectrogram using a wide band analysis (172 Hz). We used time cursors to measure (1) the total duration (in seconds) of each LV and (2) the time interval between successive sound pulses (inter-pulse interval). The fundamental frequency in Hz (pulses per sec) was calculated as 1/(average inter-pulse interval). One LV included a pause of approximately 0.25 s; we considered the two sound components of this record as separate LVs.

All significance levels are two-tailed values unless otherwise noted. We used one-tailed tests when we felt justified in predicting the direction of the difference. All sample sizes (n) reflect the maximum number of colonies, LVs, or oscillations available for a particular data analysis. All oscillation frequencies (rates) have been adjusted for the time a wasp spent on the nest.

Results

Description of LVs and larval responses to LVs from video and audio analyses

Immediately before performing an LV, the female raised and spread her wings slightly (~5 to 10°) and then depressed her gaster so that only the posterior third contacted the nest surface. At about this time the female also appeared to grip the nest surface firmly with her tarsi. The female then moved her gaster rapidly from side to side (Fig. 1) with the gaster in contact with the nest surface. In at least two LVs that were performed on the tops of small (<20 cells) combs, we were able to discern a high frequency movement of the entire comb during the LV. In some LVs the pivotal point of the oscillation was the petiole, and only the abdomen (but not the head and thorax) moved extensively during the LV. In other LVs, the pivotal point of the oscillation appeared to be the thorax and all three body regions moved extensively during the LV. In these oscillations the head moved in opposition to the abdomen.

The durations, numbers, frequencies, and amplitudes of oscillations for LVs were highly variable. The durations of LVs ranged from 0.17 s to 0.63 s ($\bar{x} = 0.45$ s, n = 8). The numbers of oscillations in LVs ranged from 4 to 10.5 ($\bar{x} = 7.2$ oscillations, n = 7) and the frequency of oscillations ranged from 11.8 to 24 oscillations per

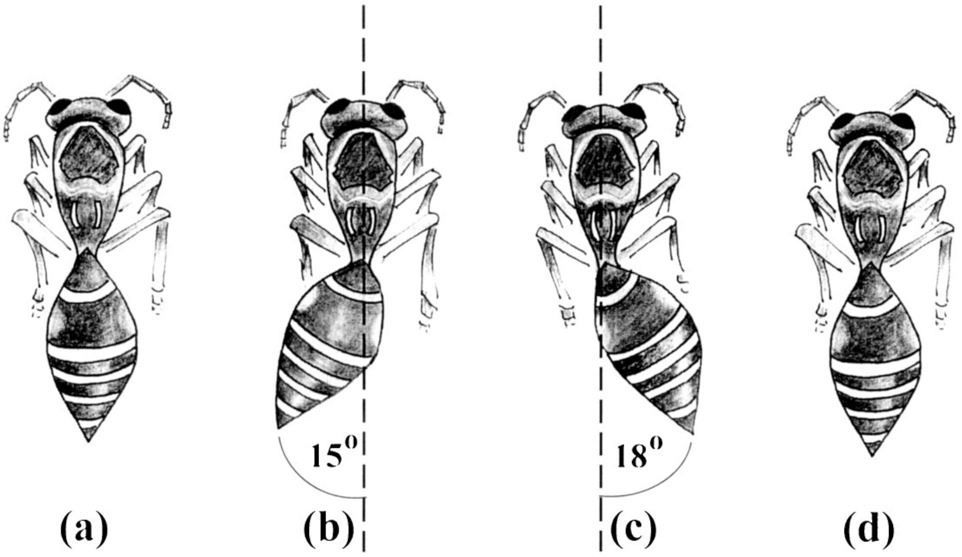

Figure 1. Two oscillations of a LV by a queen of the wasp, *Polistes fuscatus*, based on tracings made from a video segment. The swing of the gaster from one extreme to the other (b to c) represents one oscillation. Note that the deflection of the gaster is not symmetric with respect to the wasp's longitudinal axis

second ($\bar{x}$ = 17.0/s, n = 7). The amplitudes of the oscillations in LVs ranged from 11° to 34° ($\bar{x}$ = 21.3°, n = 12). The sample sizes for the number and frequency of oscillations were reduced to 7 since we were unable to determine these parameters in 1 of the 8 LVs. Interestingly, the oscillation frequencies of the three foundresses were substantially higher than those of the four workers. The small sample sizes, however, precluded statistical comparison.

