

Age Polyethism and Defense in a Tropical Social Wasp (Hymenoptera: Vespidae)

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*Although tapping the nest in simulated vertebrate attack caused all but 1-day-old workers of *Polybia occidentalis* to rush from inside and cover the envelope, defense itself—attack of a target—was shown to be carried out only by workers older than about 10 days. While foraging was also performed by older workers, the frequency–age distribution of defensive behavior was skewed to a significantly younger age than was that of foraging. The plot of mean individual probability of defending as a function of age was logistic, leveling off at 0.11 by the age of about 13 days. The distribution of the probability of defending among workers ≥ 13 days of age was random, indicating that there is no specialized defender class among older workers. Workers that defended were recruited from among both nest workers and foragers. Although foragers were more likely to defend than were nonforagers, nonforagers contributed more individuals to the pool of defenders because they were more numerous.*

KEY WORDS: defensive behavior; polyethism; social wasps; *Polybia occidentalis*.

INTRODUCTION

Age polyethism, or temporal division of labor within the worker caste, is widespread among social Hymenoptera (Wilson, 1971). The age-related specializations of workers are well developed in honey bees, stingless bees, and bumble

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bees (Michener, 1974; Sommeijer, 1984; Winston, 1987). A similar ontogenetic specialization among workers occurs in the eusocial wasps, especially in species characterized by a large colony size (Potter, 1964; Akre *et al.*, 1976; Simões, 1977; Jeanne *et al.*, 1988; Jeanne, 1991).

Despite its importance for colony success, the defensive response to vertebrate attack is typically missing from studies of temporal division of labor because defense of the colony is normally too rare an occurrence to provide meaningful data on polyethism. Thus we know more about the behavioral physiology of defense—releasers, chemical communication of alarm, relation to colony size, the stinging response, biochemistry of venom—than we do about which colony members perform it.

In a recent study that dealt directly with the ontogeny of defense in *Apis mellifera* L., Breed and his colleagues (1990) concluded that defense and foraging are performed by different subgroups of workers. In other words, there appear to be specialized defenders. Our understanding of age polyethism of defense in the social wasps is limited to indirect evidence that it is older workers that are most likely to respond to vertebrate predators with a stinging attack (Potter, 1964; Akre *et al.*, 1976; Edwards, 1980), but it is not known whether defense is carried out by specialists.

We undertook this study to determine how defense against vertebrates fits into the age polyethism system of the swarm-founding epiponine wasp, *Polybia occidentalis* (Olivier). We followed an experimental approach using known-age workers to obtain answers to the following questions: What is the shape of the defense-response curve as a function of age? and Are defenders drawn from the worker population at large, or do they constitute a separate group of specialists?

MATERIALS AND METHODS

Study Site

The study was conducted during June and July 1990 at Centro Ecológico "La Pacifica," near Cañas, Guanacaste, Costa Rica (10° 25' N, 85° 7' W), the site of several previous studies on *P. occidentalis* (Forsyth, 1978; Jeanne, 1986; Jeanne *et al.*, 1988; Raveret-Richter 1988). The native vegetation of the region is tropical dry forest, but this has been widely replaced at our site by pasture and cropland.

The Wasp

Polybia occidentalis is a Neotropical wasp common in disturbed habitats in Central and South America (Richards, 1978). A swarm-founding species, it typically suspends its multitiered enclosed nests from thin twigs 0.3–10 m above

the ground. In Guanacaste mature colony populations range from a few hundred to 1000–2000 adults in nests 10 to 30 cm long (Forsyth, 1978; R. Jeanne, personal observation). Since colonies initiate brood rearing with the onset of the rains in late May (Jeanne *et al.*, 1988), our observation nests contained immatures of all stages.

Two moderate-sized colonies (Nos. 39 and 40) were used in this study. To facilitate observation and experimental manipulation, both nests were moved from their original locations after dark and attached to the trunks of separate trees at heights of approximately 0.75 m. Both new sites were shaded during the warmer parts of the day.

