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SHORT COMMUNICATION

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The function of dart behavior in the paper wasp, *Polistes fuscatus*

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Abstract Dominance behavior in *Polistes* wasps is a composite trait consisting of various discrete behaviors such as darts, lunges, bites, and mounts. The majority of these behaviors are considered 'aggressive', and these aggressive behaviors are considered to form a continuum from mild (e.g., darts) to severe (e.g., falling fights). In this paper we focus on darts, the most common of the dominance behaviors, and investigate their function in unmanipulated post-emergent colonies of the primitively eusocial wasp *P. fuscatus*. Here we show that darts are correlated with the more severe dominance behaviors, and that dominance ranks do not change with the addition or exclusion of darts. We find no correlation, however, between receiving darts and receiving more severe dominance behaviors. This result suggests that darts are not indicative of aggressive reinforcement of dominance, but rather may serve a different function. Our data suggest that the function of darts is to regulate activity on nests. Both foundresses and workers dart inactive workers significantly more often than by chance, and workers respond to a foundress's (but not a worker's) dart by becoming less inactive. We also found that active workers who receive a dart from either a foundress or worker respond mostly by switching from one activity to another. Thus, our data suggest that darts are not aggressive behaviors, that foundresses use this signal to initiate activity, and that foundresses and workers both use the signal to regulate worker activity.

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Introduction

Polistes wasps are primitively eusocial, display slight caste differentiation, and exhibit a great deal of behavioral plasticity (see Turillazzi and West-Eberhard 1996). In temperate regions, the wasp has a defined four-stage colony cycle consisting of founding, worker, reproductive, and intermediate phases. Of interest has been the founding phase, during which time females initiate a nest alone, initiate a nest in association with another female (Reeve 1991), or wait to adopt an orphaned nest (Starks 1998). These characteristics make *Polistes* a model system for the study of the evolution of eusociality, kin recognition, and reproductive conflicts (see, e.g., Starks et al. 1998; Reeve et al. 2000).

Because *Polistes* wasps construct un-enveloped nests and often contain less than 100 individuals, the behavior of individual wasps across the colony cycle has been well documented (Reeve 1991). Given the potential conflict of reproductive interests, attention has been focused on the dominance hierarchy that develops between cooperating foundresses (Pardi 1948). A dominance hierarchy refers to a social organization where group members have different status levels, and studies show that the level that individuals occupy is linked to reproduction and task performance (Pardi 1948; Gamboa et al. 1978; Strassmann 1981).

Dominance behavior is a composite of multiple behaviors such as darts, lunges, bites, mounts, chases, and falling fights (Pfennig et al. 1983), the majority of which are considered aggressive. Both aggressive and non-aggressive dominance behaviors exist, however, and comprise the suite of characteristics that correlate with true dominance (Pardi 1948). The terms aggression and dominance have a specific meaning in this context, and can be defined as: aggression – hostile or threatening behavior; and dominance – control or command over others. *Polistes* researchers often consider aggression a means of displaying dominance, and thus a wasp's position in a hierarchy can be determined by observing the relative frequencies of initiating and receiving aggressive behavior (Pardi 1948).

In addition to difficulties in understanding what is considered 'hostile or threatening' to a wasp, researchers are faced with examining a multilevel correlative relationship. Specifically, aggression is often considered the proximate link in maintaining behavioral dominance, and behavioral dominance an indicator of reproductive dominance. Röseler and Röseler (1989) showed that the latter relationship is not absolute when ovariectomized *P. dominulus* foundresses maintained dominant status while incapable of laying eggs. Nonacs et al. (2004) showed that the former relationship is not absolute when dominance behavior was found to be unpredictive of the degree of reproductive partitioning between *P. fuscatus* co-foundresses. These studies indicate that we do not fully comprehend the functional significance of dominance behavior.

