

## Worker Age, Ovary Development, and Temporal Polyethism in the Swarm-Founding Wasp *Polybia occidentalis* (Hymenoptera: Vespidae)

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*I measured oocyte sizes of Polybia occidentalis workers to assess whether ovary development corresponded with adult age or with individual variation in behavior. Workers exhibited temporal polyethism by first working inside the nest, then performing on-nest tasks, and later foraging and defending the nest. Individuals varied in their ages at first performance of each of these sets of behavioral acts. Ovary development corresponded strongly with adult age. Workers' ovaries declined quickly after an initial phase of partial development. The period of ovary decline overlapped with the age range at which most workers began performing tasks on the exterior nest surface. However, after accounting for age effects, individual behavioral differences (rate of temporal polyethism and performance of foraging and defense tasks) did not correspond with ovary development. These data suggest that ovary development had little or no effect on variation in task performance by P. occidentalis workers on the nest surface.*

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**KEY WORDS:** division of labor; Epiponini; polyethism; reproductive physiology.

### INTRODUCTION

Reproductive physiology has long been known to influence the behavioral roles of females in some eusocial insect species (Pardi, 1948; West-Eberhard, 1969). Females with greater capacity for direct reproduction, indicated by

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greater ovary development, are often dominant over their nestmates (Röseler, 1991). Females with better-developed ovaries often specialize on queen-like tasks such as brood care and avoid worker-like tasks such as foraging (West-Eberhard, 1981). These patterns apply both to reproductive females that cooperate to initiate new colonies, and to offspring worker females, in primitively eusocial paper wasps (Haggard and Gamboa, 1980; Hughes and Strassmann, 1988). However, the degree of division of labor between queens and workers, and among workers, generally increases with colony size in eusocial Hymenoptera (Jeanne, 1986; Bourke, 1999). Research on honey bees (*Apis mellifera*) suggests that the role of reproductive physiology in worker division of labor has decreased as their large, complex societies evolved (Robinson, 1987; Robinson *et al.*, 1989). Little is known about how reproductive physiology affects polyethism among other advanced eusocial taxa, such as swarm-founding (advanced eusocial) wasps of the vespid tribe Epiponini.

Epiponine wasp colonies are typically one to four orders of magnitude larger than those of primitively eusocial paperwasps (Jeanne, 1991a). Neotropical swarm-founding wasps exhibit some of the most complex worker division of labor yet documented in insect societies, similar in complexity to honey bee polyethism (Jeanne, 1991b). Epiponine workers have stronger temporal polyethism than their independent-founding relatives (Jeanne, 1991b; O'Donnell, 1998a). In one well-studied species, *Polybia occidentalis*, workers pass through a predictable series of task sets as they grow older, shifting abruptly from in-nest work to tasks performed on the exterior surface of the nest envelope. Foraging is performed later in life (Jeanne *et al.*, 1988). However, the age-task sequence is not deterministic, and individuals vary greatly in their rates of temporal polyethism. For example, simultaneously observed nestmate workers varied in age from 5 to over 40 days at initiation of foraging [mean, 19 days (O'Donnell and Jeanne, 1992a)]. *Polybia occidentalis* workers also exhibit stronger specialization on tasks than workers of primitively eusocial wasps (Jeanne, 1991b; O'Donnell and Jeanne, 1992a; O'Donnell, 1998a).

The first goal of this study was to quantify variation in ovary development in *P. occidentalis* workers and to determine whether worker age influenced ovary development. The second goal was to determine whether variation in *P. occidentalis* workers' temporal polyethism and task performance correspond to their degree of ovary development. I collected data on behavioral development of marked, known age workers, then measured their ovary development. I first tested whether workers' ovary development was correlated with adult age. I then analyzed correlations of individual variation in task performance, and in the rate of temporal polyethism, with ovary development.

## MATERIALS AND METHODS

### Study Site and Population

Fieldwork was conducted in the wet season of 1991 near Centro Ecológico La Pacifica, in Guanacaste Province, Costa Rica (10°25'N, 85°07'W). Local habitats include savannalike pasture with scattered shrubs and gallery forest. The area is artificially irrigated throughout the year. *Polybia occidentalis* is abundant at this location, where several previous studies of behavior were conducted (Jeanne *et al.*, 1988; O'Donnell and Jeanne, 1992a).

