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Bobbi J. Harding
Oakland University

George J. Gamboa
Oakland University

THE SEQUENTIAL RELATIONSHIP OF BODY OSCILLATIONS IN THE PAPER WASP, *POLISTES FUSCATUS* (HYMENOPTERA: VESPIDAE)

Bobbi J. Harding[1] and George J. Gamboa[1,2]

ABSTRACT

Three kinds of body oscillations by foundresses of the paper wasp, *Polistes fuscatus*, were analyzed from 100 h of videotapes of 17 multiple- and 16 single-foundress, preworker colonies. The three kinds of oscillations were observed to be temporally proximate only after prey returns. Their sequential occurrence was always antennal drumming (AD), abdominal wagging (AW), and lateral vibration (LV). This sequence is consistent with the hypothesized communicative meanings of ADs, AWs, and LVs. In particular, ADs may signal larvae to withold salivary secretions prior to receiving a liquid meal from an adult female; oscillations AW and LV may signal larvae to secrete and withold saliva, respectively. Additional studies are required to provide causal evidence of the communicative meanings of ADs, AWs, and LVs.

Body oscillations have been reported in adult females of at least 15 species of wasps, and thus appear to be widespread among social wasps. The communicative meaning of these oscillations, however, is poorly understood (Savoyard et al. 1998). The species of social wasp whose oscillatory behavior has been studied most extensively is the paper wasp, *Polistes fuscatus* (Fabr.). Three distinct kinds of oscillations have been described in *P. fuscatus*: antennal drumming (AD), abdominal wagging (AW) and lateral vibration (LV). ADs consist of a female positioning her head over the opening of a cell containing a larva and rapidly hitting her antennae against the rim of the cell (Pratte and Jeanne 1984). AWs consist of slow (2–7 oscillations/s), side-to-side movements of a female's gaster against the nest as she walks over brood cells (Gamboa and Dew 1981). LVs consist of a stationary female rapidly (17 oscillations/s) moving her abdomen from side-to-side against the surface of the nest producing a short (<1s), audible sound (Savoyard et al. 1998).

All three types of oscillations are thought to be signals by adult females to larvae (Gamboa and Dew 1981, Pratte and Jeanne 1984, Downing and Jeanne 1985, Savoyard et al. 1998). The behavioral repertoire of larvae and the kinds of signals from female adults to larvae are thought to be quite limited (Savoyard et al. 1998). Larvae receive malaxated prey and liquid food from adults and, in turn, provide saliva to adults (West-Eberhard 1969, Pratte and Jeanne 1984, Hunt 1991). Adult females may signal larvae to secrete or withhold saliva (Savoyard et al. 1998). Larval saliva contains sugars,

[1]Department of Biological Sciences, Oakland University, Rochester, MI 48309.
[2]Corresponding author.

amino acids, and proteins (Hunt et al. 1982) and has been postulated to play an important role in the evolution of eusociality (Hunt 1991).

Although ADs, AWs, and LVs are presumed to be signals by females to larvae, their specific communicative meanings are not well understood. Savoyard et al. (1998) reported that the three kinds of oscillations are sometimes associated with each other. More specifically, Savoyard et al. (1998) documented that the numbers of LVs were significantly, positively correlated with both the numbers of ADs and AWs. We examined these three kinds of oscillations to determine if there is a specific temporal and sequential relationship among them. Such information might provide additional insight into their communicative meanings.

METHODS

We videotaped 17 multiple- and 16 single-foundress, preworker colonies of *P. fuscatus* nesting in plywood nestboxes near Rochester, Michigan. The nestboxes were suspended from wood crossbars attached to metal fenceposts. Foundresses were marked for individual identification on 17 and 19 June 1997, approximately one week prior to the beginning of videotaping. Each of five Sony TR910 Hi8 video cameras was positioned on a tripod approximately 0.9m beneath a nestbox so that the field of view consisted of the wasps on the face and side of the comb. The video, filmed at 30 frames per second with a 15X optical telephoto, provided a field of ~7cm in diameter. We videotaped 17 multiple-foundress colonies from 22–27 June and 16 single-foundress colonies from 27–29 June. We completed all videotaping between ~1000 h and ~1730 h when ambient air temperatures were $\geq$21°C. We completed 4 h of videotaping for each multiple-foundress colony (68 h) and 2 h of videotaping for each single-foundress colony (32 h).

Videotapes were viewed in a laboratory and the behavior of foundresses was recorded on a microcassette audio recorder. We recorded departures, returns, items foraged, body oscillations, and their associated times for all foundresses. To increase observer reliability and to minimize observer bias, one individual (GJG) observed all videotapes and completed all transcriptions.