Colony 40 abandoned its nest on July 5, following a period of decline in brood rearing. This is a common event in the colony cycle of *P. occidentalis* at this time of year in this region (Jeanne *et al.*, 1988) and was not the result of our manipulations. The swarm was located a day later at a site 40 m distant, where it was constructing a new nest. By July 12 the nest was large enough to house the swarm, so we relocated it and resumed observations for another 4 days, after which the study ended. Because of the resulting 9-day gap in observations, data from colony 40 were not available for some analyses.

Marking of Adult Wasps

Two sets of wasps from each colony were marked on the scutum for individual recognition. Decocolor paint pens were used to apply to each wasp a five-color/four-position code corresponding to a number. The first set of wasps consisted of adults of known age. One-day-old adults emerging from brood-containing combs collected from other colonies and incubated at ambient temperature were lightly etherized, marked, and introduced into each of the observation nests after dark. Following a brief period of allogrooming by the resident workers, these adults appeared to integrate into the colony in every way. A cohort of 20 such one-day-old workers was placed into each nest every other day until 120 adults had been introduced. The same procedure was carried out for the second colony on alternate days.

The second set of wasps consisted of resident adults marked while they were engaged in nest work, foraging, or defense. Each wasp was carefully removed from the nest with forceps, held lightly while the color code was applied to its thorax, then released. An attempt was made to mark all workers engaged in nest work and foraging during a period of 5 days prior to the beginning of observations. Additional workers were marked throughout the study as they took up nest work or foraging or as they were captured in the act of defense (see below). This second group of marked workers comprised 172 and 164 wasps from colonies 39 and 40, respectively.

Terminology

Nest workers are defined herein as individuals that engaged in nest construction, nest maintenance (ventilation fanning, water bailing), and/or received foraged loads. Not included are grooming, allogrooming (grooming of a nest-mate), walking, or inactivity. Foragers are workers that returned to the nest with water, wood pulp, nectar, or prey. Nonforagers are workers that were never observed to forage. We define defenders as wasps that flew at the target in response to the stimulus we provided (described below).

Experimental Apparatus

The target consisted of a 12-cm-diameter hollow plastic ball covered loosely with black cloth. This was fixed to the top of a flexible 1-m stick pushed into the ground 1 m in front of the nest. Centered over the target was a cone of white nylon mosquito netting, 2 m long and tapering from 120 cm diameter at the ground to 11 cm at the top. This net was held open by a sand-filled hula hoop at the bottom and a smaller metal ring at the middle. The upper end of the net led into a clear plastic funnel attached to an inverted clear plastic collection bottle. The net/funnel/bottle apparatus was fixed vertically to a rigid supporting arm attached to the tree so that when the net hung loosely its lower end just reached the ground. The net was set by raising the smaller hoop and suspending it from three lines held by a pin through the supporting arm. This raised the bottom of the net to approximately 0.5 m over the top of the target. The net could be released and dropped over the target by pulling on a line attached to the pin.

Data Collection

Each colony was scanned at 5-min intervals for one hour daily. At each scan the activity of each marked worker was recorded. Return of foragers and reception of foraged materials were noted as they occurred.

Prior to issuing the alarm stimulus, we recorded the presence of all marked workers on the nest. Working from behind the tree and out of sight of the wasps on the nest, the experimenter set the target swinging on its stick by means of a line attached to it. The colony was then incited to attack the target by sharp taps with a stick on the twig bearing the nest. At the moment the first large group of attacking wasps reached the target, the net was dropped, capturing them. Immediately thereafter the identities of all marked wasps on the nest were again recorded. Wasps that had flown at the target but were not captured in the net were noted as they returned to the nest. Captured wasps were coaxed to the upper end of the net and into the bottle, where they were lightly etherized for identification. Previously marked individuals were recorded and released; unmarked individuals were marked and released.

We used the following protocol on a 2-day cycle.

Morning. Hour 1 (colony 39)—mark all unmarked nest workers and foragers; hour 2 (colony 40)—scan sample behavior of all marked workers on the outside of the nest at 5-min intervals, plus all occurrences of returning foragers along with the type of load carried and the identity of the receiving individuals; hour 3 (colony 40)—elicit defensive response, followed by a recovery period of 15–20 min.

Afternoon. Same sequence, with the order of the colonies reversed; plus hour 4 (colony 40)—mark unmarked nest workers and foragers and note the return of marked foragers.

