ISSN 0044-3573 / InterCode: ZETIAG

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Antennal Drumming Behavior in *Polistes* Wasps (Hymenoptera: Vespidae)

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With 4 figures

Received: April 18, 1983
Accepted: November 23, 1983

Abstract and Summary

Antennal drumming, in which *Polistes* queens rapidly beat the antennae on the rims of nest cells, is described in detail for *P. fuscatus* and shown to be performed in the context of feeding prey to the larvae. Following the distribution of solid food to the larvae, the queen goes from cell to cell on the nest, drumming her antennae on the cell rims, producing an audible sound. After several min of this, each drum on a cell is followed by contact with a larva, usually the one in the drummed cell, during which the queen regurgitates prey juice to the larva. The average burst of drumming lasts just under one s. The two antennal flagella strike the cell rim together at an average frequency of 29 strokes per s. Similar behavior is documented in 10 other *Polistes* species. We hypothesize that antennal drumming communicates to the larva that it is about to receive liquid food from the adult and should withhold the release of salivary secretion. This predicts that a larva that has received the drumming signal will exude less secretion than if it has not been recently signaled. An experimental test of this hypothesis yielded the predicted result, and we therefore conclude that our hypothesis is supported.

Introduction

Various authors have mentioned that in paper wasps (*Polistes* Latreille) the production of sound often accompanies trophallactic contact between the females and the larvae. RAU (1928: 154), describing this sound production in *P. fuscatus* (F.) (=*pallipes*), states that the queen "stood on a nest with her head at the opening of a cell and her antennae inside, probably touching the larvae. Her head was then rapidly rammed or beaten against the wall of the cell; the whole body was in motion, seeming to actuate the head, and this rapid vibration of the head against the paper wall caused the sound." RAU believed that this behavior induced the larvae to give up a droplet of salivary secretion,

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which the adult would then imbibe (RAU 1928, 1938). OWEN (1962: 6) described the behavior in the same species as a vigorous "vibrating (of) a braced head and forelegs inside the opening of the cell." She also suggested that the behavior stimulates the larvae to produce salivary secretion. EVANS and WEST EBERHARD (1970: 137) observed that while the female is dispensing solid food or nectar to larvae she "signals her presence by rapidly knocking her head against the edge, the resulting vibration of the nest producing a brief buzz audible to the human ear." They state that the larva responds by extending its body, bringing its mouth clear of the cell's edge. YAMANE (1971: 208) working with *P. biglumis* (L.) and *P. snelleni* Saussure in Japan, noticed that the feeding of the larvae is accompanied by the "trembling of antennae inserted in the cell. CORN (1972: 154) observed similar behavior in *P. carnifex* (F.), stating that the wasps "rapidly antennated the opposite wall of the cell (producing a sound) easily audible at a distance of 1 m from the nest." She suggested that the behavior alerted the larvae to a food offering.

Here we provide the first detailed description of this behavior. We also describe the context in which the behavior is performed, and test a hypothesis about its function.

Methods

The study was carried out on *Polistes fuscatus* colonies maintained in a rearing room under fluorescent lights on a light/dark schedule of 12 : 12, increasing to 15 : 9 in weekly steps of 15 min. Temperatures ranged from 20—25 °C at night to 25—30 °C during the day. Gynes collected in the field in the fall and overwintered in the lab were placed together in a plastic-fronted cardboard box (60 × 30 × 30 cm) until they initiated nests. They were fed water, honey, and wax moth (*Galleria mellonella*) larvae. Nests, along with the founding queen (6 nests) or the queen and a joiner (6 nests), were transplanted a few days after founding to individual Lucite cages (20 × 20 × 20 cm). These colonies were observed from 15 February to 1 April 1981.

An additional 9 nests with adults, collected in the vicinity of Madison on June 9 were transplanted into individual plastic boxes. All of these nests were monogynous and in the pre-emergence phase. Observations were made from 15 June to 15 July. The first adult emerged on 23 June.

Only the first worker was allowed to remain on each nest; subsequent workers were removed as they emerged. Prior to each observation or experiment joiners and any newly emerged workers were temporarily removed from the cage, leaving only the queen. An "observation" consisted of the record of acts performed by the queen from the time she obtained a prey item until she finished distributing it and its juices to the larvae. Drumming behavior was filmed with a 16-mm Beaulieu movie camera at speeds up to 64 frames/s, and sounds were recorded on a Uher 4000 tape recorder for sonagraphic analysis.