In the spectrograms, LVs appeared as short bursts of rapidly repeating, low pitched pulses. The sound patterns varied among lateral vibrations (Fig. 2a, b, and c). The total durations of the LVs ranged from 0.174 s to 0.944 s ($\bar{x}$ = 0.416 s, n = 14); these values are similar to those from the video analysis. The fundamental frequency (number of sound pulses per second) ranged from 16.72 Hz to 69.06 Hz ($\bar{x}$ = 36.7 Hz, n = 14). The sound frequency range measured by the audio analysis was higher than the oscillation frequency range measured by the videotape analysis. This suggests that the sound pulses do not coincide directly with abdominal oscillations and that the audible properties of the LV were created by contact with the substrate on which the LV occurred. Regression analysis revealed that shorter duration LVs had higher fundamental frequencies ($r = 0.61$, $p = 0.02$).

All four LVs that occurred on the top of the comb were characterized by high frequency, irregular pulse patterns (Fig. 2a). By comparison, five of the eight LVs that occurred on the face of the comb, where the wasp's abdomen contacted the rims of cells, were characterized by lower frequency, regular pulse patterns (Fig. 2b). This association between the sound pattern and the location

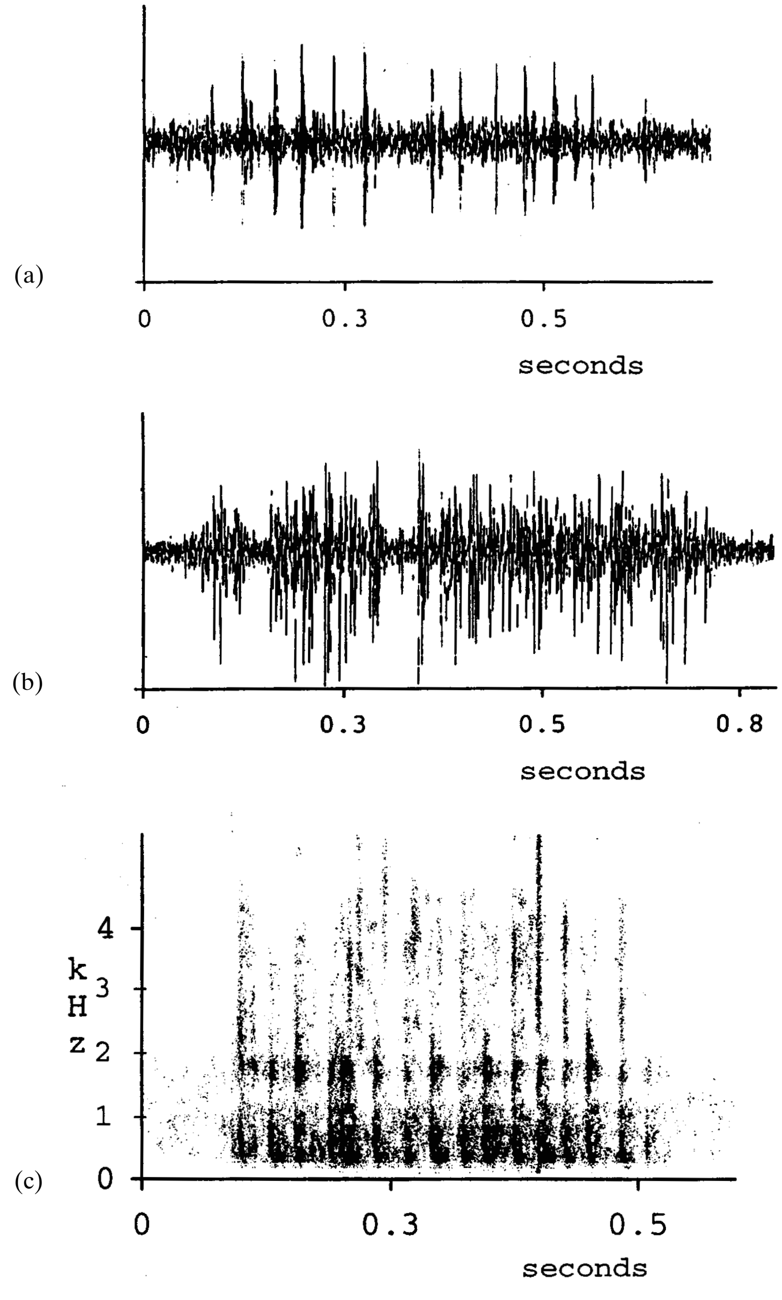

Figure 2. Spectrograms of three LVs in the wasp, *Polistes fuscatus*. The three spectrograms represents (a) a regular pulse pattern from an LV by a worker on the face of the comb, (b) an irregular pulse pattern (i.e., variable inter-pulse intervals) from an LV by an unknown female on the top of the comb, and (c) a depiction of the fundamental (< 1 kHz) and harmonic (> 1 kHz) frequencies of a LV from an unknown female on the face of the comb. The peaks in the spectrograms represent sound pulses, not oscillations

of the LV provides further evidence that the sound is produced by contact with the substrate.

In 20 LVs performed on the face or top of the comb, we had an unobstructed view of from 4 to 12 third, fourth, and fifth instar larvae before, during, and after the LV. In all 20 of these sequences, we observed a marked response by larvae to the LV. Almost simultaneously with the performance of each LV, we observed all of the visible larvae retract their head capsule. In some cases we observed that the head capsule was both retracted and shifted toward or away from the cell wall in response to the LV.

Which foundresses perform LVs and when and where on the comb are they performed?