### Observation Colonies

I selected two observation colonies (henceforth, colonies A and B) based on ease of access. The colonies were moved several hundred meters from their initial nesting sites to shelters where they were protected from rain and direct sun. Foragers were observed returning to the colonies the day after they were moved, and the colonies were left undisturbed for at least 3 days. A mirror was mounted behind each observation colony's nest, opposite the nest entrance hole, so that data could be collected from the entire nest surface.

### Marking and Introductions of Subject Workers

I collected brood combs from several additional *P. occidentalis* nests as sources of subject workers. The brood combs were housed indoors at ambient temperature in gauze-covered plastic containers. I cleared the brood combs of adults when they were collected and every 24 h afterward. Newly emerged ( $\leq 24$ -h-old) adults were used as subjects or discarded. I added 10–15 individually marked workers to each colony on days alternating with behavioral observations, beginning 30–31 August and ending 18–19 September 1991. I introduced a total of 150 females to colony A and 145 females to colony B.

### Behavioral Observations and Worker Collections

I observed worker behavior at each colony every 2 days from 31 August to 22 September 1991. I recorded behavioral data during continuous observation sessions of 1.5 h in the morning and 1 h in the afternoon on each observation day. During these sessions, I scanned the surface of the nest and the nest entrance and noted the identity and activity of all marked wasps that were visible inside the nest through the entrance or on the exterior nest

surface (see the ethogram in the Appendix). I also recorded all occurrences of arrivals and departures of marked foragers at the nest. *Polybia occidentalis* workers make short orientation flights at around the age of onset of foraging (O'Donnell and Jeanne, 1992b); these flights comprised less than 1% of foraging observations in this study and were not distinguished from other foraging trips in the analyses.

I collected the subject colonies after dark on the evening of the last day of behavioral observations. I placed each colony in a plastic bag with ether, then removed the adults wasps from the nest material. I separated marked from unmarked adults and placed all adult wasps into formalin:acetic acid:ethanol fixative.

### Dissections and Ovary Measurements

All dissections and measurements were performed blind to the age and behavior of the wasps. I transferred the wasps into 70% ethanol immediately prior to dissection, then dissected the gasters of all marked females under a binocular microscope. Ovaries of all dissected females were located and examined. If no opaque oocytes could be discerned by two observers at 40× magnification, I scored the ovaries as filamentous and a mean oocyte size of zero was recorded for that female. If any opaque, swollen oocytes were visible, the ovaries were photographed onto black-and-white film at 40× magnification with a 35-mm camera body mounted on the microscope. The 35-mm negatives were developed and scanned into computer files at 300-lpi resolution. I measured the length of the largest oocyte in the left and right ovary for each female using the ruler tool of Adobe PhotoShop software. I used the mean length of these two oocytes as an index of ovary development for each female. To determine the size of mature oocytes, I measured the length of eggs collected from the brood comb of a *Polybia occidentalis* nest with dial calipers.

### Statistical Analysis

I tested for relationships of age and behavioral variation with ovary development using multiple linear regression. The results of multiple linear regression tests that I present are type III sums of squares, indicating the relationship of each age or behavior covariate with ovary development when that covariate was entered as the last term in the regression model (Sokal and Rohlf, 1981). I pooled behavioral acts into groups based on where they were performed (on-nest acts versus foraging). I also distinguished defense tasks from other on-nest acts, since defense is often performed later in life and

overlaps in age at performance with foraging behavior (Jeanne *et al.*, 1992). I scored the ages at first observed performance of on-nest acts, foraging, and defense for each worker. Estimates of colony distributions of age at first performance of behavioral acts included workers that did not survive until colony collection. I used survival analysis with censoring to analyze the distributions of age at first performance of the task sets.