Additional species of *Polistes* were observed for drumming in the field in France, Mexico, Costa Rica, Brazil, and the U.S.

Description of Antennal Drumming

The wasp performs the antennal drumming by positioning her head over the opening of a cell containing an egg or a larva and rapidly hitting the rim of the cell with her antennae (Fig. 1). The behavior produces an audible drumming, or rattling sound. If the drumming is particularly vigorous, the wasp's entire body is moved rapidly forward and backward, as if emphasizing

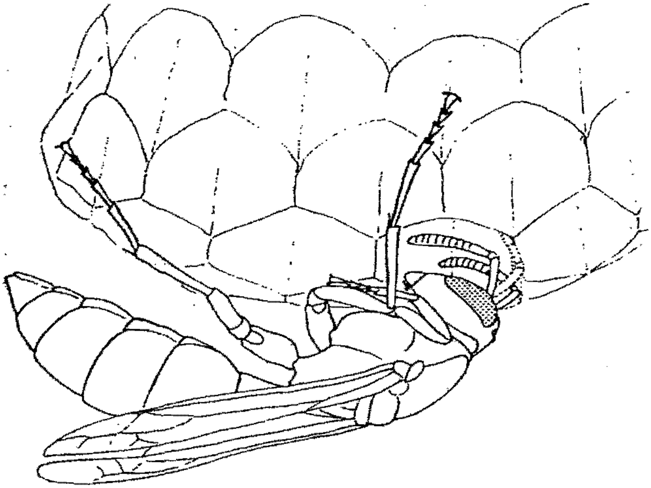

Fig. 1: Antennal drumming behavior by a *Polistes fuscatus* queen. She has paused at the opening of a larval cell and is drumming the antennal flagella on the opposite rim of the cell. Drawn from a frame of 16-mm movie film

the movement of the antennae. Analysis of high speed movie film reveals that the dorsal surface of the antennal flagellum strikes the cell rim, that both antennae move synchronously rather than alternately, and that the forelegs are held off the nest and against the prothorax.

24 bursts of drumming from 9 wasps were recorded on tape and analyzed by means of sonagrams (Fig. 2). The average burst lasted 0.94 s (SD = 0.27), and the average frequency was 28.96 antennal strikes per s (SD = 2.49). During the course of a single burst, however, the strike frequency steadily decreased from 32.32 (SD = 3.22) to 25.26 (SD = 2.05) (Fig. 3).

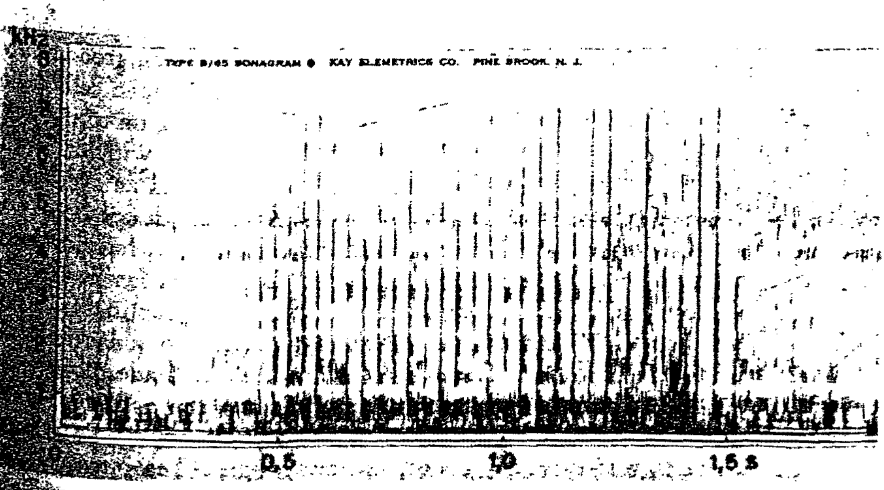

Fig. 2: Sonagram of airborne sound produced during a burst of drumming in *Polistes fuscatus*