Of 504 LVs recorded during the combined 1989, 1991, and 1994 preworker observations, 329 (65%) were performed by queens and 175 (35%) were performed by subordinate cofoundresses. The mean numbers of LVs recorded per hour differed significantly among queens, alpha subordinates, and beta subordinates ($p = 0.037$; Table 1). Queens performed LVs at about 1.5 times the frequency of alpha subordinates and 3.2 times that of beta subordinates. The mean LV frequencies for queens, alpha subordinates, and beta subordinates were all significantly different ($p < 0.04$; Table 1) with higher ranked foundresses performing LVs at higher frequencies than lower ranked foundresses.

The mean LV frequency for queens and for alpha subordinates did not change significantly over the three observation periods of the preworker phase of the colony cycle (Table 2). Overall, the trend was a decrease in the frequency of LVs by

Table 1. Mean numbers of lateral vibrations (LVs) per hour for queens, α subordinates, and β subordinates in preworker colonies of the paper wasp, *Polistes fuscatus*

Queen LV/h (± SD)	α Subordinate LV/h (± SD)	β Subordinate LV/h (± SD)	No. of colonies	Significance level
1.52 (0.68)@	0.96 (0.69)@	0.48 (0.44)@	11	0.037*

* Friedman test.

@ All three means significantly different (p < 0.04), SNK test.

Table 2. Mean numbers of lateral vibrations per hour for queens and α subordinates of the paper wasp, *Polistes fuscatus*, during three periods of the preworker colony cycle

Class of female	Mean number of lateral vibrations (± SD)			No. of colonies	Significance level*
	Period 1	Period 2	Period 3		
Queen	1.29 (2.07)	1.02 (1.14)	0.61 (0.88)	29	0.13
α Subordinate	0.54 (0.66)	0.69 (0.95)	0.56 (0.59)	27	0.92

* Friedman test.

queens (but not alpha subordinates) over the three preworker observation periods (Table 2). In fact, the frequencies of LVs for queens and alpha subordinates were virtually identical in the third observation period (Table 2) and thus LV rates are not diagnostic of foundress dominance rank at this phase of the colony cycle.

Most LVs performed by queens during the preworker phase in 1989 and 1991 were performed on the top of the nest (369 of 465, 79.3 %, n = 34 colonies). The percentage of queen LVs performed on the top of the nest did not change significantly over the three periods of the preworker phase of the colony cycle ($p = 0.763$, Friedman test). Similarly, the majority of LVs in late preworker and early postworker colonies in 1995 were also performed on the top of the nest (55 of 86, 64 %, and 33 of 60, 55 %, respectively), and these percentages did not differ significantly ($p > 0.40$; n = 12 colonies, Wilcoxon Matched-Pairs test). However, in later postworker colonies when combs were much larger, most LVs were performed on the face of the comb. In fact, 80 % (32 of 40) of LVs recorded in mid-July to mid-August in 1996 were performed on the face of the comb. The differences between these later colonies and earlier colonies with respect to the locations of LVs (i.e., top vs. face of comb) were highly significant ($p < 0.005$, chi square).

