

Mechanisms regulating functional monogyny in a Japanese population of *Leptothorax acervorum* (Hymenoptera, Formicidae) : dominance hierarchy and preferential egg cannibalism

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ABSTRACT. Queen behaviour of *Leptothorax acervorum* collected in northern Japan was observed in four functionally monogynous colonies (one functional mated egg-laying queen with some supernumerary mated but sterile queens) and two monogynous colonies with some virgin queens. In three functionally monogynous colonies, dominance behaviour including antennation, biting, pulling, and remarkable avoidance where queens fled approaching the functional queens, were frequently observed among queens. In two of the three colonies, an almost linear dominance hierarchy was established among queens and only the top ranked queen laid eggs. However, the hierarchy was not stable : in one colony the queens in second and third ranks and the second ranked queen in the other colony were expelled from colonies. Such queen antagonism was very rare in the other functionally monogynous colony, where workers expelled the fertile queen, and the other queen replaced the egg-layer. In monogynous colonies with virgin queens, virgin queens showed worker-like behaviour, and dominance interactions completely lacked among queens. Oophagy was often observed among nestmates : this always occurred just after oviposition. Eggs of functional queens were not eaten while most eggs laid by supernumerary queens were eaten by functional queens and workers. Supernumerary queens never showed oophagy. Workers laid trophic eggs and reproductive eggs : the former ones were always eaten while one third of the latter survived.

KEY WORDS : dominance hierarchy, ants, functional monogyny, oophagy.

INTRODUCTION

In ants, many species show polygyny in which there are several functional queens per colony (HÖLLDOBLER & WILSON, 1990). Polygyny in mature colonies is usually a secondary polygyny where new queens are added by adoption into an already existing monogynous colony (HÖLLDOBLER & WILSON, 1990). In general, secondary polygyny maintains the reproductive function of most queens without aggressive display among them (BOURKE & FRANKS, 1995). However, some ant species show a remarkable reproductive skew among coexisting queens. The most remarkable case is "functional monogyny", in which only one mated individual lays eggs while the other inseminated individuals are sterile (e.g. BUSCHINGER, 1968). This social structure is known from seven Formicoxenini, and the queenless ponerine *Pachycondyla* sp. (BUSCHINGER, 1968, 1990; ITO, 1990, 1993). Functional monogyny is proximately regulated by antagonistic behaviour leading to dominance hierarchy among nestmates in *Leptothorax* sp. A., *L. gredleri* Mayr, 1855 and *Pachycondyla* sp. (HEINZE & SMITH, 1990; HEINZE et al., 1992; ITO, 1993).

To know how and why such high reproductive skew exists is very important for understanding the evolution of social life in animals (reviewed in REEVE & KELLER, 2001). *Leptothorax acervorum* Fabricius, 1793 is an interesting subject for understanding this problem, since

its social structure varies geographically : in central, western and northern Europe, many colonies show functional polygyny, i.e. several egg-laying queens occur per colony (BUSCHINGER, 1968; BOURKE, 1991; STILLE et al., 1991; HEINZE et al., 1995) while in northern Japan and central Spain, colonies having multiple mated queens always show functional monogyny (ITO, 1990; FELKE & BUSCHINGER, 1999). In Alaska, both functional monogyny and functional polygyny were found in the same population (HEINZE & ORTIUS, 1991). In this paper, I demonstrate the mechanisms regulating functional monogyny in a Japanese population of *Leptothorax acervorum*, and compare the results with studies in other populations (BOURKE, 1991; HEINZE & ORTIUS, 1991).

METHODS

The ants

Leptothorax acervorum is a common holarctic ant, distributed through Europe, Asia and northernmost North America. In Japan, the ants are found in Hokkaido and mountain areas of Honshu and Shikoku (TERAYAMA et al., 1992). In Furano, northern Hokkaido, 50% of the colonies have multiple dealate queens per colony, however, there is only one principal egg layer having well developed ovaries even if there are multiple mated queens (ITO, 1990). A few colonies have additional egg-laying queens;

however, the ovaries of these queens are distinctively less-developed than those of the principal egg layer. In this paper, I use the term "functional queens" for principal egg layers and "supernumerary queens" for the non-reproductive mated queens and mated queens who lay eggs at a very low rate, and "virgin queens" for unmated queens.

The colonies for the present paper were collected from dead twigs fallen on sunny rocky outcrops in Shikaoi, eastern Hokkaido, northern Japan, in mid May (colony code A, B, C, D) of 1992 and early July (E, F) of 1990. This collection site is located ca. 50 km east of Furano. In

the colonies collected in early July (colonies E and F), one queen per colony already had a swollen abdomen and there were several eggs in the nests. The colonies collected in mid May had neither such queens nor eggs. The numbers of dealate queens and workers in these colonies are shown in Table 1. Colonies C and D had only one functional queen and some virgin queens. The remaining four colonies had one functional queen with a few virgin queens and/or multiple supernumerary queens (functional monogyny).

