

ECOLOGY, BEHAVIOR AND BIONOMICS

The Acceptance Rate of Young Wasps by Alien Colonies Depends on Colony Developmental Stages in the Swarm-Founding Wasp, *Polybia paulista* von Ihering (Hymenoptera: Vespidae)

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**ABSTRACT** - In social insects, newly emerged individuals learn the colony-specific chemical label from their natal comb shortly after their emergence. These labels help to identify each individual's colony of origin and are used as a recognition template against which individuals can discriminate nestmates from non-nestmates. Our previous studies with *Polybia paulista* von Ihering support this general pattern, and the acceptance rate of young female and male wasps decreased as a function of their age. Our study also showed in *P. paulista* that more than 90% of newly emerged female wasps might be accepted by conspecific unrelated colonies. However, it has not been investigated whether the acceptance rate of newly emerged female wasps depends on colony developmental stage of recipient colonies. We introduced newly emerged female wasps of *P. paulista* into different colony developmental stages of recipient colonies, i.e., worker-producing and male-producing colonies. We found that the acceptance rate of newly emerged female wasps by alien colonies was pretty lower by male-producing colonies than worker-producing colonies. This is the first study to show that the acceptance rate of young female wasps depends on stages of recipient colonies.

**KEY WORDS:** Swarm-founding wasp, nestmate recognition, kin recognition, Epiponini

In social insects, nestmates are characterized by a distinct chemical label, which is determined by the interaction of genetic and environmental cues (Breed 1983, Carlin & Hölldobler 1986, Stuart 1987, Waldman *et al* 1988, Ratnieks 1991, Downs & Ratnieks 1999, Pirk *et al* 2001). Newly emerged individuals learn the colony-specific chemical label from their natal comb shortly after their emergence (e.g. Gamboa *et al* 1986a). In *Polistes* wasps, it has been demonstrated that colony-specific cuticular chemical labels mature between one and three days after emergence (Panek *et al* 2001, Lorenzi *et al* 2004). These labels help to identify each individual's colony of origin and are used as a recognition template against which individuals can discriminate nestmates from non-nestmates (Gamboa *et al* 1986b, Fletcher & Michener 1987, Crozier & Pamilo 1996, Ozaki *et al* 2005).

In polistine wasps, there are some studies to show that newly emerged individuals are accepted by unrelated colonies (Arathi *et al* 1997, Kudô & Zucchi 2006, Kudô *et al* 2007). In the swarm-founding wasp *Polybia paulista*, for example, the percent acceptance of <2-days-old female wasps into alien colonies was much higher than that of >2-days-old wasps, suggesting that the percent acceptance decreased as a function

of their age (Kudô *et al* 2007). Similarly, acceptance of young males of *P. paulista* into unrelated colonies decreased as a function of their age (Kudô & Zucchi 2006).

In the present paper, we report that the acceptance rate of newly emerged female wasps of *P. paulista* depends on developmental stages of recipient colonies.

### Material and Methods

Field experiments were carried out at the campus of Universidade de São Paulo – USP, in Ribeirão Preto city (21°11'S, 47°48'S), SP, during the dry season (winter) between July and August 2005. We put combs with numerous numbers of pupae, obtained from two colonies (PP0539 and PP0540) nesting at Cajuru city, into plastic containers (25 x 20 x 10 cm). We checked the containers each day at 0900h, and when newly emerged wasps were present, we marked day-specific marks on their thorax. We introduced these wasps (0-2 days old) into four recipient colonies (PP0540, PP0541, PP0543 and PP0548) nesting on the campus of USP. PP0540, PP0541 and PP0543 were male-producing colonies, and those colonies abandoned soon after our field

experiments. PP0548 was a worker-producing colony. The donor wasps were apparently unrelated to recipient colonies because the donor and recipient colonies were always more than 50 km apart.

Prior to introduction, each wasp was put into a plastic tube (15 ml) and immobilized by cooling with a portable freezer bag to force her to become passive. All tests were carried out by introducing a live, cooled wasp into a colony. Introduced wasps were held with forceps and placed gently onto the surface of envelopes. The observer noted the behavior of host residents towards the introduced wasp and classified it into three categories: 1) tolerant behavior (residents groomed the introduced wasp); 2) intermediate behavior (resident bit or lunged at the introduced wasps and then groomed them); and 3) aggressive behavior (at least one resident bit or stung the introduced wasps, and the introduced wasps ultimately flew away from the nest or fell down due to wing damage). In addition to the above categories, host residents often carried the introduced wasps from the nest. These cases were also regarded as category (3). In this paper, categories (1) and (2) were regarded as 'acceptance' and category (3) as 'rejection'. Field experiments were carried out between 0900h and 1800h on days without rain. Each introduced wasp was used no more than once, and wasps were introduced into recipient colonies at intervals of at least 60 min.