On alternate days the sequence of the two colonies was switched, that is, the morning protocol began with colony 40.

This schedule was continued for 21 days (June 27 through July 17). The oldest known-age cohort attained age 28 days on July 17, while the youngest cohort reached 18 days. On July 17 both colonies were collected and all adult wasps were preserved in Kahle's fixative.

Data Analysis

Age Distribution of Defensive Behavior. To compare the age–frequency distribution of defense with nest work and foraging, we plotted the total numbers of each task performed by all workers as a function of age, using 1-day age intervals. In order to compare more closely the distributions of defensive and foraging behavior, we used the technique of Jeanne *et al.* (1988): we estimated for each forager the age in days at which it made the transition from nest work to foraging. For individuals making the transition abruptly, such that foraging did not overlap with nest work, the age of the first foraging trip was taken as the transition age. For individuals in which the two roles overlapped by several days, we defined the point of transition as the age midway between the start of foraging and the end of nest work. We then plotted the task distributions so as to center each individual's transition age on the same point on the x axis. Thus the independent variable becomes age relative to the age of switching from nest work to foraging. We used the Kolmogorov–Smirnov test or a form of chi-square to compare frequency distributions.

Probability of Exiting from the Nest as a Function of Age. The mean probability of exiting from the nest in response to the tapping stimulus was computed for each age as the ratio of the number exiting to the number inside immediately prior to the stimulus. The number inside the nest was obtained by subtracting the number on the envelope immediately prior to the stimulus from the number known to be alive. The number exiting comprised the wasps present on the envelope following the tapping, plus the wasps attacking the target, minus those on the envelope prior to the stimulus. There are two sources of potential

error. (1) Because of the large numbers of wasps on the envelope following the stimulus it is possible that some marked individuals were overlooked, and (2) foragers that were away from the nest during the test would have been counted as inside and not exiting. Both errors would reduce the computed probabilities below their true values.

Probability of Defending as a Function of Age. For known-age workers we computed the group mean probability, P , of attacking the target for each age. We defined P as the ratio of the number of defending wasps of age x to the total number of wasps of age x present on or in the nest when the stimulus was issued. Because younger cohorts did not achieve the ages reached by older cohorts at the termination of the study, older ages would be represented in our analyses by the older cohorts only. Unless all cohorts behaved alike, this bias could affect the results. To preclude this possibility, data were analyzed only through age 18 days, the maximum age at which all six cohorts were represented in our samples.

RESULTS

During daylight hours there were always several workers on the outer envelope of our observations nests. These were concentrated nearest the entrance and included foragers, nest maintenance workers, and receivers of foraged loads. We saw no evidence of "guards" of the sort found in honey bees, that is, workers stationed at the entrance that contact individuals entering the nest (Butler and Free, 1952). The nest entrance, a circular hole in the envelope 1–1.5 cm in diameter, was typically unencumbered with stationary workers. Most returning foragers, as well as ants that made their way onto the nest, were contacted by the workers scattered over the outer surface of the envelope.

Tapping the twig bearing the nest always elicited alarm recruitment, causing large numbers of wasps to run out of the entrance and fan across the outer surface of the nest (for details see Jeanne, 1981). Wasps flying from the nest to attack the target came from among these alarmed workers.

Age Distribution of Defensive Behavior

Results for colony 39 show that although the age range for defense and foraging overlapped broadly (Fig. 1), the frequency distributions of the two roles differed significantly ($P < 0.05$). The age distribution of the defensive response was skewed toward younger individuals. This is seen more clearly when individual differences in age of transition from nest work to foraging are factored out by plotting frequencies relative to the age of switching to foraging for each individual (Fig. 2). On this relative age scale the age distribution of the defensive response differs even more strongly from foraging ($P < 0.001$)