## RESULTS

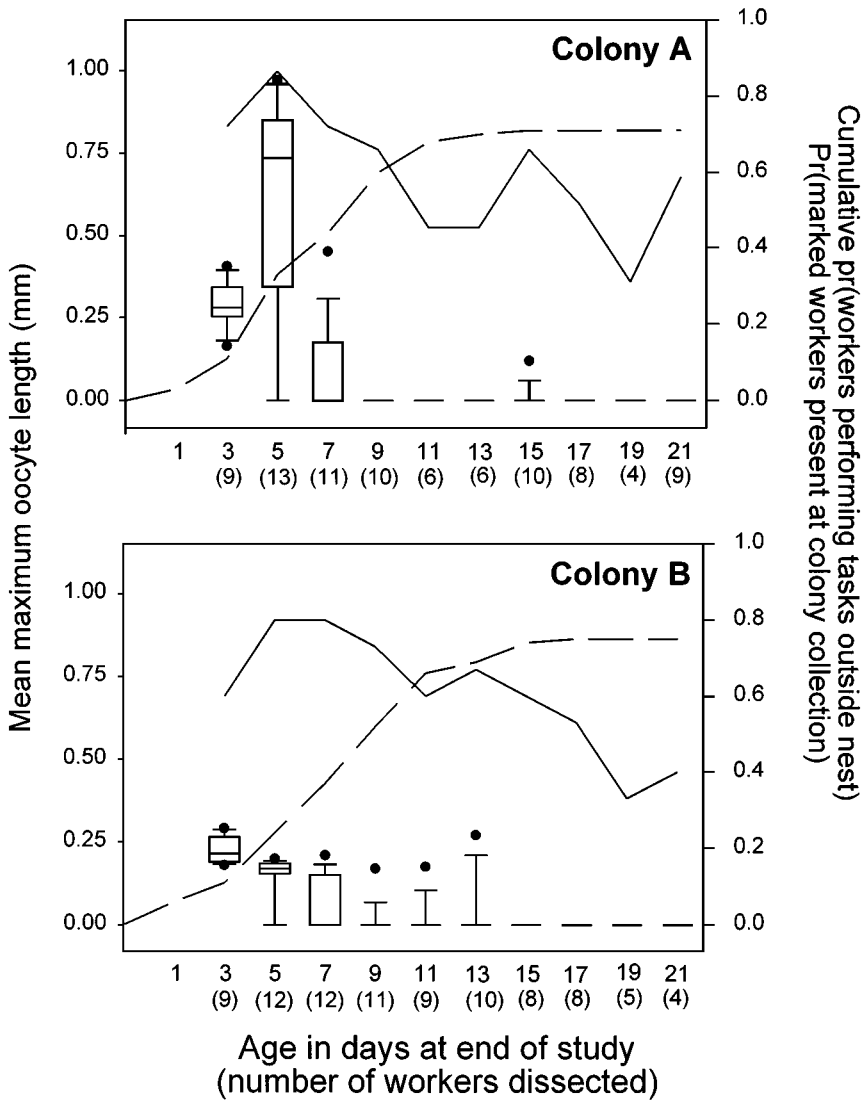
### Colony Characteristics

The observation colonies and the worker-source brood combs were in the growth phase of development, producing workers but not males. The observation colonies' brood combs contained eggs, larvae of different sizes, and pupae, and few empty cells were present. The observation colonies were of intermediate size for the La Pacífica population (colony A—592 unmarked adults, five layers of nest comb; colony B—276 unmarked adults, three layers of nest comb). I collected behavioral and/or ovary data on 134 workers in colony A and 131 workers in colony B. I dissected and measured ovary development on the marked workers that were present when their colonies were collected (colony A, 86 workers; colony B, 87 workers). Dissected workers ranged from 3 to 21 days of age in both colonies. Worker survival decreased slightly in the older cohorts, but 33 to 87% of marked workers in each cohort were present when the colonies were collected (Fig. 1).

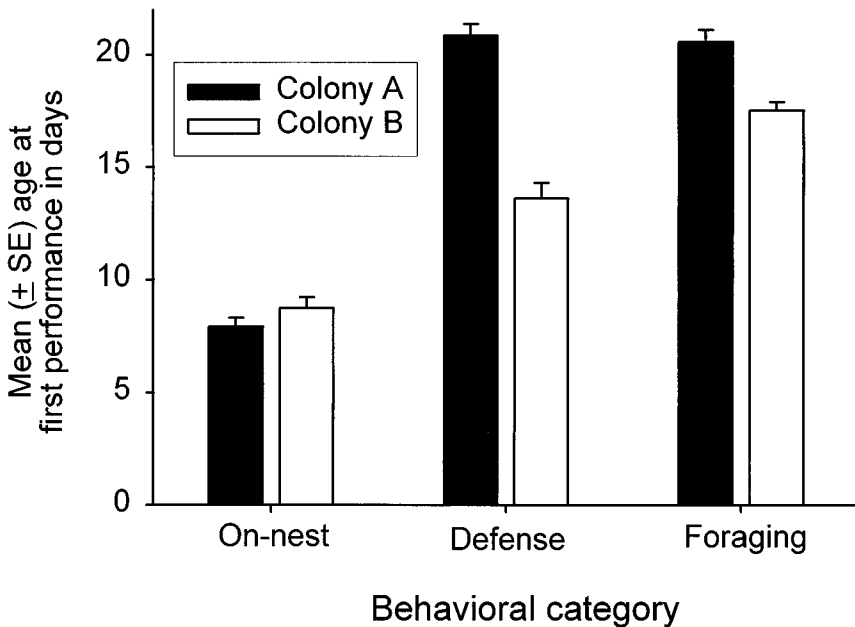
### Ovary Development, Age, and Behavior