Are LVs associated with either tolerance or dominance?

Neither the queen's LV rate nor the alpha subordinate's LV rate was significantly correlated with mean tolerance ($r_s = -0.09$, $p = 0.57$ and $r_s = -0.23$, $p = 0.18$ for queens and alpha subordinates, respectively; n = 35 colonies, one-tailed Spearman Rank Correlation tests). Similarly, there were no significant correlations between the differences in dominance indices between cofoundresses and the frequencies of LVs for either queens or alpha subordinates ($r_s = -0.12$, $p = 0.48$ and $r_s = -0.12$, $p = 0.49$ for queens and alpha subordinates, respectively; n = 35 colonies, one-tailed Spearman Rank Correlation tests). Thus, there was no evidence of an association between tolerance or dominance differences and frequency of LVs.

If LVs are involved in adult-adult communication, we would expect foundresses to perform LVs preferentially in the presence of other foundresses. For 1989, 1991, and 1994 preworker observations of two-foundress colonies, foundresses were together on the comb 52.7 % of the total observation time, and the percentage of LVs recorded while foundresses were together on the comb was 70.3 %. The observed and expected percentages, 70.3 % and 52.7 %, were significantly different ($p = 0.0004$; n = 24 colonies, Wilcoxon Matched-Pairs test). Therefore, foundresses preferentially performed LVs in the presence of other cofoundresses.

It may be that LVs are positively associated with high activity levels rather than with the presence of other cofoundresses. To investigate this, we examined the temporal relationship between LVs and activity level for 1989 and 1991 observations. We first examined queen activity levels immediately before and after an LV. The queen activity levels immediately before an LV (0.93) and immediately after an LV (0.71) were significantly greater than 0.34, the overall queen activity level ($p < 0.001$; n = 33 colonies, Friedman test, SNK test). Therefore, the queen is almost always active immediately before (and frequently after) she performs an LV. Interestingly, queens were significantly less active ($p < 0.01$, SNK test) after performing an LV than before.

We also examined the relationship between the rate of queen LVs and queen activity level. Queen activity level and queen LV rate were highly positively correlated ($r_s = 0.61$, $p < 0.001$; n = 35 colonies). This analysis, like the previous analysis, demonstrated that queen LVs were associated with high queen activity levels. Since most queen activity (approximately 95%) involves cell inspection (Reeve and Gamboa, 1983), queens typically are inspecting cells immediately before and after performing LVs.

Are LVs associated with foraging or other body oscillations?

The total numbers of LVs recorded in a colony were not significantly correlated with either the total number of departures ($r_s = 0.26$, $p = 0.14$; Table 3) or the total number of returns ($r_s = 0.32$, $p = 0.062$; Table 3). The weak association between returns and LVs may be a reflection of the finding of Reeve and Gamboa (1987) that forager returns stimulate colony activity. There were no significant correlations between the total numbers of LVs recorded in a colony and numbers of pulp returns, empty returns, or prey returns ($p = 0.21$, 0.09, and 0.37, respectively; Table 3). In summary, we found no evidence that LVs are associated with any foraging-related variables.

We also examined the possible association between LVs and two other oscillations, abdominal wagging and antennal drumming. Lateral vibrations were strongly positively correlated with both abdominal wagging ($r_s = 0.56$, $p = 0.0005$) and antennal drumming ($r_s = 0.67$, $p = 0.00001$; n = 35 colonies for both, one-tailed Spearman Rank Correlation tests).

Are LVs associated with other foundress behaviors?