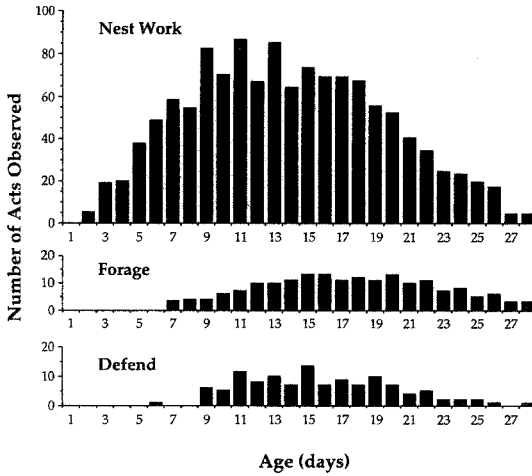


Fig. 1. Frequency of task performance as a function of worker age, colony 39. Number of nest work tasks, foraging trips, and defensive responses observed in daily 1-h scans. Sample sizes: nest work, 82; foraging, 27; defense, 49 workers.

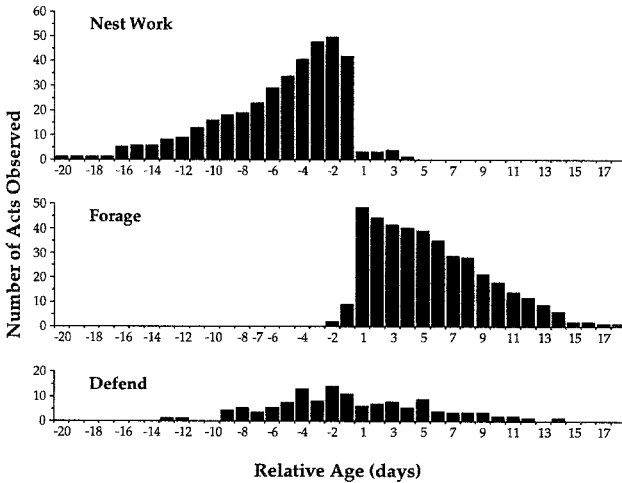


Fig. 2. Frequency of task performance as a function of relative age, colony 39. Age is relative to each individual's transition from nest work to foraging. Includes known- and non-known-age marked individuals. Sample sizes: nest work, 101; foraging, 112; defense, 113 workers.

and nest work ($P < 0.001$). The temporal displacement of defense with respect to foraging was also apparent in the mean age to first observed act, which was significantly lower ($P = 0.027$) for defense (13.6 ± 4.2 days) than for foraging (15.5 ± 5.1 days). (Data were too few to compute means for colony 40.) Of the 20 known-age individuals in colony 39 that both defended and foraged, 17 (85%) defended at least 1 day before they foraged. In colony 40, five of seven (71%) were in this category.

Probability of Exiting from the Nest as a Function of Age

The likelihood of exiting from the nest in response to tapping was zero for 1-day-old workers but increased with age for workers older than 1 day (Fig. 3).

Probability of Defending as a Function of Age

The probability of exhibiting a defensive response was zero through a worker's first few days of adult life, increased sharply from age 8 to age 12 days, then leveled off (Fig. 4). Our data did not differ significantly from a logistic model (Fig. 4) that adjusted the asymptote ($P \approx 0.7$). The mean maximum probability that a worker responded defensively (value of the asymptote) was estimated to be 0.11. The age at which 90% of this value was achieved was approximately 11 days.

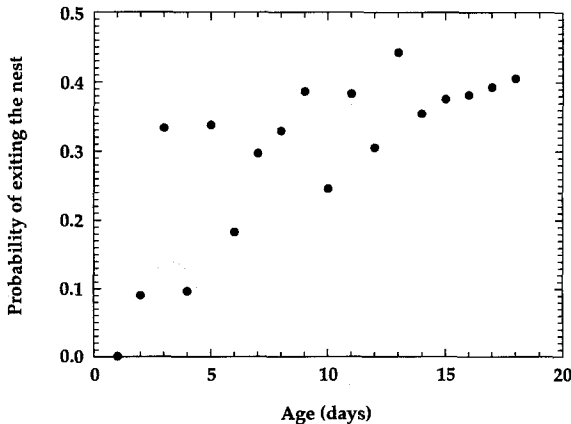


Fig. 3. Probability of exiting from the nest in response to the tapping stimulus as a function of age, colony 39; $n = 108$ workers. Data are lumped for all cohorts of known-age workers. Each age along the x axis thus includes data from six dates, one for each of the six cohorts.