We compared the percent acceptance of young wasp among four recipient colonies by using Fisher's exact probability tests. A sequential Bonferroni procedure was applied after Fisher's exact probability tests. For each colony, the differences in percent acceptance between two donor colonies were tested Fisher's exact probability tests, and the probabilities were combined across recipient colonies using a Fisher's combined probability test.

## Results

The percent acceptance of young wasps into alien colonies varied among recipient colonies (Fig 1). Only two out of 25 introduced wasps (8%) were accepted in PP0540, while 24 out of 25 introduced wasps (96%) were accepted in PP0548, and the difference in acceptance between these colonies was statistically significant (Fig 1). In PP0541 and PP0543, 68% (17/25) and 48% (12/25) of introduced wasps were accepted from recipient colonies, respectively, and both percent acceptances were greater than that in PP0540, but smaller than that in PP0548 (Fig 1). Overall, 55% of introduced wasps were accepted from four recipient colonies. We found that there was no significant difference in the percent acceptance between two donor colonies ( $\chi^2_8 = 3.246$ ,  $P = 0.918$ ).

## Discussion

In this study, 55% of young wasps were accepted from unrelated colonies. However, this frequency is far lower than those of previous studies in polistine wasps (Arathi *et al* 1997, Kudô *et al* 2007). Arathi *et al* (1997) showed

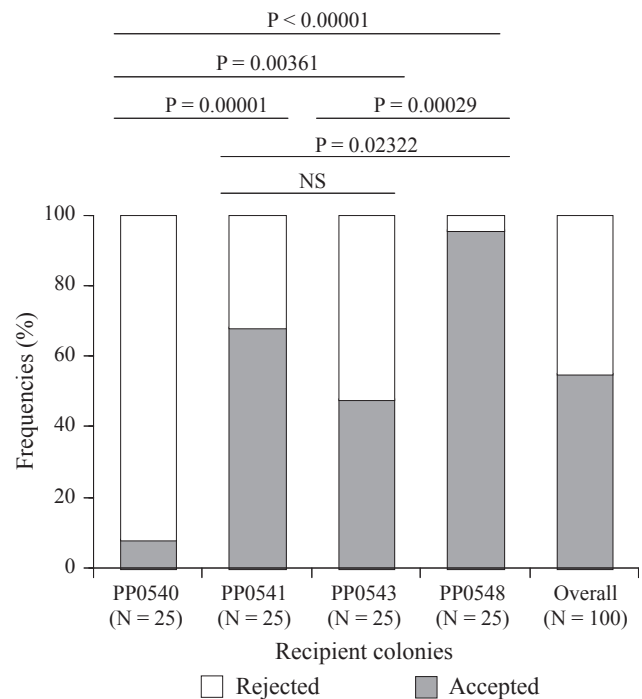


Fig 1 Comparisons in the acceptance rate of newly emerged female wasps between four recipient colonies.

in *Ropalidia marginata* Lep. that all 1-day-old wasps (<24 h) were accepted from unrelated alien colonies. Kudô *et al* (2007) also showed in *Polybia paulista* that approximately 90% of newly emerged wasps were accepted from unrelated colonies. Because colony-specific cuticular chemical profiles mature between 1 and 3 days in female polistine wasps (Panek *et al* 2001, Lorenzi *et al* 2004), we predicted that most of introduced wasps must be accepted by unrelated colonies in this study.

While the percent acceptance was very high in a worker-producing colony (PP0548), it was pretty low in male-producing colonies (PP0540, PP0541 and PP0543). In our previous study with *P. paulista*, we introduced young wasps into alien worker-producing colonies, and the percent acceptance was very high (Kudô *et al* 2007). Our experimental design was the same in our previous study (Kudô *et al* 2007), clearly meaning that the lower acceptance rate by recipient male-producing colonies in the present study was not caused by the experimental design. Thus, our studies suggest that acceptance of young female wasps in *P. paulista* depends on the stages of recipient colonies. In *P. paulista*, the male-producing period is the end of colony cycle. As the nests are not in expansion in this period, wasps in male-producing colonies might aggressively reject introduced newly emerged wasps.

To our knowledge, the lower acceptance rate of young female wasps by alien male-producing colonies is not known in any other polistine species. In this study, however, we used only one worker-producing recipient colony. A number of colonies should be used to compare the acceptance rate of newly emerged females between worker-producing and male-producing colonies in future works.

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