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ORIGINAL ARTICLE

Factors affecting internest variation in the aggressiveness of a polygynous ant, *Camponotus yamaokai*

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Abstract

The facultatively polygynous ant *Camponotus yamaokai* shows various degrees of internest hostility. We examined the relationship between aggressiveness and possible factors that affect the level of hostility, such as internest distance, numbers of queens and workers, and brood size. We found that the aggression level did not significantly correlate with these factors. Our study suggests that information on the colony genetic structure is important in understanding variation in the aggressiveness of polygynous colonies.

Key words: aggression, Formicidae, Hymenoptera, polygyny, super-colony.

INTRODUCTION

Polygynous ants, which have many egg-laying queens in a single colony, generally show reduced levels of intercolonial hostility compared to monogynous and oligogynous species, which have only one and two to several functional queens per colony, respectively (Janzen 1973; Hölldobler & Wilson 1977; Yamauchi *et al*. 1981; Brian 1983). At least two possibilities can explain such reduced hostility. First, ant polygyny is usually associated with fission reproduction (Passera & Keller 1990). Fission reproduction results in neighboring colonies being genetically related and sharing common environments. Second, the presence of more than one queen should complicate nestmate recognition cues or colony specific odor, and may reduce the efficiency of nestmate recognition (Keller & Passera 1989). In a monogynous carpenter ant, it was revealed that recognition chemicals produced by the single queen were disproportionately important in nestmate recognition compared to those produced by workers and to environmental odors (Carlin & Hölldobler 1983, 1986, 1987). If the former is more important, it is predicted that hostility increases as intercolony distance increases, whereas the latter predicts that a colony reduces general hostility with increasing queen number.

Camponotus yamaokai Terayama and Satoh nests in hollows of dead twigs and bamboo grasses and is facultatively polygynous; that is, a single colony often has multiple functional queens (Satoh 1989). The ant is common in an arboreal ant community of evergreen broad-leaved forest in central Japan. In this study, aggression between workers from adjacent nests as well as between those from distant nests was compared to evaluate the importance of the two possibilities presented above. Colony size and composition, which may potentially affect aggression and thus hostility level, were also analyzed.

MATERIALS AND METHODS

Nest collection

At Mount Tsukuba (site A) and Tokorozawa (site B) nests within a defined area (5×5 m^2 and 5×6 m^2, respectively) were mapped (Fig. 1), and all nest members, including immatures, were collected in October 1986 (Table 1). They were kept by nest in a plastic box (120 mm in diameter, 60 mm in depth) at room temperature (20–27°C) and fed with honey–water mixture and freshly killed *Drosophila* flies.

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Table 1 Composition of nest members of the nests used in aggression tests

Nest	Composition						
	Queen	Minor worker	Major worker	Alate female	Male	Larva	Egg
Site A (Mount Tsukuba)							
A1	1	143	18	0	2	91	0
A2	0	155	16	0	3	146	2
A3	2	188	38	0	7	341	1
A4	0	40	4	0	0	3	0
A5	3	357	44	0	0	304	0
A6	2	183	20	0	0	200	0
A7	5	223	18	0	0	115	0
A8	9	339	41	0	0	418	16
A9	1	87	5	0	0	108	0
A10	1	74	10	0	0	31	0
A11	1	258	27	0	5	180	13
A12	5	64	10	0	0	79	2
Site B (Tokorozawa)							
B1	0	8	2	0	0	8	0
B2	7	189	35	0	0	273	0
B3	15	388	72	1	7	436	2
B4	19	751	124	0	8	585	5
B5	2	188	24	10	5	130	0
B6	6	204	21	0	0	188	2
B7	5	126	26	0	1	225	1
B8	19	983	173	2	14	487	4

Table 2 Aggression scale used in scoring the responses of workers from different nests in aggression tests

Score	Description
0	Acceptance: mutual tolerance, huddling, grooming, trophallaxis
1	Avoidance: retreat, escape from the opponent
2	Alarm: open-mandible threat, posture of spraying formic acid
3	Weak attack: nipping, leg pulling, body jerking
4	Full attack: locking together, biting, spraying formic acid

positively correlated with the genetic distance between colonies (Beye *et al*. 1998) and the intranest relatedness of the recipient colonies (Pirk *et al*. 2001). In species that show aggression correlated with queen number and nest distance, the number of queens may be negatively correlated with intranest relatedness, and nearby nests may be much more closely related to each other than to distant nests, through fission reproduction of colonies. In the case of *C. yamaokai*, however, estimates of average intranest relatedness are very high (more than 0.75) and some colonies show clonal genetic structure (Satoh *et al*. 1997). Successive intranest mating (inbreeding) and adoption of queens might be responsible for such a high level of intranest relatedness. This species has either a uni- or a multicolonial population structure (for definition, see Hölldobler & Wilson 1977), and in most cases, a large proportion of nests within the same habitat belonged to a single super-colony as found at site B (Satoh 1990). In such cases, queen number does not correlate with intranest relatedness, and internest distance does not correlate with genetic distance, suggesting that neither the queen number nor the nest distance affect the aggression level as observed in the present study. We expect that the polygynous species that show no correlation between queen number and aggression should have high intranest relatedness independent of queen number because of intranest mating and queen adoption. Stuart (1991) noted the possibility that intranest relatedness of polygynous colonies of *L. ambiguus* might not be low enough to produce a correlation between queen number and aggression (see also Herbers & Stuart 1990).

Table 3 Internest aggression at site A (Mount Tsukuba)

	Aggression score (average)											
Nest	A1	A2	A3	A4	A5	A6	A7	A8	A9	A10	A11	A12
A2	0	0	0.1	0	0	0	0	0	0.1	0	0.3	0.9***
A3	0	0.1	0	0	0.1	0.1	0	0.1	0.2	0.1	0.1	1.8***
A12	–	0.9***	1.8***	–	2.3***	2.2***	1.8***	0.6*	0.6*	–	0.9***	0

Distributions of scores were compared with control by Mann–Whitney *U*-test: *$0.05 > P > 0.01$; **$0.01 > P > 0.001$; ***$P < 0.001$; –, not tested.

In this study, both the number of workers and eggs in the nest did not correlate with aggression level. Positive correlation between colony size and aggressiveness was reported in *L. ambiguus* (Stuart 1991), but not in *R. confusa* (Crosland 1990) and *L. longispinosus* Roger (Stuart & Herbers 2000). Stuart (1991) suggested that such a phenomenon is important in territorial competition and defense against the social parasite (= *L. longispinosus*) in *L. ambiguus*.

In conclusion, our study suggested that a polygynous colony with high intranest relatedness might function as a monogynous colony with respect to nestmate recognition. Thus, information on colony genetic structure should be important in understanding variable degrees of aggressiveness in polygynous colonies.

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