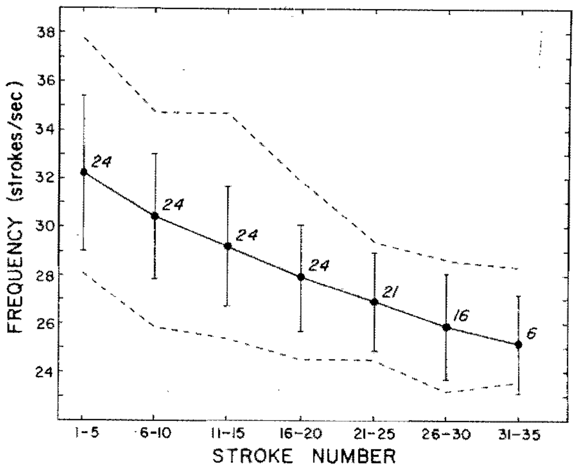

Fig. 3: Decrease in average frequency of antennal strikes during a burst of drumming. Numbers are sample sizes. Mean, standard deviation (bars), and range (dashed lines) of frequencies of 5-strike intervals are shown. Strokes (horizontal axis) are numbered from the beginning of the burst

Context of Antennal Drumming

Despite extensive observation of all on-nest activities, including nectar feeding, cell inspection, or nest construction, we found that antennal drumming occurred only in the context of the feeding of prey to larvae. The typical sequence of behavior began with the return of the queen to the nest with a prey load, and proceeded as follows (Fig. 4). Step 1: The queen spent several min (up to 25 min for a large load) malaxating the prey. The mass became visibly drier during the process, suggesting that the queen was extracting and ingesting liquid from it. Step 2: She then fed small bits of the prey to the larvae, often pausing to malaxate between feedings. In small nests such as were used in our observations, most or all of the larvae received prey during a feeding bout. Step 3: When the solid food was gone, the queen groomed for several min. Step 4: She then began to drum on the rims of open cells (cells containing eggs or larvae), pausing for several s before moving on to the next cell, but without contacting larvae. This phase of drumming without larval contact occurred in 73 sequences of feeding (86.9 %) and lasted an average of 170.8 s (SD = 80.8). In a typical such round of drumming, each open cell was drummed several times. Step 5: Antennal drumming continued, but now each drum was followed by a few s of regurgitation of liquid to a larva. Usually the adult fed the larva in the cell that was just drummed, but in 24.7 % of 67 cases she drummed in one cell and then regurgitated to a larva in an adjacent cell. In some of these cases (46.3 %) the switch was made because the drummed cell was empty or contained an egg. This phase occurred in 82 (97.6 %) sequences, and lasted an average of 269.6 s (SD = 157.4). Each larva in these small nests was typically contacted many times. The intensity and duration of drumming bursts gradually diminished during this phase until the antennae were only twitched lightly against the cell prior to some of the larval exchanges. The duration of both phases of drumming (steps 4 and 5) averaged 413.5 s (SD = 181.6; n = 83). Step 6: The wasp continued to contact larvae without drumming, the length of each contact gradually increasing to many seconds or even a minute or more. Step 7: Finally, visits to larvae ceased and the wasp groomed.

There were occasional variations in this sequence (Fig. 4). In three of 84 observed sequences, for example, the wasp drummed while feeding solid food to the larvae. In a few cases antennal drumming did not begin until after liquid transfer to the larvae had begun, and in 6 sequences drumming did not ocur at all.

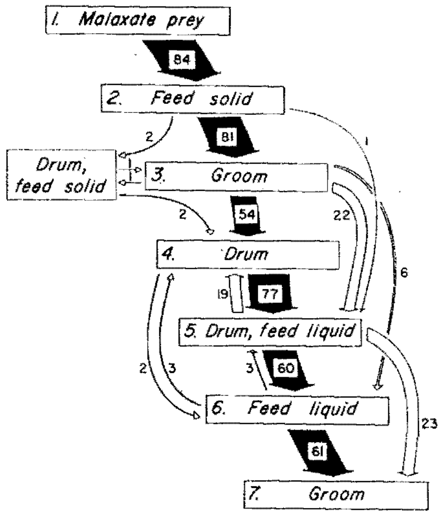

Fig. 4: Kinematic graph of the acts associated with feeding prey to the larvae. Steps 1 through 7 are described in the text. Small numbers represent absolute numbers of each transition. Widths of arrows represent relative numbers of each transition. Most common transitions are shown in black. Based on n = 502 transitions

We could not confirm that the larvae responded to the drumming in any consistent way. In a few instances they appeared to stretch somewhat toward the cell opening, as though reaching toward the adult. Contrary to what EVANS and WEST EBERHARD (1970) imply, this by no means occurred invariably.