The colonies differed in distributions of ovary development (Fig. 1) (multiple linear Regression,  $F = 17.41$ ,  $P < 0.001$ ), and the interaction effects of colony and age on ovary development were marginally significant ( $F = 3.95$ ,  $P < 0.05$ ). Therefore, I analyzed the relationships of workers' age and behavior with ovary development separately for each colony.

Most workers had filamentous ovaries in both colonies (dissected workers with filamentous ovaries: colony A, 70%; colony B, 69%). Among workers with ovary development, the largest oocytes were typically much smaller than mature eggs (Fig. 1). Mature eggs collected from a *P. occidentalis* nest averaged  $1.16 \pm 0.10$  mm (SD) ( $n = 7$ ) in length. Several 5-day-old workers in colony B had single oocytes that were approximately 1 mm long, 85% as long as the average mature oocyte. Workers' ovary development was strongly related to age. Younger workers had partially developed ovaries, and ovary



**Fig. 1.** Distribution of ovary development (box plot), cumulative proportion of workers performing acts on the nest surface (dashed-line plot), and proportion of marked workers present upon colony collection (solid-line plot) versus age for two *Polybia occidentalis* colonies. The upper limit of the left X axes (1.16 mm) indicates the mean length of mature eggs laid in *P. occidentalis* nests. Box plots indicate medians (central line), interquartiles (box limits), 10th and 90th percentiles (whisker limits), and all more extreme values (points outside whiskers).



**Fig. 2.** Mean ( $\pm$ SE) age at first performance of on-nest, defense, and foraging tasks for *Polybia occidentalis* workers from two colonies.

development declined exponentially with age (Fig. 1) (multiple linear regression: colony A—age effect  $F = 28.5$ ,  $P < 0.0001$ , age<sup>2</sup> effect  $F = 16.1$ ,  $P < 0.0001$ ; colony B—age effect  $F = 50.0$ ,  $P < 0.0001$ , age<sup>2</sup> effect  $F = 28.0$ ,  $P < 0.0001$ ).

Marked workers exhibited temporal polyethism, moving from in-nest to on-nest and, later, to defense and foraging tasks as they aged. First ages at performance differed among on-nest tasks, defense, and foraging (Fig. 2) (survival analysis Wilcoxon test: colony A— $\chi^2 = 150.65$ ,  $df = 2$ ,  $P < 0.0001$ ; colony B— $\chi^2 = 97.26$ ,  $df = 2$ ,  $P < 0.0001$ ). Workers varied in their rates of behavioral development. For example, some workers in each colony began working on the nest surface at 1 day of age, while some of their nestmates were first observed on the nest at 13 to 15 days of age (Fig. 1). However, after accounting for age effects, behavioral variation showed no significant associations with ovary development. The number of days elapsed since workers were first observed working on the nest surface was not related to ovary development (multiple linear regression: colony A— $F = 0.1$ ,  $P > 0.70$ ; colony B— $F = 1.25$ ,  $P > 0.25$ ). Workers that had performed foraging or defense tasks did not differ in ovary development from those that had not (multiple linear regression: foraging—colony A  $F = 0.33$ ,  $P > 0.50$ , and colony

B  $F = 0.01$ ,  $P > 0.90$ ; defense—colony A  $F = 0.05$ ,  $P > 0.75$ , and colony B  $F = 0.25$ ,  $P > 0.50$ ).