RESULTS

Pratte and Jeanne (1984) reported that ADs occurred only after wasps returned with prey. Thus we examined the sequence of oscillations that followed prey returns since this was the only context in which we observed all three kinds of oscillations. In single-foundress colonies, we recorded nine prey returns of which six were followed within 30 min by all three kinds of body oscillations. In multiple-foundress colonies, we recorded 80 prey returns of which eight were followed within 30 min by all three kinds of body oscillations. Fifteen of these oscillation sequences were interrupted by the returns of other foundresses. This may at least partly explain why single-foundress colonies had a higher proportion of prey returns that were followed by all three oscillations than did multiple-foundress colonies.

When there was more than one complete sequence of oscillations for a colony, we averaged the values from multiple sequences so that each colony contributed a single datum for calculating a mean value. This resulted in a sample size of five single- and six multiple-foundress colonies for which we had at least one complete sequence of three different oscillations. We found

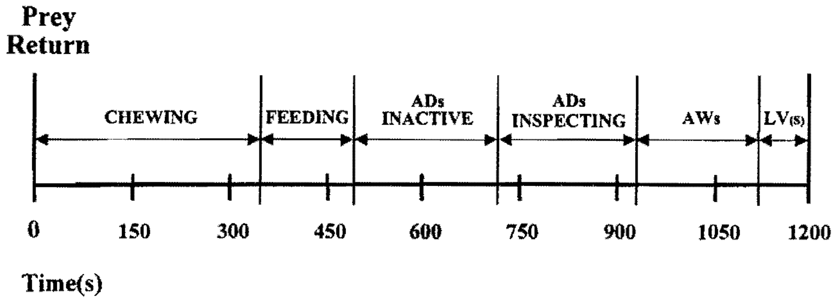

Figure 1. The sequence of activities performed by foundresses of *Polistes fuscatus* after returning with a prey item. The seconds spent in each activity are mean values based on five single- and six multiple-foundress colonies. Prey returns and LVs are the initial and terminal events, respectively, of the sequence of activities.

no significant differences between single- and multiple-foundress colonies in the nine parameters discussed below ($p \geq 0.09$; Mann-Whitney U Test with a Bonferroni Correction).

Upon returning with a prey item, the wasp chewed the prey item ($\bar{x}$ = 312s, range = 150–735s), which became noticeably smaller as the wasp extracted fluids from the prey (Fig. 1). Female *Polistes* extract hemolymph from prey as they malaxate it (Hunt 1984). The wasp then distributed the prey mass to larvae ($\bar{x}$ = 51s, range = 5–100s). After feeding the prey to larvae, the wasp began performing ADs ($\bar{x}$ = 12.9 ADs, range = 2–20ADs) while displaying inactivity between episodes of ADs ($\bar{x}$ = 205s, range = 30–470s). The wasp then began to inspect cells between episodes of ADs ($\bar{x}$ = 8.6 ADs, range = 1–29 ADs; $\bar{x}$ = 139s, range = 30–405s). During cell inspections, adult wasps lowered their heads into cells containing larvae. Next, the female performed AWs ($\bar{x}$ = 2.3 episodes of AWs, range = 1–6 episodes) as she inspected and walked over cells ($\bar{x}$ = 207s, range = 5–660s). Finally, the wasp performed one to five LVs ($\bar{x}$ = 2.0 LVs), which were the terminal oscillations of the sequence.

DISCUSSION

The sequence of the three types of oscillations was invariant: for all 14 recorded sequences, the order of the oscillations was AD, AW, and LV. This sequence is consistent with the suggested communicative meanings hypothesized for ADs, AWs, and LVs from previous studies. Pratte and Jeanne (1984) provided evidence that ADs follow the feeding of solid prey to larvae. They postulated that ADs inform larvae that they are about to receive a liquid meal from an adult and that the larvae should withhold their salivary secretions. Our observations that ADs occurred after larvae were fed prey and that wasps extracted liquid from prey items shortly before performing ADs is consistent with Pratte and Jeanne's (1984) hypothesized function of ADs. Savoyard et al. (1998) speculated that AWs and LVs might signal larvae to secrete and to withhold larval salivary secretions, respectively. Our findings that AWs always preceded LVs and that LVs were the terminal oscillations of the sequence are consistent with the hypotheses that AWs stimulate larval secretions and LVs inhibit larval secretions.

It has been hypothesized that much of the adult-larval communication in social wasps is mediated by the substrate vibrations produced by body oscillations (Savoyard et al. 1998). Since the durations and oscillation frequencies of ADs, AWs, and LVs are known (Pratte and Jeanne 1984; Savoyard et al. 1998), it should be possible to mechanically reproduce the three kinds of body oscillations in combs containing larvae. This, in turn, could be utilized in experimental studies to provide causal evidence of the communicative meanings of ADs, AWs, and LVs.

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