TABLE 1

Composition of *Leptothorax acervorum* colonies observed in laboratory. Numbers in parentheses show duration of observation only for egg laying activity. All colonies had only one principal egg layer each.

Colony code	No. individuals			Worker	Dates observed	Hours observed
	Queens					
	Total	Mated	Virgin			
A	6	5	1	48	June 15 – July 15	44 + (24)
B	5	5	0	23	May 28 – July 12	72 + (24)
C	10	1	9	45	June 10 – 29	20 + (24)
D	5	1	4	30	June 17 – July 12	13 + (24)
E	7	6	1	36	July 2 – 10	18
F	7	7	0	29	July 8 – 22	16

Laboratory observation

The colonies were kept in an artificial nest measuring 14.5 x 8.0 x 3.0 cm at room temperature condition (ca. 20 ~ 25 °C). The bottom of each nest box was covered with plaster and brood chambers (2 x 6.5 x 0.5 cm) were excavated in the plaster floor. The chambers were covered with glass plates. Small mealworms and diluted honey were given as prey every day. All dealate queens were individually marked by enamel paint. In four colonies (A-D), observation started from just after the winter season (late May to mid June). These colonies were kept for one to two months and observation ended in the egg-laying season. For the other two colonies (E and F), behavioural observation started during the egg-laying season in early July.

Behaviour of queens and workers was observed by scan sampling using a binocular dissecting microscope. The interval of scans was one to three minutes. Scan sampling was repeated for 30 to 60 minutes. Such observation session was replicated 20 to 60 times. The total observation time was 13 to 48 hours per colony. During the observation, I recorded all behaviours shown by queens, and oviposition and oophagy by workers. Furthermore, to detect egg-laying activity of individual queens and workers, only oviposition and subsequent behaviour was recorded from the observation under a binocular dissecting microscope for 24 hours per colony in colonies A-D. Survival of eggs was estimated from observations of oviposition and the subsequent behaviour of nestmates. After the observation, all queens were dissected under a binocular microscope to check insemination, ovarian development, and yellow bodies as in Ito (1990).

RESULTS

Aggressive interactions and dominance hierarchy among queens, and queen expulsion

Aggressive antennation, biting, and pulling between queens were frequently observed in three functionally monogynous colonies (colonies A, E and F), but it was rare in one functionally monogynous (colony B) and the two monogynous colonies with virgin queens (C and D). These behavioural interactions were similar to those described for workers or intercastes of other species of formicoxenine ants, *Harpagoxenus sublaevis* Nylander, 1849, *Leptothorax allardycei* Mann, 1920, and *Leptothorax* sp. A (FRANKS & SCOVELL, 1983; COLE, 1981; HEINZE & SMITH, 1990).

In colony A, observed just after hibernation, aggressive interactions among queens were frequent, but a clear dominance hierarchy was not found because aggressive interactions were observed only three dyads (Fig. 1). However, one queen started to lay eggs. In colony B, which comprised five mated queens, queen-queen aggressive interactions were quite rare. In this colony, the expulsion of a queen by workers was observed (Fig. 1). On day 3 after the start of observation, the abdomen of one queen (Q3) in colony B became swollen but she did not lay eggs yet. From day 5 to day 6, Q3 was frequently attacked by Q2 and workers in the nest chamber. On day 7, she was always in the foraging arena and received aggressive attacks from workers and Q2 who often engaged in foraging. Q3 did not enter the nest chamber after this day. Two days later, the other queen (Q1) became fertile, having a swollen abdomen, and subsequently started oviposition. After the expulsion of Q3, Q1 laid six eggs, all of which survived. In colonies C and D where there was only one mated queen with some virgin queens, no aggressive

behaviour was observed among queens. In these two colonies, virgin queens frequently showed foraging just like workers.

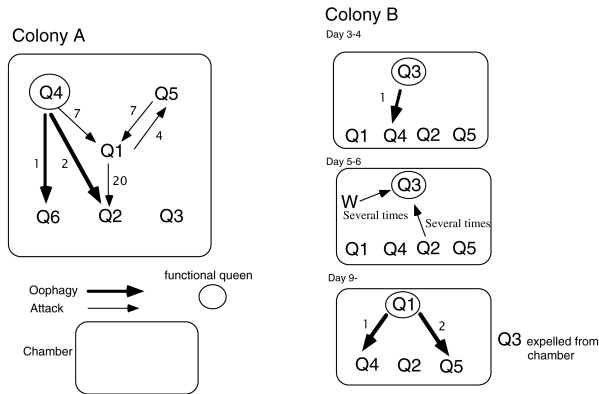


Fig. 1. – Dominance structure in colony A (Q3 was virgin and other queens mated) and successive change of dominance structure in colony B (all queens mated). A numeral on each arrow means the number of observation episodes.