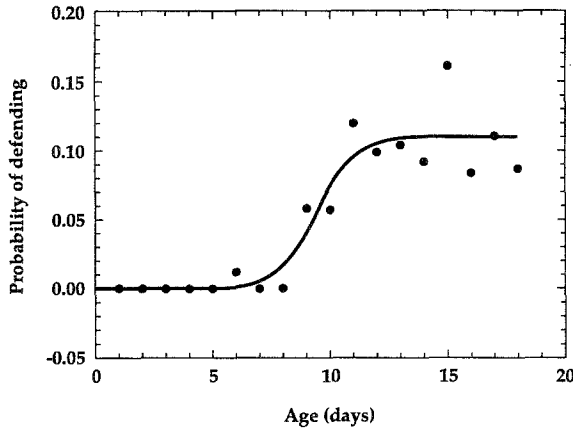


Fig. 4. Probability of defending as a function of age, colony 39; $n = 101$ workers. Probability is computed as the number of workers of a given age attacking the target divided by the number of that age that were on the nest at the time of elicitation of attack. Data are lumped for all cohorts of known-age workers. Each age along the x axis thus includes data from six dates, one for each of the six cohorts. Sample sizes for individual cohorts were too small to detect substantial deviations in shape from one another. The curve is truncated at age 18 days, the maximum age attained by the youngest cohort. The fitted curve is given by the logistic equation $p = 0.110 \times \{\exp(-11.36 + 1.21 \times \text{age}) / [1 + \exp(-11.36 + 1.21 \times \text{age})]\}$.

Are There Specialized Defenders Among the Older Workers?

The result that the probability of defending is essentially flat beyond age 13 days (Fig. 4) makes it possible to control for age while testing whether defenders constitute a subset of individuals among the population of older workers at large. That is, we can ask if there is any evidence for specialization among individuals after they reach the age past which group probability of defending does not change.

To test for this we used the subset of known-age workers that were on the nest and therefore available to defend during a minimum of four of the daily experimental assays of defensive behavior subsequent to reaching age 13 days. (The subset included 24 workers that were not observed to perform tasks but were present in the nest at the end of the study; we assumed that because they did not forage, they were inside the nest during the experimental assays.) A test for Poisson distribution of the days defending, adjusting for days under observation, showed only mild evidence of a nonrandom pattern ($P = 0.079$). Therefore the data are consistent with defense at random, suggesting that there is no specialized defender class among workers ≥ 13 days of age.

Do Defenders Perform Other Tasks?

Marked workers (of known and unknown age) on the envelope at the time the stimulus was issued were significantly more likely to defend than were marked workers emerging from inside the nest in response to the stimulus (Table I). Nevertheless, because of the greater numbers of wasps in the latter category, the bulk of the defending force consisted of workers that had been inside the nest before the nest was tapped.

A breakdown of marked workers into major behavioral categories (foraging, nest work, and neither) based on lifetime repertoires reveals that defenders were drawn from among workers that performed nest work and foraging as well as those that performed no work outside the nest (Table II). The tabulation suggests, however, that defense cooccurs in the same individual more often with foraging than with the other two behavioral categories.

To assess the interaction between defense and foraging more closely, we examined the subsample of known-age workers in colony 39 that performed one or more foraging or defensive act(s) or survived at least to age 20 days (mean age of onset of foraging plus 1 standard deviation). The latter criterion was established to include individuals that neither foraged nor defended, despite having lived well past the mean age of first performance of these tasks. The relationship between foraging and defense for these workers is summarized in Table III. The null hypothesis that foraging and defense are independent was rejected; there was a positive association between the two tasks ($P < 0.01$). This means that within the subset of workers used in this test, if an individual foraged there was an enhanced probability that it also defended.

This pattern is borne out when we examine the relative contributions to the average defensive response of foragers and nonforagers (Table IV). Although nonforagers significantly outnumbered foragers in responding defensively, foragers as a group were two to three times more likely to defend. Similarly, the probability of defending as a function of age was consistently and significantly higher for foragers than for nonforagers (Fig. 5; $P < 0.05$).