Drumming before feeding (step 4) was directed to egg- and larva-containing cells approximately in the proportion they occurred in the nest. But after feeding began (step 5), drumming was more likely to be performed in larval cells than in egg cells (Table 1). In 7 observations the distributions of drums during feeding were skewed significantly, often highly so, toward larval cells, while in only three observations did the distribution of drums before feeding differ significantly from expected, and not always toward larvae (e.g., nest 5 on 2/26). The 6 nests tested showed the tendency in varying degrees; nests 3, 5, and 6 showed it clearly, while nest 2 showed little difference between pre- and during-feeding distribution of drums. Nest 4 had few egg cells, so there was little potential for the tendency to be detected.

Table 1: Distribution of antennal drumming among egg and larval cells before (step 4) vs. during feeding the larvae (step 5). "Brood" gives the numbers of egg and larval cells in the nest when each test was done. "Number of drums" gives the number of times each type of brood cell was drummed. χ^2 was used to test the level of difference between the observed ratio of egg to larval cells drummed and the ratio expected based on the numbers of egg and larval cells in the nest

Nest	Date	Brood		Number of cells drummed per observation			
		Stage	No.	Pre-feeding	χ^2 test	During feeding	χ^2 test
1	25 Feb.	Eggs	11	3	.025	0	.005
		Larvae	17	18		16	
	27 Feb.	Eggs	8	0	.05	0	.025
		Larvae	21	7		15	
2	18 Feb.	Eggs	12	7	NS	3	NS
		Larvae	2	0		1	
	20 Feb.	Eggs	8	5	NS	7	NS
		Larvae	6	4		3	
	24 Feb.	Eggs	6	3	NS	4	NS
		Larvae	8	9		7	
	26 Feb.	Eggs	6	1	NS	1	NS
		Larvae	7	6		6	
3	26 Feb.	Eggs	11	6	NS	3	.001
		Larvae	3	1		6	
4	20 Feb.	Eggs	2	2	NS	2	NS
		Larvae	19	11		17	
	23 Feb.	Eggs	2	2	NS	0	NS
		Larvae	21	11		15	
	25 Feb.	Eggs	2	0	NS	0	NS
		Larvae	21	6		3	
	27 Feb.	Eggs	4	1	NS	1	NS
		Larvae	19	8		17	
5	24 Feb.	Eggs	11	5	NS	5	.001
		Larvae	5	2		13	
	25 Feb.	Eggs	11	6	NS	2	.001
		Larvae	5	2		17	
	26 Feb.	Eggs	11	11	.05	0	.001
		Larvae	5	0		6	
6	27 Feb.	Eggs	5	2	NS	2	.005
		Larvae	4	1		11	
Total		Eggs	110 (40 %)	54 (38 %)		30 (16 %)	
		Larvae	163 (60 %)	86 (62 %)		153 (84 %)	
		Total	273	140		183	

Data combined from the 6 nests reveal an overall slight bias toward feeding the larger larvae during the drumming phase of the sequence (step 5), and toward smaller larvae after drumming had ceased (step 6) (Table 2).

Drumming was performed by single foundresses before workers emerged, as well as by foundresses with joiners and/or workers. We never observed it, however, on young nests containing only eggs, regardless of the number of foundresses present. The behavior first appeared within a day after the emergence of the first larvae in the nest.

Table 2: Accompaniment of feeding by drumming as a function of relative age of larval recipient. Queens tended to concentrate more on feeding young larvae after ceasing drumming than while drumming. Data from 6 nests. $G = 8.95$, $df = 1$, $p < .005$

	Number of Larvae Fed	
	During drumming (step 5)	After drumming (step 6)
Young larvae (instars 1-3)	176	188
Old larvae (instars 4-5)	160	105

The Direction of Trophallactic Transfer during Antennal Drumming

In trophallactic exchanges accompanied by drumming (step 5), the direction of liquid flow was from adult to larva. This was readily confirmed by giving an adult prey macerated with vegetable dye, allowing the adult to pass through the normal feeding sequence described above. In each case the colored liquid was visible on the mouthparts of the larva following trophallactic contact. (Because trophallactic transfer from larva to adult involves a secretion and not a regurgitate, liquid moving in this direction would have been clear, even after the larva had ingested colored prey.)