Here we evaluate dart behavior, a behavior traditionally viewed as aggressive. Darts are defined as sudden movements of one wasp towards another, which do not result in physical contact. Darts are performed by foundresses and workers, and are the most common of the dominance behaviors seen between nestmates. We examine the relationship between darts and other dominance behavior, the role that darts play in determining a wasp's position in a dominance hierarchy, the context in which darts are performed, and the effect that receiving a dart has on a wasp's behavior.

Methods

We collected data from 16 post-emergent *P. fuscatus* colonies located in Ithaca, New York. All colonies contained wasps individually paint-marked. Data were collected from videotapes, which were recorded during May–July 1995. Videotapes were transcribed using two methods. *Method 1* involved 11 colonies (a subset of the original 16) containing 4.2±2.4 (mean ± SD) wasps and represented 4.4±2.2 h of observation per colony. All dominance interactions, and the identity of interacting wasps, were recorded. The following behaviors were recorded: darts, lunges (a dart with contact), bites, mounts, grapples, stings, and falling fights. *Method 2* involved 11 colonies (a different subset) with 5.8±2.6 wasps were observed for 5.67±4.53 h. We recorded 1,002 focal darts and noted the identity of the pair involved. In addition, the behavior performed by the wasp before (pre-dart) and after (post-dart) receiving the dart was noted.

To calculate a dominance hierarchy, one can sum all interactions into a single value (Pardi 1948), weight the severity of each behavior prior to summing (Pfennig et al. 1983), or separate the behaviors into mild and severe categories (Premnath et al. 1996). To remove subjective evaluation, we calculated our dominance score by dividing number of dominance acts initiated by the total number of dominance acts initiated and received. Colony-specific individual dominance scores were arranged in descending order (Reeve and Gamboa 1987). This process was repeated after excluding darts and after including only darts. The resultant values are referred to as rank 1, rank 2, and rank 3, respectively. The relationship between darts and other dominance behaviors was examined by regressing (1) the number of darts initiated against the number of other dominance behaviors initiated and (2) the number of darts received against the number of other dominance behaviors received.

χ^2 tests were used to examine whether darts were preferentially directed at wasps based on activity states, whether darts influenced the behavior of recipients, and (if yes) what the likely outcome of the behavioral change was. Expected values were generated using the assumption that darts would be directed at random to wasps in one of four behavioral states: active (e.g., walking), inactive (e.g., sitting, grooming), darting, and inspecting cells. These behaviors were selected because they constituted 92% of all behaviors and activity states observed prior to the focal dart. In order to determine the expected values for the consequences of darts, we calculated the pre-dart proportions at which each behavior under consideration was performed and multiplied this value by the total number of transitions occurring in the post-dart period. To calculate the expected value of an active wasp to change behavior, we assumed that she had only three options: to become inactive, switch behavior, or continue performing the same behavior.

Results

Darts and other dominance behaviors

In this study, 77.0±32.0% of the total dominance behavior observed was darts. A positive correlation was detected between the number of darts and other dominance behavior initiated by an individual (Fig. 1A). There was no relationship, however, between the number of darts and other dominance behavior an individual received (Fig. 1B).