Gamboa and Dew (1981) reported anecdotal observations that LVs in *P. metricus* appeared to occur shortly before the departure of a foundress. The queen might perform an LV to signal her departure to either the brood or other cofoundresses. To investigate this, we examined the two minute period immediately preceding a queen departure to determine what proportion of queen departures were preceded

Table 3. Correlation of numbers of lateral vibrations (LVs) with numbers of (1) foraging departures, (2) foraging returns, (3) prey returns, (4) pulp returns, and (5) “empty” returns in preworker colonies of the paper wasp, *Polistes fuscatus*

	No. of colonies	Correlation coefficient	Significance level*
LVs vs. departures	35	0.26	0.14
LVs vs. returns	35	0.32	0.06
LVs vs. pulp returns	35	0.22	0.21
LVs vs. empty returns	35	0.29	0.09
LVs vs. prey returns	35	0.16	0.37

* Spearman Rank Correlation tests.

by a queen LV. Of 281 queen departures in 35 colonies, only 18 departures (6.4%) were preceded by a queen LV.

Some LVs appeared to occur in the context of pedicel licking or pedicel rubbing. To investigate this, we examined the numbers of LVs that occurred within 2 min of pedicel licking or pedicel rubbing. Of 504 LVs recorded, only 35 (6.9%) occurred within 2 minutes of pedicel licking or pedicel rubbing.

Are LVs associated with the presence of larvae in the comb?

In 1996 observations, we compared the numbers of LVs in 1) early colonies that contained eggs only, and 2) the same colonies later in the colony cycle when both eggs and larvae were present. There was a significantly greater frequency of LVs in colonies containing eggs and larvae than in colonies containing only eggs ($p = 0.004$; Table 4). In fact, we recorded only two LVs in 20 h of observation of 10 colonies containing eggs only. For 1989 and 1991 observations, we observed the frequencies of LVs for queens and alpha subordinates separately for colonies containing eggs only and for other colonies containing both eggs and larvae. For both queens and alpha subordinates, there was a significantly greater frequency of LVs in colonies containing eggs and larvae compared with colonies containing eggs only ($p = 0.00012$ and 0.0014 for queens and alpha subordinates, respectively; Table 4).

To further test the hypothesis that the performance of LVs is associated with the presence of larvae, in 1996 we removed larvae from their combs and then recorded the frequency of LVs in these colonies. In the six colonies in which larvae had been removed (treatment), we recorded only two LVs by foundresses, both in one colony. In contrast, we recorded 27 LVs in six undisturbed colonies with all six colonies displaying LVs. The mean number of LVs recorded per hour in undisturbed controls (2.25) was significantly greater than that recorded in treatment colonies ($\bar{x} = 0.17$, $p < 0.01$, Mann-Whitney test). In the six colonies in which larvae had been removed and replaced (disturbance controls), we recorded 14 LVs by foundresses in 4 of the 6 colonies. The frequency of LVs in treatment colonies (0.17/h) and disturb-

Table 4. Mean numbers of lateral vibrations/hour for queens and α subordinates in early and mid-preworker colonies of the paper wasp, *Polistes fuscatus*. Early colonies contained eggs only and mid-preworker colonies contained eggs and larvae only

Class of female	Year of observation	Number of colonies	Mean No. of lateral vibrations (± SD)		Significance level
			early colonies	mid-colonies	
Queens	1989, 1991	9, 10	0.131 (0.156)	2.97 (2.33)	0.00012*
α Subordinates	1989, 1991	9, 10	0.16 (0.25)	1.27 (0.70)	0.0014*
All Foundresses	1996	10	0.10 (0.21)	2.50 (1.56)	0.004@

* One-tailed Mann-Whitney tests.

@ One-tailed Wilcoxon Matched-Pairs test.

ance control colonies (1.17/h) was almost significantly different ($p = 0.06$, one-tailed Mann-Whitney test). The lack of significance was probably due to our small sample size.

Discussion

Lateral vibrations in *P. fuscatus* consisted of a rapid lateral oscillation of the gaster against the nest carton that produced a short, loud burst of repeating, low-pitched (~ 17 to 70 Hz) sound pulses. Video analysis revealed that the duration, number, frequency, and amplitude of the oscillations were variable. Nevertheless, LVs differed markedly from previously published descriptions of abdominal wagging, another oscillation that also involves a lateral oscillation of the gaster. Specifically, LVs were shorter in duration (~ 0.45 s vs. ≥2 s) and had a greater oscillation frequency (~ 17/s vs. 2–7/s) than values reported by Gamboa and Dew (1981) for abdominal wagging.