Behavior of adult and larva during trophallaxis provides further clues as to the direction of flow. A wasp offering liquid food to a larva brushes the sides of the larva's body with the tips of her antennae, opens her mandibles, and regurgitates a droplet while slowly moving her head into the cell to bring the droplet into contact with the larva's mouthparts. The mouthparts of the adult remain still, while the mouthparts of the larva quiver slightly as it imbibes the liquid. During the few seconds required for the typical transfer, the gaster of the adult can be seen to telescope inward as liquid is pumped out of the crop.

On the other hand, a wasp soliciting a larva for salivary secretion actively stimulates the larva's head and mouthparts with chewing movements of her mandibles, causing the wasp's body to move slightly forward and backward. Adults do not perform antennal drumming when they are soliciting larval secretion.

Although the brief trophallactic contacts accompanying antennal drumming (step 5 above) always involved liquid flow to the larvae, as drumming diminished in intensity then ceased and the contacts became more prolonged (step 6), each contact appeared to end with solicitation of larval secretion by the adult.

Drumming in Other Species of *Polistes*

One of us (RLJ) has observed antennal drumming in several other species in the field (Table 3). In each of these species, the behavior is performed in the same context as in *P. fuscatus*, that is during regurgitation of crop content food to larvae. *P. exclamans* Viereck is unusual in that it frequently issues two distinct bursts of drumming prior to entering a cell. *P. annularis* (L.) drums

Table 3: Occurrence of antennal drumming in *Polistes*. Average drumming frequencies for species other than *P. fuscatus* were determined from sonagrams made from tape recordings taken in the field

Species	Locality	Frequency (strokes/s)	Sample size
P. (Fuscopolistes) fuscatus (F.)	Wisconsin	29.0	24
P. (Fuscopolistes) bellicosus Cresson	Florida	23.6	3
P. (Fuscopolistes) metricus (Say)	Florida	35.6	4
P. (Fuscopolistes) carolinus (L.)	Florida	37.8	7
P. (Onerarius) carnifex (F.)	Mexico		
P. (Aphanilopterus) annularis (L.)	Florida		
P. (Aphanilopterus) exclamans Viereck	Florida	37.2	1
P. (Aphanilopterus) instabilis de Saussure	Mexico		
P. (Aphanilopterus) versicolor (Olivier)	Brazil		
P. (Aphanilopterus) erythrocephalus Latreille	Costa Rica		
P. (Aphanilopterus) canadensis (L.)	Brazil		

very lightly, almost inaudibly. Drumming in *P. canadensis* (L.) (and possibly other species) occurs throughout the night (RLJ pers. obs.).

Despite its being the subject of numerous intensive behavioral studies, *P. gallicus*, a European species in the subgenus *Polistes*, has not been observed to perform antennal drumming (MP pers. obs.; J. GERVET, pers. comm.), although HELDMANN (1936) and ISHAY and SCHWARTZ (1973) state that females often waggle the gaster from side to side prior to giving up liquid — especially juice from prey — to the larvae. Their description of this behavior is similar to what GAMBOA and DEW (1981) call "lateral vibration" in *P. metricus* (Say).

A Test of a Hypothesis on the Function of Antennal Drumming

It seems likely that antennal drumming is a signal that conveys information, probably via vibration of the nest carton, to other members of the colony. The observation that solitary foundresses perform the behavior prior to the emergence of any workers and that the behavior does not appear until the day the first larva hatches, strongly suggest that the signal is meant for the larvae and not for adult nestmates. Because the drumming is clearly associated with the regurgitation of liquid food to the larvae, it is likely that the signal provides information about adult-larva trophallaxis. Specifically, we hypothesize that antennal drumming communicates to the larva that it is about to receive liquid food from the adult and should withhold the release of larval salivary secretion. Especially if a larva has not been milked of its secretion recently, it will exude copious amounts of it in response to only a light touch. A signal that reduces the likelihood that larval secretion will be mixed with the liquid protein offered by the adult would be advantageous to the larva in that it would not dilute and thereby reduce the amount of liquid food ingested. The less of its own secretion the larva ingests, the less energy it must expend absorbing and resecreting the amino acids and sugars in the secretion (MASCHWITZ 1966; HUNT et al. 1982). Prevention of inadvertent release would be advantageous to the adults in maximizing the amount of larval secretion they could obtain when they solicit it.

