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ARTICLES

Caste-biased acceptance of non-nestmates in a polygynous ponerine ant

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We investigated the influence of caste on nestmate discrimination in the ponerine ant *Pachycondyla luteipes*, where workers lack functional ovaries and are totally sterile. Both a mark-and-recapture field experiment and an introduction experiment in the laboratory revealed intermixing of both nestmate and non-nestmate workers between nests. In the laboratory experiment, conspecific workers, both nestmate and non-nestmates, were almost always accepted. Workers' internest hostility was weak and did not correlate with the distance between nests over the geographical scale studied (<130 m). However, workers responded differentially to nestmate and non-nestmate workers, grooming non-nestmates more frequently than nestmates. In contrast, non-nestmate queens were usually violently attacked by resident workers, and as a result only 30% were accepted. Nestmate queens were always accepted with no aggression. Our results indicate that *P. luteipes* workers have the ability to recognize nestmates but are not aggressive when the non-nestmates are sterile workers. Such caste-biased acceptance has been predicted by kin selection in relation to the avoidance of intraspecific social parasitism and regulation of queen numbers.

Keywords: caste; nestmate recognition; *Pachycondyla luteipes*; polygyny; ponerine ant

In most social Hymenoptera, kin discrimination is well developed and there is strict nestmate discrimination (Crozier & Pamilo 1996). The ability to discriminate kin is important for the evolution and maintenance of altruism by workers through kin selection (Hamilton 1987). Nestmate and/or kin discrimination consists of three parts: the production of recognition cues, the perception of these cues and subsequent behavioural discrimination (Reeve 1989; Sherman et al. 1997). The perception of recognition cues, however, does not always lead to discrimination. For example, in a unicolonial population of the wood ant, *Formica paralugubris*, workers showed no aggression towards non-nestmate workers, but they did engage in trophallaxis more frequently with nestmate workers than with non-nestmate workers (Chapuisat et al. 2005). This implies that, although *F. paralugubris* workers are able to discriminate nestmates from non-nestmates, they do not show aggression against the latter. Reeve (1989) indicated that the expression of kin discriminatory behaviour will depend on the costs and benefits of discrimination, and predicted that when the cost of accepting is high, the probability of rejecting both nonkin and kin should increase. Conversely, if the fitness cost of accepting is low, the probability of rejecting may decrease. Empirical support for Reeve's (1989) model has been observed from studies of honeybees, *Apis mellifera* (Downs & Ratnieks 2000).

Intrusion by non-nestmates leads to various costs for recipient colonies, ranging from parasites and disease transmission to selfish reproduction by the intruders (Schmid-Hempel 1998; Neumann & Moritz 2002; Lopez-Vaamonde et al. 2004). Given that cost, the acceptance probability might be influenced by the reproductive ability of the potential invaders. In ants, the difference in reproductive potential between queens and workers is usually pronounced and in some species workers are totally sterile (Bourke & Franks 1995). A colony accepting non-nestmate workers will suffer relatively low costs if the non-nestmate workers are sterile, since the cost of selfish reproduction by nonkin is absent, unless the workers resort to another selfish behaviour (e.g. food robbing in

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honeybees, slave making in some ants). Therefore, acceptance of alien workers would be more likely to occur in species with totally sterile workers than in species where workers retain reproductive ability. Vander Meer & Porter (2001) reported that in polygynous colonies of *Solenopsis invicta*, in which workers are completely sterile, acceptance probability differs between queens and workers: workers from other nests are accepted, whereas alien queens are attacked by resident workers. Such caste-biased non-nestmate acceptance is, however, known only in *S. invicta*. Furthermore, in *S. invicta* it is unclear whether the absence of aggression is due to a lack of kin recognition. Apart from the concept of the potential cost of selfish reproduction by nonkin, there is much evidence of fundamental differences in underlying nestmate recognition mechanisms between castes and between developmental stages (Smith 1983; Shellman-Reeve & Gamboa 1985; Hölldobler & Wilson 1990; Layton et al. 1994; Hare 1996; Sundström 1997; Vander Meer & Porter 2001; Tentschert et al. 2002; Brown et al. 2003; Moritz & Neumann 2004).