Are LVs involved in adult-adult communication?

Even though the rate of LVs was associated with the dominance rank of a cofoundress, there was no evidence that LVs were associated with dominance communication, tolerance, or aggression. Neither the queen's LV rate nor the alpha subordinate's LV rate was significantly correlated with tolerance or aggression. If LVs are associated with dominance communication, we might expect cofoundresses of similar dominance rank to be less tolerant of each other and have greater LV rates than cofoundresses of more disparate dominance ranks. However, we found no association between differences in dominance rank and LV rates. In short, we found no evidence that LVs were involved in dominance communication among cofoundresses.

Some of our results, as well as the findings of previous studies, suggested that LVs might be involved in some type of adult-adult communication. For example, we found that LVs were preferentially performed in the presence of other cofoundresses. Gamboa and Dew (1981) reported the same for preworker colonies of *P. metricus* and also reported that in postworker colonies, the number of LVs was significantly, positively correlated with the number of workers. In contrast, Downing and Jeanne (1985) reported that in *P. fuscatus*, the queen rate of LVs did not increase with the presence of other cofoundresses or with increasing numbers of workers. However, it is not clear whether Downing and Jeanne (1985) adjusted their rates of LV for the time a particular wasp spent on the nest. For this reason and because our results were highly significant and based on an extensive data set, we believe that LVs are indeed preferentially performed in the presence of cofoundresses in preworker colonies of *P. fuscatus*.

Reeve and Gamboa (1987) reported that the number of adults on the nest was positively associated with activity level. If numbers of LVs are positively correlated with activity level, we would expect to see a positive association between the performance of LVs and the presence of cofoundresses on the nest. Indeed, our results demonstrated a strong association between LVs and activity level. Queen activity level was significantly, positively correlated with queen LV rate. Furthermore, most LVs (~93%) were directly preceded by activity, particularly cell inspection. Thus, we believe the association between the presence of cofoundresses and the performance of LVs to be a byproduct of the association between LVs and activity. We also believe that the association of LVs with both dominance rank and the presence of other cofoundresses misled Gamboa and Dew (1981) into postulating that LVs were associated with the communication of dominance.

We also found that lone foundresses of *P. fuscatus* frequently performed LVs. Of 251 LVs recorded in two-foundress colonies in 1989, 1991, and 1994, 76 were performed when only one foundress was at the nest. Downing and Jeanne (1985) reported that single foundresses of *P. fuscatus* actually performed LVs at higher rates than multiple foundresses. Both of these findings are inconsistent with the hypothesis that LVs function in any kind of adult-adult communication, and they lend further support to our hypothesis that LVs are associated with activity level rather than with the presence of other cofoundresses.

Are LVs associated with other foundress behaviors?

Gamboa and Dew (1981) suggested that foundresses perform LVs in the context of departures, either to stimulate the departure of another foundress or to signal their own departure to brood or other foundresses on the comb. We found no evidence for these suppositions. Lateral vibrations were not significantly associated with either departures or returns. Furthermore, only a small minority of queen departures (6.4%) were preceded within 2 min by a queen LV.

We did, however, find that LVs were strongly associated with abdominal wagging and antennal drumming, both of which have been implicated in adult-larval communication. Downing and Jeanne (1985) reported that LVs were associated with abdominal wagging although they provided no statistical evidence for this statement. In short, there is a strong, positive association among all three oscillations in *P. fuscatus*.

Are LVs involved in adult-larval communication?

There are several lines of evidence that strongly suggest that LVs involve communication between adult females and larvae. We found that LVs were rarely recorded in early colonies that contained only eggs. In fact, LVs began to appear in colonies at about the time that eggs hatched into larvae. Gamboa and Dew (1981) also reported that LVs were uncommon in early nests of *P. metricus* that contained only eggs. They found that the number of LVs peaked at about the time that the numbers of larvae in the comb were increasing rapidly. Furthermore, Gamboa and Dew (1981) reported that the number of LVs in postworker colonies was significantly, positively correlated with the numbers of larvae in the comb.