This hypothesis about the function of antennal drumming predicts that a larva that has just received the signal will exude less of its secretion than if it has not recently been signaled. We attempted to test this prediction in the following experiment.

Methods

The lab-reared colonies described above were used. All tests were done in the mornings, in conjunction with the first prey offering of the day. The test consisted of measuring the volume of secretion given up by individual larvae in a nest on which the queen had just drummed, and comparing this to the amount each produced in the absence of drumming. We took advantage of the temporal separation of antennal drumming and regurgitation by a queen to provide the necessary stimuli to the larvae. Collections of secretion from larvae in the absence of drumming were made while the queen groomed after feeding a lump of prey (step 3 of the feeding sequence). Collections from larvae that had just experienced drumming were made during step 4, that is while the queen was drumming without yet regurgitating liquid to the larvae.

Since the amount of secretion a larva produces depends in part on its size, we held the size variable constant by using each larva as its own control. One subset ($n = 69$) of larvae in the sample was tested first just after drumming, then 24 h later without drumming. With the other subset ($n = 68$) secretion was collected first without drumming, then 24 h later after drumming. The subsets were separated by 24 h. One day was felt to be adequate time for the larvae to fully regenerate the amount of secretion removed in our test. Larvae are normally solicited many times by the adults in a 24-h period. 52 larvae were tested once in each subset. Another 33 were used in only one subset. These included larvae that were excluded from the first subset because they were too small to work with and others that were excluded from the second subset because they had pupated. As no consistent patterns were found relating observations on larvae tested in both subsets, the ($n = 137$) trials were viewed as independent.

The method of collection of secretion was standardized for all larvae tested. The upper end of a 5 μl capillary pipette, held vertically at one end of a light lever arm, was touched to the mouthparts of the larva for 5 s. The lever was adjusted so that the pipette exerted an upward pressure of 0.6 mg against the mouthparts of the larva (larvae hang head-down in the cells). At least a light contact with the mouthparts is necessary to elicit the exudation of secretion.

Results

Exploratory analysis of the data showed that the distributions of differences in secretion amounts between "with drumming" and "without drumming" were similar, so data for the two subsets were combined. 90 (66 %) of the larvae yielded less secretion with drumming than without ($\chi^2 = 13.5$, df = 1, $p < .001$). One larva yielded the same amount with as without drumming. Over all trials ($n = 137$), larvae yielded a mean of 2.66 (SD = 1.89) μl of secretion in the absence of drumming, and only 2.06 (SD = 1.70) μl with drumming. Drumming caused a 22.6 % drop in the mean amount of secretion yielded by this sample of larvae.

Conclusion

Because antennal drumming caused a significant reduction in the amount of secretion a larva would yield, we reject the hypothesis that drumming has no effect on the release of salivary secretion by larvae. Therefore we tentatively accept our alternative hypothesis, that antennal drumming inhibits the release of larval secretion.

Two features of our experimental procedure may have limited to only 22.6% the reduction of secretion obtained following drumming. First, the contact of the pipette with the larvae may have partially countered the inhibitory effect of drumming on exudation of secretion. When an adult regurgitates to a larva following drumming, contact with the mouthparts of the larva is light or via the droplet only. The pressure of the pipette, even though light and steady, may have been perceived by the larva as a solicitation of secretion.

Second, it may be that the queen's drumming-only sequence (step 4) is necessary because many repetitions of drumming are required before complete inhibition of secretion is imposed. By collecting secretion before this stage was complete, we may have failed to measure the full effect of the drumming behavior on the larvae.

Discussion

Our interpretation is that previous authors (RAU 1928; OWEN 1962; EVANS and EBERHARD 1970) were incorrect in ascribing sound production in this context to the knocking of the head against the cell wall. To overlook the involvement of the antennae is understandable, given the forward-backward motion of the whole body accompanying vigorous antennal drumming. We believe that the "longitudinal vibration" observed by GAMBOA and DEW in *Polistes metricus* is identical to what we are calling antennal vibration (GAMBOA and DEW 1981; DEW 1983).