Despite the 20 known-age individuals that both defended and foraged (Table III), the fact that 29 other defenders did not forage leaves open the possibility that most defenders specialize in that task to the exclusion of foraging. If this were so, such specialists might be expected to differ quantitatively from defender-foragers in their performance of defense and other tasks. We found this not to be the case. There was no difference between known-age defenders that did and did not forage with respect to (1) the probability of defending, i.e., the ratio of number of days defended to number of days on nest at time of test, beginning with the first defensive act performed by each individual ($P = 0.058$), (2) the age-frequency distribution of defensive acts ($P = 0.90$), (3) the distribution of age at the first defensive act ($P = 0.48$), (4) the probability of performing nest

Table I. Relative Contribution to the Defense Response of Marked Workers Present on the Envelope and Inside the Nest (Known-Age and Non-Known-Age Workers Included)

	On envelope			In nest			P value ^a
	Number defending	Number available	Proportion defending	Number defending	Number available	Proportion defending	
Colony 39 (N = 20) ^b							
Mean	4.50	14.55	0.31	12.90	59.15	0.22	<0.001
SD	±2.48	±6.27		±6.44	±16.66		
Colony 40 (N = 10) ^b							
Mean	2.60	10.90	0.24	5.60	45.10	0.12	<0.002
SD	±10.90	±4.46		±2.69	±11.48		

^a Chi-square test.

^b N = number of test days.

Table II. Numbers of Known-Age Workers in Colony 39 Performing Other Tasks According to Whether They Defended or Not, over Their Entire Observed Lives

Other behavior	Defended		Total
	Yes	No	
Foraging only	0	3	3
Nest work only	15	31	46
Foraging + nest work	20	4	24
Seen only ^a	14	18	32
Not seen ^b	—	15	15
Total	49	71	120

^aIncludes workers that appeared on the nest envelope during at least one scan but did not forage or perform nest work.

^bIncludes workers that were never recorded on the nest envelope. Only two of these were still in the nest at the end of the study.

Table III. Two-Way Table of Foraging and Defense for Known-Age Workers, Colony 39^a

Forager	Defender		Total
	Yes	No	
Yes	20 (14.9)	7 (12.1)	27
No	29 (34.1)	33 (27.9)	62
Total	49	40	89

^aValues are observed (expected) numbers of individuals, based on life-long repertoires.

work before their first defensive act (ratio of number of days seen doing nest work to total number of days since first observation of nest work through first defensive act) ($P = 0.57$) or (5) the probability of performing nest work subsequent to their first defensive act (ratio of number of days seen doing nest work to total number of days on nest subsequent to first defensive act) ($P = 0.12$).

Colony Populations and Composition

Colony 39 contained 636 adult females when it was collected in the evening of July 17. Of these, 68 (11%) foraged and 126 (20%) defended during the preceding 21 days. Colony 40 contained 892 adult females when collected on the same evening. Because of the 9-day gap in observations on this colony, data on numbers of foragers and defenders were incomplete. Neither colony con-

Table IV. Relative Contributions of Foragers and Nonforagers to the Defensive Response (Known- and Non-Known-Age Workers Included)

	Foragers ^f			Nonforagers			P value ^b
	Number defending	Number available ^a	Proportion defending	Number defending	Number available	Proportion defending	
Colony 39 (N = 20) ^c							
Mean	6.30	16.25	0.39	10.50	56.30	0.19	<0.001
SD	±3.77	±6.38		±5.15	±16.38		
Colony 40 (N = 20) ^c							
Mean	2.30	6.70	0.34	5.90	48.50	0.12	<0.001
SD	±1.19	±2.57		±3.18	±14.06		

^aNumber of foragers available based on only those foragers present at the time the alarm stimulus was issued.

^bChi-square test.

^cN = number of test days.