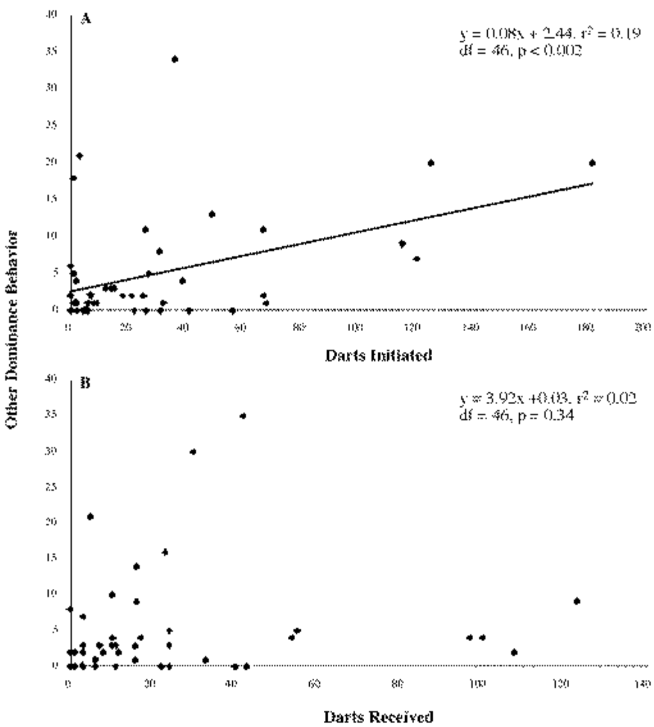

Fig. 1A, B Relationship between darts and other dominance behaviors. **A** Relationship between initiating darts and initiating other dominance behaviors. **B** Relationship between receiving darts and receiving other dominance behaviors

Table 1 χ^2 values for different behaviors observed immediately prior to receiving the focal dart (pre-dart) and just after the focal dart (post-dart). All the comparisons for pre-dart behaviors were between the observed number of wasps carrying out a task and the expected number of wasps that would be doing the same task by chance alone. All comparisons for post-dart behaviors were between the number of wasps carrying out a task in the post-dart period and the number of wasps carrying out the same task in the pre-dart period. Analysis was carried out separately for darts initiated by workers to other workers and initiated by foundresses to workers. Significant (P<0.05) values are in bold

	Behavior	Observed/ expected	χ^2 Worker darts	Observed/ expected	χ^2 Foundress darts
Pre-dart	Inactive	161/128	**8.51**	100/76.25	**7.40**
	Active	116/128	1.12	69/76.25	0.69
	Dart	134/128	0.28	94/76.25	**4.13**
	Cell inspection	101/128	**5.70**	42/76.25	**15.38**
Post-dart	Inactive	141/161	2.48	72/100	**7.84**
	Active	113/116	0.08	67/69	0.06
	Dart	151/134	2.16	116/94	**5.15**
	Cell inspection	104/101	0.09	41/42	0.02

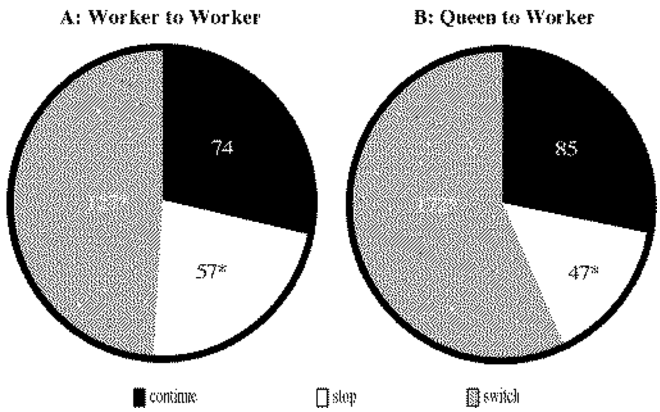

Fig. 2A, B There are three possible responses for an active wasp once darted: become inactive (*white area in the pie chart*), continue performing the activity (*black area*), or switch to a new activity (*gray area*). The *pie chart* shows the relative amount of each possible response. Within each section the number of wasps in each category is mentioned and significantly different ones are *marked with an asterisk* (χ^2 analysis, P<0.05, df=1). **A** Response of the active wasps to a dart by another worker. **B** Response of active wasps to a dart by the foundress

Darts and dominance hierarchies

Position in the dominance hierarchy did not differ when darts were excluded from the analysis, or when only darts were considered (Wilcoxon, P>0.05). Although 52% of individuals changed ranks when comparing rank 1 and rank 2, and 26% when comparing rank 1 and rank 3, there was no consistent pattern in the changes and many changes resulted from tied ranks.