The case of *Polistes gallicus* is intriguing. If the behavior is indeed absent, there is the possibility that oscillation of the gaster has the same function. This requires further investigation.

Females in several other social wasp genera also perform sound-producing movements in the same context as antennal drumming in *Polistes*. In the Polistinae, *Mischocyttarus drewseni* Saussure vibrates the gaster rapidly up and down against the comb just before entering a cell to regurgitate to a larva (JEANNE 1972). *Belonogaster grisea* (F.) and *B. juncea* (F.) tremble the wings, trill the antennae, and vibrate the gaster (ROUBAUD 1916; MARINO PICCIOLI and PARDI 1970). *Ropalidia cincta* (Lepeletier) females vibrate the wings prior to feeding solid food to each larva (DARCHEN 1976). *R. revolutionalis* (Saussure) foragers are said to drum their heads inside the cell before feeding the larva inside (HOOK and EVANS 1982). Audible abdominal drumming accompanying the feeding of liquid to larvae has been reported for vespines in queens of *Dolichovespula arenaria* (Fabricius) (GREENE et al. 1976; JEANNE 1977), and workers of *Vespa orientalis* (L.) (ISHAY 1975; ISHAY et al. 1974; ISHAY and SCHWARTZ 1973). Such behavior in the context of adult-larva trophallaxis is apparently absent in Nearctic species of *Vespula* (GREENE et al.

1976). If, indeed, these sounds serve to communicate information to the larvae, such communication appears to be widespread though not uniform in occurrence or performance among the social wasps.

The outcome of our experimental test in support of the hypothesis that drumming communicates to the larvae that liquid food is coming does not preclude the possibility that the behavior may have additional functions. The observation that *P. canadensis*, at least, drums during the night is hard to reconcile with our interpretation of drumming's function. Secondly, although our study focussed entirely on queens, other observations both on *P. fuscatus* (R. L. Jeanne, unpubl. obs., D. C. Post, pers. comm.) and on *P. metricus* (Dew 1983) indicate that queens continue to do most of the antennal drumming (= "longitudinal vibration") even after workers are present in the colony. This suggests that drumming may play some role related to the particular interests of the queen but not the workers. A resolution of such questions will require further investigation.

Zusammenfassung

Feldwespen-Königinnen trommeln mit raschen Antennenschlägen auf die Ränder von Nestzellen. Das wird im Detail für *Polistes fuscatus* beschrieben. Hier tritt es zusammen mit der Beuteübergabe an die Larven auf: Nach dem Verteilen fester Nahrung an die Larven geht die Königin von Zelle zu Zelle, trommelt die Antennen gegen den Zellrand und erzeugt damit ein hörbares Geräusch. Nach mehreren min geht die Königin dann nach dem Trommeln zu einer Larve (meist der, auf deren Zellrand sie trommelte) und übergibt Beutesaft. Ein Trommelwirbel dauert im Mittel knapp 1 s, die Antennengeißeln schlagen mit im Mittel 29 Schlägen/s. 10 weitere *Polistes*-Arten machen es genauso.

Das Trommeln scheint der Larve anzukündigen, daß sie jetzt flüssige Nahrung bekommt und ihre Speichelsekretion einstellen soll. Tatsächlich produzieren Larven, die das Trommelsignal erhielten, weniger Speichel als solche, die es nicht wahrnahmen. Dieser experimentelle Befund bestätigt die vermutete Bedeutung des Signals.

Acknowledgments

We gratefully acknowledge Holly Downing for assistance with the collection and maintenance of the laboratory colonies. Thomas Walker and Jeffrey Baylis loaned us tape recording equipment, and Jack P. Hailman let us use his sonagraph. We thank Richard Richlan for his assistance with a preliminary study of antennal drumming. Erik Nordheim generously provided advice on our statistical analyses. Jeffrey Baylis offered constructive criticism of the manuscript. The senior author was supported by a grant from the French Ministry of Foreign Affairs. Research was supported by the College of Agricultural and Life Sciences, University of Wisconsin, Madison, and by National Science Foundation Grant BNS 77-04081 to R. L. Jeanne.

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