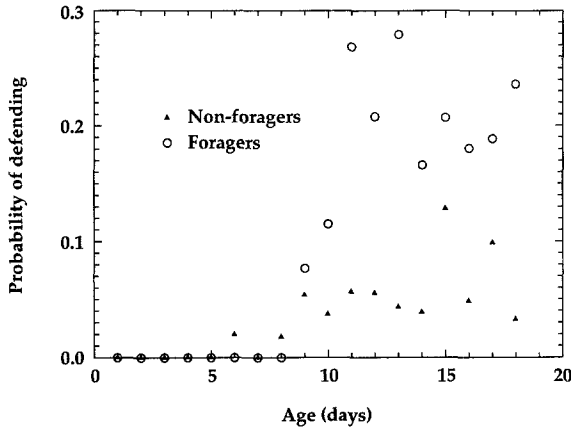


Fig. 5. Probability of defending as a function of age for foragers and nonforagers, colony 39; $n = 26$ foragers and 75 nonforagers. All cohorts lumped. Probabilities computed as for Fig. 4. Foragers differ significantly from nonforagers ($P < 0.05$).

tained males. Both contained known-age individuals that neither foraged nor defended.

DISCUSSION

There is age polyethism with respect to defense in *Polybia occidentalis*. Defense against vertebrates is clearly a task that is performed by older workers. The mean probability that a worker will respond defensively does not increase linearly with age but rises sigmoidally, becoming essentially constant by the third week of adult life. It is possible that the probability of defending changes from the asymptotic value of 0.11 among much older individuals than we were able to sample. However, recent work on honey bees has shown no discernible change in the probability of defending among very old individuals (Breed *et al.*, 1990).

The result that the mean probability of defending is 0.11 among older workers as a group could have two explanations at the individual level. At one extreme, all older individuals could have a probability of defending of 0.11, which would mean that there is no individual specialization for defense. Alternatively, there could be a subgroup of specialized defenders characterized by having significantly higher probabilities of defending than the remaining individuals. We take the position that demonstration of a specialized caste of defenders among older workers would require evidence of a bimodal distribution of the probability of defense within the class of older workers. Although our distribution of frequency of defense shows a slight tendency toward bimodality, it

does not differ significantly from random. While it is possible that more extensive data could bring a bimodal pattern into focus, the conservative conclusion is that a specialized subgroup of defenders among older workers does not exist in *Polybia occidentalis*. This conclusion is supported by our failure to find any differences between defenders and nondefenders with respect to the performance of other tasks. Defenders as a group performed all the other tasks performed by older individuals at large.

Unlike the honey bee, which has recently been shown to have a specialized "soldier" caste, apparently distinct from foragers (Breed *et al.*, 1990), in *P. occidentalis* there is a positive interaction between foraging and defense such that foragers have a significantly higher probability of defending than nonforagers. This suggests that the thresholds for performance of the two tasks are linked in some way. Since both are risky tasks, perhaps both thresholds decline in response to age-related decrease in risk aversion as a fitness-maximizing strategy among older workers whose chances of direct reproduction are approaching zero. However, thresholds for the two tasks appear to be only loosely linked because (1) increases in readiness to forage and defend did not reach threshold together and (2) a substantial number of older workers defended but did not forage.

The fact that even young individuals rush out from the nest in response to a mechanical stimulus, while only the older individuals among them actually attack the intruder, makes it clear that exiting and attack are distinct responses. This point was made by Jeanne (1981), who showed that attack behavior in this species is released only by an appropriate visual stimulus after the wasps are in an alarmed state. The participation of large numbers of nondefending individuals in the exiting response suggests that this behavior may function in part to present a visual aposematic signal to an intruding vertebrate.

The quantitative results of this study must be treated with caution. It is possible, for example, that our finding of a 2-day temporal separation between the onset of defense and that of foraging could be an artifact of our sampling method and that the onsets of the two tasks really occur simultaneously. This could come about if we undersampled foraging with respect to defense. We believe this not to have been the case. Foragers were given at least 2 h each day to show themselves (hours 1 and 2 of protocol, plus hour 4 on alternate days), while the defensive response was sampled once per day, so it seems unlikely that the average age of the onset of foraging was underestimated compared with defense. A similar result has been reported for honey bees, in which the first appearance of defensive behavior also ontogenetically preceded foraging by about 2 days (Breed *et al.*, 1990).

Similarly, social context could cause the observed temporal separation as well as the value of 0.11 for the asymptote of the probability of defending to vary. If demand for foraging were high while the colony had little to defend,

as might occur during founding, workers might first show a readiness to defend after they begin foraging and/or the asymptotic value for probability of defending might be much lower than 0.11. Further study will be required to quantify the effects of social context on these variables.

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