In two colonies (E and F) observed in July, antennation and biting were frequently observed among the supernumerary queens. Top-ranking functional queens never showed such antagonistic behaviour. The supernumerary queens showed remarkable avoidance behaviour against these functional queens: they fled approaching the func-

tional queens. Such avoidance behaviour, only shown against functional queens, was not observed in other colonies. Aggressive interactions including remarkable avoidance behaviour occurred in the same direction in most of a given pair of queens in colony E (Table 2). Therefore, an almost linear dominance hierarchy among dealate queens was established until day 4 (index of linearity, $K' = 0.82$, $P = 0.057$; DE VRIES, 1995). However, this relationship was not stable: on day 4, Q7 who ranked third, was frequently attacked by workers and Q2. The second ranked queen (Q6) was also attacked by workers. On day 6 after the start of observation, Q6 and Q7 always spent their time in the foraging arena. They often tried to enter the nest chamber; however, they were always attacked by workers. I removed them from the nest and dissected them on day 7: they had mated but were sterile without yellow bodies. After removal of the two queens, the dominance order was not changed: the fourth ranked queen (Q2) became the second rank, however, she immediately became the target of attacks by workers and Q4. Finally, she was also expelled from the nest chamber on day 9. A similar dominance hierarchy was observed in colony F ($K' = 0.82$, $P = 0.057$). In this colony, the second ranked queen (Q3) was expelled from the nest chamber by intensive attacks from the fifth ranked queen (Q4). After the expelling, the third-ranked queen (Q5) moved to 2nd place.

TABLE 2

Dominance hierarchy and reproductive condition of queens in colonies E and F. Frequencies of aggressive antennation, biting, and pulling were summed. Frequency of remarkable avoidance behaviour was shown in parenthesis.

Colony E	Subordinate							Total
	Q1	Q6	Q7	Q2	Q4	Q5	Q3	
Dominant								
Q1	---	(3)	(1)	(8)	(4)	(4)	0	(20)
Q6	0	---	15	14	8	5	5	47
Q7	0	0	---	8	4	1	2	15
Q2	0	0	5	---	29	13	5	52
Q4	0	0	0	8	---	4	2	14
Q5	0	0	0	0	0	---	1	1
Q3	0	0	0	0	0	0	---	0
Total	0	(3)	20 (1)	30 (8)	41 (4)	23 (4)	15	129 (20)
Insemination ¹	+	+	+	+	+	-	+	
Ovarian development ²	+++	-	-	-	-	-	-	

Colony F	Subordinate							Total
	Q6	Q3	Q5	Q2	Q4	Q1	Q7	
Dominant								
Q6	---	(4)	(3)	(1)	(3)	0	(3)	(14)
Q3	0	---	34	6	28	6	1	75
Q5	0	0	---	21	80	50	1	152
Q2	0	0	0	---	5	2	1	8
Q4	0	10	0	0	---	4	0	14
Q1	0	0	1	1	2	---	4	8
Q7	0	0	0	0	0	0	---	0
Total	0	10 (4)	35 (3)	28 (1)	115 (3)	62	7 (3)	257 (14)
Insemination ¹	+	+	+	+	+	-	+	
Ovarian development ²	+++	-	-	-	-	-	-	

1.+ mated, - virgin

2.+++ well developed ovaries having many mature oocytes, - undeveloped ovaries

TABLE 3
Egg laying and oophagy in six *L. acervorum* colonies.

Egg layers (No. individuals)	No. eggs laid	No. eggs eaten by				No. eggs survived (%)
		Functional queens	Supernumerary queens	Virgin queens	Workers	
Functional queens (6)	31	0	0	0	0	31 (100)
Supernumerary queens (19)	9	7	0	0	1	1 (10)
Virgin queens (15)	1	0	0	0	1	0 (0)
Workers (211)						
reproductive eggs	17	5	0	0	6	6 (35)
trophic eggs	9	4	0	0	5	0 (0)
Total	67	15	0	0	14	38