Darts and activity

Foundresses initiated more darts than workers (45.8±34.4 vs 12.1±9.2; Wilcoxon, P=0.054) and wasps inspecting cells received significantly fewer darts than anticipated (Table 1). Inactive workers received significantly more darts than expected from both foundresses and workers. Workers responded to the foundress's dart by becoming less inactive, but did not respond to a worker's dart (Table 1). When active wasps received a dart from either a foundress or a worker, they were significantly more likely to switch behaviors than to continue performing the previous behavior or to become inactive (Fig. 2A, B).

Discussion

In this study we attempted to identify the function of darts, a very common behavior observed between wasps. Because this easily observed behavior occurs so frequently, adaptive explanations for it have been proposed. For example, Reeve and Nonacs (1992) suggest that darts and other low-cost dominance behaviors are used to set the degree of reproductive skew between cooperating foundresses. On closer examination, however, the relationship between darts and reproductive opportunities vanishes (Nonacs et al. 2004). This is disturbing, given that dominance hierarchies, which presumably correlate with fitness, are often calculated using darts.

Our data show a positive relationship between initiating darts and initiating other aggressive dominance behaviors (Fig. 1A). In addition, dominance hierarchies developed using only darts, excluding darts, and including all 'classic' aggressive behaviors do not differ significantly. Accordingly, darts appear to be reasonable correlates of behavioral dominance, and thus inclusion of darts is unlikely to result in faulty dominance hierarchies. However, there was no correlation between the receipt of a dart and the receipt of other dominance behaviors (Fig. 1B). This finding suggests that, although a correlate of seemingly aggressive behavior, darts are not aggressive.

What then is the primary purpose of a dart? In many primitively eusocial insects, foundresses are known to regulate activities and act as the central pacemaker of the colony (Breed and Gamboa 1977; Reeve and Gamboa 1983, 1987). Research using incapacitated (chilled) wasps examined the effect of foundress behavior on worker behavior and discovered that foundresses regulate worker foraging (Reeve and Gamboa 1987). We examined whether darts, a behavior unavailable to chilled foundresses, regulate activities within the colony. In support, we find that foundresses initiate significantly more darts than do workers, and that darts are directed at inactive individuals more often than expected by chance (Table 1). Our data also suggest that the status of the darter is important: although both workers and foundresses darted inactive workers, only darts by foundresses resulted in the recipient becoming active (Table 1). This result suggests that foundresses directly influence the level of activity in a nest.

Although they do not increase activity, darts by workers do influence behavior. Active workers respond to darts from both workers and foundresses by switching activities (Fig. 2). Dart behavior may induce a specific switch, or induce a general change in activity pattern. Further studies are required to discern the level of control. Our data do suggest, however, that there are two levels at which tasks are regulated, first by foundresses activating workers and second by foundresses and workers influencing active workers to switch tasks.

If darts are activity-regulating social signals, then it is appropriate to examine them within a communication system framework. Darts could be visual signals, vibrational signals, chemical signals, or a combination of these signal forms. Our data suggests that darts may be visual signals: individuals who were performing cell inspection—and thus had their heads within a cell—were significantly less likely to receive a dart than expected (Table 1). Although the exact form of the signal has not been investigated, the meaning of the signal is becoming clearer: darts appear to regulate activity within the nests. In this signaler/recipient relationship, the effect of the signal is dependent on the status of the signaler (i.e., foundress or worker) and the activity state of the recipient (i.e., active or inactive).

Based on the complexity of these findings, and the definition of language as the use of signs, gestures, or sounds to communicate (see National Institute of Deafness), it is tempting to label darts as a form of language used by wasps to communicate colony task requirements. Our perception of language, as exemplified by the honeybee dance language, is so complex that we hesitate to do so. However our data do suggest that the communication system in paper wasps is more complicated than previously assumed. It is apparent that we need more studies where each of dominance behaviors are investigated separately in order to tease out the roles they perform in the regulation of both reproductive and non-reproductive activities for the colony.

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