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Short communication

Hard working nurses rather than over-aged nurses permit *Ropalidia marginata* to respond to the loss of young individuals

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Summary. The primitively eusocial wasp *Ropalidia marginata* exhibits a remarkably well-developed honey bee like age polyethism. Individuals perform different tasks sequentially as they age, starting with intranidal tasks (nursing and building in that order) and ending with extranidal tasks (foraging for pulp and food in that order). As in the case of honey bees such age polyethism is rather flexible; in the absence of old individuals (in young-cohort colonies), precocious foragers forage at abnormally young ages. Here we demonstrate that the absence of young individuals (in old-cohort colonies) does not result in over-aged nurses nursing at abnormally old ages, as seen in the case of honey bees. Instead it results in hard working nurses who nurse at abnormally high rates. The possible reasons for the absence of over-aged nurses and the presence of hard working nurses are discussed.

Key words: Age polyethism, eusociality, social wasps, *Ropalidia marginata*, division of labor.

In spite of its primitively eusocial status, the social wasp, *Ropalidia marginata* shows a remarkably well-developed honey bee like age polyethism. Individuals begin their life with intranidal tasks, performing nursing (feeding larvae) and building the nest, in that order. Older individuals perform extranidal tasks, foraging for pulp and for food, in that order (Naug and Gadagkar, 1998a). Age polyethism is however considerably flexible; in cohorts of young individuals, precocious foragers perform the task of foraging at abnormally young ages and do so in larger numbers and at higher rates compared to foragers in normal colonies (Naug and Gadagkar, 1998b). Here we report the results of the converse situation involving cohorts of old individuals and demonstrate that such colonies respond with hard working nurses rather than with over-aged nurses, the latter being the case in honey bees (Huang and Robinson, 1996).

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Methods

Nine naturally occurring *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae) nests were used in this study. All eclosing wasps were marked with a unique color code on the day of eclosion. Experiments were initiated after all the unmarked individuals (present when the colony was located) had died or disappeared so that the ages of all individuals now present on the colonies were known.

Experiment 1: Four (normal) colonies were observed without any manipulation. In another four (old-cohort) colonies all individuals younger than 20 days of age were removed just before the commencement of the experiment. Twenty days is about the mean age at which individuals begin extranidal tasks (Naug and Gadagkar, 1998a).

Experiment 2: Another colony was observed first as a normal colony, then as an old-cohort colony (by removing individuals younger than 20 days old) and once again as a normal colony (after returning the individuals previously removed). Individuals removed from normal colony to create the old-cohort colony were held individually in cages and provided *ad libitum* food and water but were denied opportunities for initiating new nests.

Behavioral observations on each of the four normal colonies and four old-cohort colonies of the first experiment and during each of the three phases of the second experiment were made over 4–7 consecutive days. Observations consisted of recording every occurrence of larval feeding (other behaviors were also recorded but were not used in this study) by every individual in 22 five min blocks spread over 2.5 h, uniformly distributed between 08:00 h and 18:00 h (see Gadagkar, 2001, for methods of observation). We obtained 100 h of data for normal colonies and 80 h of data for old-cohort colonies for the first experiment and 20 h of data for each of the two normal colony phases and 30 h of data for the old-cohort phase of the second experiment. Since nursing, at least at a low rate, is performed by most individuals, here we designate as nurses, those individuals who nurse at a rate higher than the mean rate of nursing (0.75 acts/hr.) computed from all the colonies.

Results

Experiment 1: The age composition of the four old-cohort colonies we created is strikingly and significantly different from that seen in normal colonies. The mean age of individuals in the old-cohort colonies was not only significantly higher than the mean age of individuals in normal colonies but also higher than the mean age of the subset of 20–82 day