Colonies in which the larvae had been removed had significantly fewer LVs than undisturbed colonies. In fact, the removal of larvae almost eliminated LVs. In addition, the replacement of previously removed larvae caused a marked increase in LVs by resident foundresses. We also found that in close-up video sequences, larvae always exhibited a conspicuous behavioral response to LVs. In short, the results of our studies of both undisturbed colonies and experimentally manipulated colonies indicate that LVs function in adult-larval communication, as originally suggested by Downing and Jeanne (1985).

What are the communicative meanings of body oscillations in P. fuscatus?

The behavioral repertoire of larvae appears to be rather limited. Larvae receive malaxated prey and liquid food from adults and, in turn, provide saliva to adults (West-Eberhard, 1969; Hunt, 1991; Pratte and Jeanne, 1984). Hunt et al. (1982) documented that larval saliva is nutritious and contains both amino acids and proteins. We believe that the communicative meanings of signals from female adults to larvae might also be rather limited. Adult females may signal larvae to reveal their nutritional needs or to secrete or withhold saliva. Since we found no association between lateral vibrations and departures, it does not appear that LVs function to stimulate larvae to reveal their nutritional needs.

Lateral vibrations may stimulate larvae to stop secreting saliva. There are several indirect lines of evidence that are consistent with this hypothesis. First, our video analysis of larval responses to LVs revealed that larvae retracted their head capsules immediately after a foundress performed an LV. This larval behavior appears to be more consistent with the detection of a signal that inhibits rather than stimulates the secretion of saliva. It may be that another oscillation, abdominal wagging, stimulates larvae to secrete saliva. If this is correct, we would expect abdominal wagging to precede LVs. Indeed, when we examined the order of performance of these two oscillations, we found that abdominal wagging was significantly more likely to precede an LV ($p < 0.001$; $n = 34$, chi square) than expected by chance. Finally, we found that foundresses were significantly more likely to be active inspecting cells immediately before than immediately after they performed an LV. This is more consistent with a signal that inhibits rather than stimulates larval secretions.

Pratte and Jeanne (1984) provided evidence that antennal drumming is performed after larvae are fed prey and signals larvae to stop secreting saliva in preparation for receiving a liquid meal from an adult female. We found that antennal drumming was indeed significantly, positively correlated with prey returns ($r_s = 0.38$, $p = 0.01$), which is consistent with Pratte and Jeanne's (1984) interpretation of function for antennal drumming.

Our results, together with those of Gamboa and Dew (1981), Pratte and Jeanne (1984), and Downing and Jeanne (1985), indicate that all three reported oscillatory behaviors in *P. fuscatus* and *P. metricus* involve adult-larval communication via substrate vibration. However, additional experimental studies are required to verify the communicative meanings of oscillations in social wasps. One approach might be to record the amount of saliva secreted by larvae before and after the performance of an oscillation. Pratte and Jeanne (1984) used such a design in their investigation of the communicative meaning of antennal drumming. Perhaps an even more powerful experimental design would be to mechanically reproduce LVs and abdominal wagging and then record the response of larvae to these oscillations.

Acknowledgements

We thank T. Fishwild, K. Jankens, R. Schemidt, and T. Wacker for their assistance in field observations and John Burt for his technical assistance in the audio analyses. N. Rudolph kindly drew the wasps in Figure 1. We also thank Dr. M. G. Keeping and Dr. Robert Jeanne for their critical review of our manuscript. The research was partially supported by the Howard Hughes Undergraduate Program – Oakland University.

References

Bura, E.A. and G.J. Gamboa, 1994. Kin recognition by social wasps: asymmetric tolerance between aunts and nieces. *Anim. Behav. 47*:977–979.

Darchen, R., 1976. *Ropalidia cincta*, guêpe social de la savane de Lamto (Côte D'Ivoire). *Ann. Soc. Entom. Fr. 12*:579–580.

Downing, H.A. and R.L. Jeanne, 1985. Communication of status in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Z. Tierpsychol.* 67:78–96.

Esch, H., 1971. Wagging movements in the wasp *Polistes versicolor vulgaris* Bequaert. *Z. Vergl. Physiol. 72*:221–225.

Gadagkar, R. and N.V. Joshi, 1984. Social organization in the Indian wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae). *Z. Tierpsychol. 64*:15–32.