Nearly all workers with ovary development were in the three youngest age cohorts, from 3 to 7 days old (colony A, 24 of 25 workers with developed ovaries were  $\leq 7$  days old; colony B, 24 of 28 workers with developed ovaries were  $\leq 7$  days old). Only the 7-day-old cohorts included many workers both with and without ovary development. Seven-day-old workers with and without developed ovaries did not differ significantly in their probabilities of having initiated on-nest behavior (pooled across colonies; Fisher's exact test  $P > 0.05$ ). All workers with ovary development that were older than 7 days had worked on the nest surface except one 13-day-old worker in colony B.

## DISCUSSION

*Polybia occidentalis* workers exhibited partial ovary development within several days of adult emergence, but their ovaries declined quickly with age. Despite differences in maximum ovary development and ages at first performance of tasks between the colonies, the relationships of age and behavior with ovary development were consistent. Workers that were 17 days of age or older never exhibited ovary development, and few workers older than 7 days of age had developed ovaries. As observed in previous studies, workers progressed from in-nest to on-nest behavior as they aged, before they began foraging (Jeanne *et al.*, 1988; O'Donnell and Jeanne, 1992a). The timing of decreases in ovary development corresponded with the ages at which most workers moved began performing acts on the nest surface. However, individual variation in the age of making this transition did not correspond with ovary development.

Other key events in *P. occidentalis* workers' behavioral development were not related to changes in ovary development. Mean ages at onset of foraging (18 to 21 days) and defense (14 to 21 days) were similar to the ages of first performance noted in previous studies on this population (O'Donnell and Jeanne, 1992a, 1993; Jeanne *et al.*, 1992). These behavioral transitions occurred well after the age at complete ovary regression for most individuals, and performance of foraging and defense tasks was not associated with variation in ovary development in this study.

The dynamics of ovary development and physiological effects on social wasp behavior are best studied in groups of potential queens that found new nests (Röseler, 1991). Few studies have investigated temporal patterns of ovary development in workers, and to my knowledge, this is the first that has used marked, known-age workers in swarm-founding wasps. However, several indirect lines of evidence suggest that temporary ovary development is common for young swarm-founding wasp workers. Richards and Richards

(1951; see also Richards, 1978) documented partial ovary development in a subset of the females in colonies of several epiponine species, but they did not obtain data on the relative ages of these females. Naumann (1970) noted that nest workers had better-developed ovaries than foragers in two colonies of *Protopolybia pumila*, but worker ages were not determined. Hastings *et al.* (1998) used cuticular darkening to estimate relative worker ages in the swarm-founding wasp *Brachygastra mellifica*. They found that *B. mellifica* workers with developed ovaries were younger than those with no ovary development. West-Eberhard (1978) reported temporary ovary development for young workers in five species of epiponine wasps from four genera, including two species of *Polybia*, but she did not present data on the degree of variation in ovary size or on the precise timing of changes in ovary development.

Several mechanisms have been proposed for ovary regression in female eusocial wasps. Failure to oviposit is thought to promote ovary regression in female Hymenoptera (Röseler, 1991). Lack of empty brood cells in the nest, and egg cell guarding by queens, may reduce epiponine workers' opportunities to lay eggs (Forsyth, 1978; West-Eberhard, 1981). Nutritional factors have also been proposed to promote ovary regression, such as decreased food intake and increased caloric expense for foragers (Hunt, 1994). In a previous study I found that *P. occidentalis* workers' lipid stores declined with time after they initiated on-nest behavior (O'Donnell and Jeanne, 1995a). These changes in lipid stores, and the ovary regression documented here, preceded the performance of foraging tasks and therefore were not caused by elevated energy expenditure during flight.

Workers of some eusocial wasps and bees can distinguish nestmates with developed ovaries, presumably via chemical cues or signals (West-Eberhard, 1977, 1978; Downing and Jeanne, 1985; Visscher and Dukas, 1995). Workers with developed ovaries are often targets of social aggression, as would be expected if workers are policing each others' reproduction (Ratnieks, 1988). In other studies, I found that *P. occidentalis* workers on the exterior nest surface frequently engaged in dominance interactions (O'Donnell and Jeanne, 1995b), but neither highly aggressive nor subordinate workers exhibited ovary development (O'Donnell, 2000). However, young workers may experience social aggression inside the nest, where they are difficult to observe.