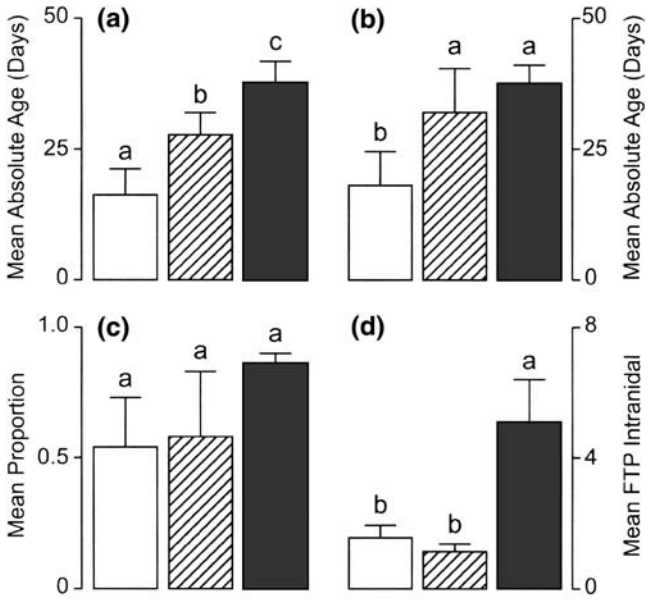

Figure 1. Mean (± SD) (a) absolute age of all individuals, (b) absolute age of nurses, (c) proportion of nurses, (d) FTP of nurses; in the entire normal colonies (open bars), the old cohort ages corresponding animals in normal colonies (diagonal hatches) and the old cohort colonies (filled bars). One-way ANOVA followed by multiple comparisons of means by Tukey-Kramer method was used to test the effect of age distribution on the above parameters. Proportions were compared using non-parametric ANOVA. Within each graph, bars with different alphabets are significantly different from each other ($p < 0.05$) while those with similar alphabets are not significantly different ($p > 0.05$)

old individuals present in normal colonies (Fig. 1 a). However, the age of nurses does not follow this pattern. While the mean age of nurses in the old-cohort colonies is significantly higher than the mean age of nurses in normal colonies, it is not significantly different from the mean age of nurses among the 20–82 day old individuals present in the normal colonies (Fig. 1 b). The proportion of individuals meeting our criterion for being labeled as nurses, in old-cohort colonies is not different from the corresponding proportion in normal colonies and also not different from the corresponding proportion among the 20–82 day old individuals present in normal colonies (Fig. 1 c). But the rate of nursing in the old-cohort colonies is substantially and significantly higher compared to the corresponding rates in the normal colonies and also compared to the 20–82 day old individuals present in normal colonies (Fig. 1 d).

Experiment 2: All 18 individuals observed increased their rate of nursing compared to their previous rate in the normal colony (Wilcoxon matched pairs signed ranks test, $T = 0$, $Z = 3.72$, $p < 0.01$), when confronted with the absence of young individuals, and reduced to a low rate of nursing when the colony demography was returned to the normal state ($T = 10$, $Z = 3.2$, $p < 0.01$).

Discussion

In honey bees, young-cohort colonies respond to the lack of old individuals by having precocious foragers who forage at abnormally young ages. Conversely old-cohort colonies respond to the loss of young individuals by having over-aged nurses who nurse at abnormally old ages (Huang and Robinson, 1996). *R. marginata*, that shows a honey bee like age polyethism in spite of being primitively eusocial, exhibits a similar phenomenon of precocious foragers in young-cohort colonies (Naug and Gadagkar, 1998a, b). It was therefore expected that old-cohort colonies of *R. marginata* would exhibit the phenomenon of over-aged nurses, an expectation that had hitherto remained untested.

Here we demonstrate that old-cohort colonies of *R. marginata* do not respond to the loss of young individuals by having over-aged nurses. Because normal colonies also have some nurses as old as the nurses in old-cohort colonies, the nurses in the old-cohort colonies do not qualify to be called over-aged nurses, in the same way that the foragers in the young-cohort colonies qualify for the label precocious foragers. Although old-cohort colonies of *R. marginata* do not respond to the loss of young individuals by having over-aged nurses, they instead respond by having hard working nurses. The rate of nursing by nurses at the colony as well as individual level in old-cohort colonies is higher than the corresponding rate in normal colonies. We suggest that these results are different from those in honey bees and those expected from the response of *R. marginata* in young-cohort colonies because both nursing in honey bees and foraging in *R. marginata* are more specialized tasks compared to nursing in *R. marginata*. Honey bee nurses require active hypopharyngeal glands in order to perform nursing; nursing is therefore restricted to younger individuals as the hypopharyngeal glands of older individuals regress. Over-aged nurses have been shown to regenerate their hypopharyngeal glands (Huang and Robinson, 1996). Similarly, foraging in *R. marginata* is rather specialized and is rarely or never performed by very young individuals (Naug and Gadagkar, 1998a). In contrast, nursing in *R. marginata*, which is also performed by old individuals, albeit at a low rate, is a rather unspecialized activity, perhaps not involving any hypopharyngeal glands, and therefore much more flexible.

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