Gamboa, G.J. and H.E. Dew, 1981. Intracolonial communication by body oscillations in the paper wasp, *Polistes metricus*. *Insectes soc. 23*:13–26.

Gamboa, G.J., B.D. Heacock and S.L. Wiltjer, 1978. Division of labor and subordinate longevity in foundress associations of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae) *J. Kans. Ent. Soc. 51*:343–352.

Gamboa, G.J., R.L. Foster, J.A. Scope and A.M. Bitterman, 1991. Effects of stage of colony cycle, context, and intercolony distance on conspecific tolerance by paper wasps (*Polistes fuscatus*). *Behav. Ecol. Sociobiol. 29*:87–94.

Gamboa, G.J., D.W. Pfennig and H.K. Reeve, 1986. The evolution and ontogeny of kin recognition ability in social wasps. *Ann. Rev. Ent. 31*:431–454.

Hunt, J.H., I. Baker and H.G. Baker, 1982. Similarity of amino acids in nectar and larval saliva: the nutritional basis for trophallaxis in social wasps. *Evolution 36*:1318–1322.

Hunt, J.H., 1991. Nourishment and the evolution of the social Vespidae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, Eds.), Cornell University Press, Ithaca, New York. pp. 426–450.

Ishay, J., A. Motro, S. Gitter and M.B. Brown, 1974. Rhythms in acoustical communication by the oriental hornet, *Vespa orientalis*. *Anim. Behav. 22*:741–744.

Jeanne, R.L., 1972. Social biology of the neotropical wasp, *Mischocyttarus drewseni*. *Bull. Mus. Comp. Zool. 144*:63–150.

Jeanne, R.L., 1977. Behavior of the obligate social parasite *Vespula arctica* (Hymenoptera: Vespidae). *J. N. Y. Ent. Soc. 50*:541–557.

Keeping, M.G., 1992. Social organization and division of labour in colonies of the polistine wasp, *Belonogaster petiolata*. *Behav. Ecol. Sociobiol. 31*:211–224.

Morimoto, M., 1961. On the dominance order in *Polistes* wasps. I. Studies on the social Hymenoptera of Japan. XII. *Sci. Bull. Fac. Agric. Kyushu Univ. 18*:339–351.

Pardi, L., 1942. Recerche sui Polistini. V. La poliginia iniziale di *Polistes gallicus* (L.). *Boll. Inst. Ent. R. Univ. Bologna 14*:1–106.

Pfennig, D.W., 1990. Nest and nestmate discrimination among workers from neighboring colonies of social wasps *Polistes exclamans*. *Can. J. Zool. 63*:268–271.

Pratte, M. and R.L. Jeanne, 1984. Antennal drumming behavior in *Polistes* wasps (Hymenoptera: Vespidae). *Z. Tierpsychol. 66*:177–188.

Reeve, H.K. and G.J. Gamboa, 1983. Colony activity integration in primitively eusocial wasps: the role of the queen. (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol. 13*:63–74.

Reeve, H.K. and G.J. Gamboa, 1987. Queen regulation of worker foraging in paper wasps: a social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behaviour 102*:147–167.

Suzuki, T., 1996. Natural history and social behaviour of cofoundresses in a primitively eusocial wasp, *Polistes stigma* (Fabricius) (Hymenoptera: Vespidae), in India: a case study. *Jpn. J. Ent. 64*:35–55.

Theraulaz, G., J. Gervet and S. Semenoff Tian-Chanski, 1991. Social regulation of foraging activities in *Polistes dominulus* Christ: A systemic approach to behavioural organization. *Behaviour 116*:292–319.

Tindo, M. and A. Dejean, 1996. Vibrations abdominales chez *Belonogaster juncea juncea* (Vespidae: Polistinae). *Actes Coll. Insectes soc. 10*:179–184.

Tindo, M., E. Francescato and A. Dejean, 1997. Abdominal vibrations in a primitively eusocial wasp *Belonogaster juncea juncea* (Vespidae: Polistinae). *Sociobiology 29*:255–261.

West-Eberhard, M.J., 1969. The social biology of polistine wasps. *Misc. Publ. Mus. Zool. Univ. of Mich. 140*:1–101.

Received 7 July 1997;
revised 8 January 1998;
accepted 15 January 1998.