The implications of rapid ovary regression for *P. occidentalis* females' reproductive options are not known. The subject colonies in this study were in the growth phase of development, when worker populations are increasing. The colony's stage of development may influence the reproductive options of newly emerging female wasps. West-Eberhard (1977, 1978) noted that *Metapolybia* wasp females emerging when reproductive opportunities were greatest, following the death of the single remaining queen, engaged in social

aggression. Some of these young females succeeded in reproductive competition by becoming queens. Partial ovary development in young wasps could represent a brief window of opportunity for females to enter the queen caste, if the appropriate social conditions are present when they emerge [(West-Eberhard, 1977); but see O'Donnell (1998b) for a review of evidence for larval caste determination in eusocial wasps].

Social organizations of advanced eusocial species of bees and wasps share several convergently evolved features, including strong temporal polyethism, task partitioning, and task specialization. The data presented here suggest that physiological effects on division of labor have also converged in different swarm-founding lineages. The division of labor among *Polybia occidentalis* workers that I measured was apparently not affected by variation in reproductive physiology. In previous field experiments I showed that application of the juvenile hormone (JH) analogue methoprene to *P. occidentalis* workers caused accelerated temporal polyethism in a dose-dependent manner (O'Donnell and Jeanne, 1993). These results suggest that, as in honey bees [*Apis mellifera* (Robinson, 1987)], variation in JH titers regulate *P. occidentalis* workers' rate of behavioral development. In adult honey bee workers, unlike most female insects, JH does not influence ovary development (Robinson *et al.*, 1992). Furthermore, ovary development does not usually play a role in division of labor among honey bee workers (Visscher, 1996; Oldroyd *et al.*, 1999). Worker polyethism can occur independently of reproductive physiology in advanced eusocial species, including species where workers possess functioning ovaries.

## APPENDIX

### Ethogram of Behavioral Acts Recorded During Scan Samples of Worker Behavior on the Nest Surface of *Polybia occidentalis* Colonies

**In-nest acts:** Recorded when workers were visible moving past the nest entrance opening or when the task required the worker's body to protrude partially out of the entrance.

Walk on comb

Bail water—Wasp regurgitates drop of water from crop, which falls to the ground

Carry trash—Wasp walks with debris in mandibles

Drop trash—Wasp expels solid debris from the mandibles, which falls to the ground

Fly with trash—Wasp flies from nest entrance carrying debris and returns within 5 min to nest entrance

Inspect cell—Wasp places head into brood cell

**On-nest acts:** Recorded when workers were visible on the exterior surface of the nest envelope, with the entire body outside the entrance. Foraging and defense acts on the nest surface are not included.

Build—Wasp adds wood pulp to nest with mandibles

Inspect nest—Wasp antennates nest surface

Chew nest—Wasp mandibulates nest surface

Chew pulp, carry pulp—Wasp handles wood pulp used in nest construction

Share pulp—Wasp exchanges wood pulp with nonforager

Chew prey

Enter, exit—Wasp walks into or out of nest entrance

Fan—Wasp flaps wings while standing in place; thermoregulatory (L. Phelps and R. L. Jeanne, unpublished data)

Bite nestmate, bitten by nestmate

Groom self—Wasp rubs own body with legs

Inactive

Solicit—Wasp approaches nonforager head-on, with head and antennae raised

Suck water, drop water—Wasp presses mandibles to nest surface without chewing movements, followed by wasp regurgitating water drop to ground

Take materials from arriving foragers

Trophallaxis—Wasp exchanges liquid with nonforager via mouth-to-mouth contact Walk

**Foraging acts:** Tasks performed at the nest exclusively by foragers.

Arrive from flight (with prey, pulp, water, or nectar, or making no transfers with nestmates)

Give prey, pulp, water, or nectar to on-nest worker

Leave—Wasp flies from nest

**Defense acts:** Performed on nest surface in response to disturbance; includes responses to vertebrates and insects (typically parasitoids).

Alert—Wasp rears up from nest surface, raising front pair of legs, and orients head toward moving objects

Buzz run—Wasp runs rapidly across nest while flapping wings in brief bursts of less than 1 s; performed in response to parasitoids and other small insects near the nest

Exit alarm, alarm run—Wasp runs rapidly out of nest or to a new position on the nest surface, with wings partially raised and assuming alert posture after running

Flying attack—Wasp flies off nest toward moving object, then returns to nest surface and assumes alert posture

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