Acceptance of non-nestmates occurs in the context of polydomy (a single colony consisting of multiple spatially separated nests) in social insects. Striking examples exist in some invasive tramp species (e.g. Passera 1994; Tsutsui & Suarez 2003) that have a unicolonial social and population structure, that is, they are polygynous (coexistence of multiple fertile queens in a colony) and polydomous. However, unicoloniality has not been rigorously demonstrated in the ant subfamily Ponerinae.

We focused on *Pachycondyla* (formerly *Brachyponera*) *luteipes* which belongs to the Ponerinae, a systematically distinct group from the myrmicine *Solenopsis*. The Ponerinae is often referred to as a primitive group, in which queen–worker dimorphism is less pronounced in many species (Peeters 1997). However, some species of *Pachycondyla*, in particular those belonging to the genus formally called *Brachyponera*, express pronounced caste dimorphism and have totally sterile workers in the species reported so far (Haskins & Haskins 1950; T. Kikuchi, unpublished data). In mangrove forests and the neighbouring evergreen forests of Iriomote island, Japan, polygynous colonies of this species are found at high density (K. Tsuji, unpublished data). In this study, we first checked whether individuals of different nests could intermix in the field. When intermixing occurred (which indicates the possibility of polydomy or, in the extreme case, unicoloniality), we examined to which geographical scale colony subunits extended. Second, we tested whether the acceptance probability of introduced non-nestmates depended on the non-nestmate's caste (queens versus workers). When internest exchanges of individuals (i.e. polydomy) occurred, we predicted that non-nestmate workers were more likely to be accepted than non-nestmate queens because of the absence of the cost of selfish reproduction in workers.

METHODS

Mark-and-Recapture Experiment

We conducted a mark-and-recapture experiment in November 2003 to quantify exchange of individuals between nests. We found 18 *P. luteipes* nests in rotten wood and rotten bamboo stems on the ground in an area of approximately 1500 m^2 (ca. 130 × 11.5 m) and measured the distances between all nest pairs. We collected eight of the 18 nests, together with their nest material, and left the rest of the nests intact. The collected nests were dissected at the Iriomote laboratory of Ryukyus University. Workers belonging to the same nest received the same coloured enamel paint spot on their thorax or abdomen and were housed in a plastic box with moistened paper. On the following day, the workers from each nest were released around the entrance (within 30 cm radius) of a randomly selected nest from the 10 intact nests in the field. Each pair of donor and recipient nests was 5–120.8 m apart (Table 1). We consider this geographical scale of nests to be appropriate to test mixing of ants between nests because in the only case of polydomy known in the Ponerinae, the nests were in an area of 50 m^2 (*Hypoponera bondroiti*: Yamauchi et al. 1996). We collected the 10 recipient nests 48 h later and counted the marked and unmarked individuals in them.

Laboratory Introduction Experiment

Eleven additional *P. luteipes* nests were collected and maintained in individual plastic cases (20 × 10 cm and 5 cm high) with plaster on the bottom to maintain high humidity in the laboratory (25°C; 12:12 h light:dark). All colonies were fed with the same diet (honey water and termites) every 2 days. After the ants were familiarized with this artificial nest for 5–7 days, we carried out the introduction experiment. A single individual, either a worker or a queen, was picked up from a donor nest and introduced into the foraging area of a recipient nest. We marked all introduced individuals with an enamel paint marker 1 day before the introduction. The intranest control consisted of the removal and reintroduction of a marked worker and a queen (also marked) into their natal nests (once for each of 11 nests). Non-nestmate introduction consisted of the introduction of a non-nestmate worker or a non-nestmate queen into a recipient nest. Worker introduction was carried out once in each of the

Table 1. The number of workers intermixing between nests in the field

Recipient nests	Introduced nests	Distance between nests (m)	Number of Marked workers	Number of Recaptured workers
A	1	30.0	54	1
B	2	37.0	73	3
C	3	38.8	84	3
D	4	5.0	92	2
E	5	81.7	302	9
F	6	18.3	145	2
G	7	15.1	296	2
H	8	31.3	331	1
I	8	120.8	361	2
J	8	81.3	394	0