Egg cannibalism

Egg cannibalism among nestmates was observed in all six colonies. Since egg-laying activity was low in all colonies, the data were summed (Table 3). During 234 hours of observation for six colonies, oviposition was observed 67 times: 31 by functional queens, 9 by supernumerary queens, one by a virgin queen and 26 by workers. Of 26 eggs laid by workers, 17 were evidently reproductive eggs which were observably indistinguishable from queen eggs in shape, size, and colour, and the remaining nine eggs were trophic eggs which were round because of an undeveloped chorion. All trophic eggs were eaten by functional queens (four eggs) or workers (five eggs). Oophagy of reproductive eggs was observed on 20 occasions, all of which occurred directly after oviposition. In an extreme case, an egg just appeared at the tip of the abdomen of a supernumerary queen was immediately picked up by the consumer. Eggs piled on the nest floor were never destroyed during the observation time. Once an egg was put on the egg-pile, it most likely escaped cannibalism and survived. The survival of reproductive eggs was significantly different among functional queens, supernumerary queens, and workers (Monte Carlo contingency table test (ENGELS, 1988), $P = 0.000 \pm 0.000SE$). The eggs of functional queens were never eaten by nestmates while all but one egg laid by supernumerary queens was immediately eaten by functional queens or workers. Supernumerary queens and virgin queens never showed oophagy. Only one egg laid by a supernumerary queen was intact during three hours after oviposition. In this case, the functional queen licked the egg just after egg laying by the supernumerary queen, but did not attack the egg. Worker-laid eggs also suffered heavy cannibalism by functional queens and workers: only six of 17 reproductive eggs survived.

DISCUSSION

To date, functional monogyny in *L. acervorum* has been reported from Alaska, Spain, and northern Japan (HEINZE & SMITH, 1990; ITO, 1990; FELKE & BUSCHINGER, 1999), while facultative polygyny is known from populations of central, western and northern Europe (BUSCHINGER, 1968; STILLE et al., 1991; BOURKE, 1991; HEINZE et al., 1995). In a Japanese population of *L. acervorum*, aggressive interactions among mated queens were observed as in an Alaskan colony of *L. acervorum* (HEINZE & ORTIUS, 1991) and other functionally monogynous formicoxenine species, *Leptothorax* sp. A and *L.*

gredleri (HEINZE & SMITH, 1990; HEINZE et al., 1992). Such queen antagonism is rarely found in European populations of *L. acervorum*. The present study indicates that the geographic difference of behavioural characteristics is an important proximate factor affecting the differences in social structures. Queen antagonism was not found in monogynous colonies with virgin queens. Virgin queens were excluded from reproductive competition among queens in *L. acervorum*, because they functioned just like workers as shown in this paper and in European populations (BUSCHINGER, 1983; BOURKE, 1991).

Even though sample size (number of colonies observed) was small, the frequency of aggressive behaviour among queens was different between two seasons. In spring, the frequency was low but functional queens showed aggressions to others while functional queens never showed actual physical aggression to other queens in summer, even aggression among subordinate queens was frequent. Previous reports on dominance hierarchy in *Leptothorax* ants showed that the aggressive interactions are more frequent after hibernation than in the reproductive season (HEINZE et al., 1992; ORTIUS & HEINZE, 1999), because during the reproductive season queens recognize ovarian development of each other and they rarely attack fertile queens (ORTIUS & HEINZE, 1999). Less aggression against functional queens during the reproductive season is also observed in Japanese *L. acervorum*. As in other species of *Leptothorax* and some other ponerine ants (ORTIUS & HEINZE, 1999; PEETERS et al., 1999; CUVILLIER-HOT et al., 2002), the fertile signal of the alpha individual may be more important than physical direct aggression after establishment of dominance. The reasons of the high frequency of aggressions among supernumerary queens during summer in the Japanese population of *L. acervorum* are unknown in this time.

Among four functionally monogynous colonies, queen expelling was observed in three colonies. In two colonies with a clear dominance hierarchy, second ranked and third ranked supernumerary queens (in total four supernumerary queens) were the target of attacks by lower ranked supernumerary queens and workers. However, it is not sure whether functionally monogynous colonies of *L. acervorum* in northern Japan become truly monogynous via such queen expelling. Queen expelling is also observed in functionally monogynous colonies of *Leptothorax* sp. A, where higher ranked individuals tend to disperse or to be attacked and expelled from colonies (ORTIUS & HEINZE, 1995). In the queenless ponerine ant *Pachycondyla sublaevis* (EMERY, 1877) which shows a

linear dominance hierarchy among workers, and where the top-ranked one is a gamergate (mated and egg-laying worker), HIGASHI et al. (1994) have reported in a colony after artificial removal of the gamergate that the second to fourth ranked workers were aggressively attacked by lower ranked workers, and were expelled from the colony. MONNIN and PEETERS (1999) also reported immobilization and expelling of high ranked workers in the queenless ponerine ant *Dinoponera quadriciceps* KEMPF, 1971. Thus, in ant colonies with a linear dominance hierarchy established by aggressive behaviour, expelling higher ranked individuals from colonies may be a common phenomenon. In ant societies where reproduction is regulated by such a dominance hierarchy, low ranked individuals seem to have a lower probability to be a reproductive individual than higher ranked individuals. These observations on ponerine and formicoxenine ants, however, indicate that the higher ranked ones risk to be attacked and expelled from colonies while lower ranked queens can safely stay in the colony and lower ranked queens still may have a probability to become future reproductives. This may be one of the reasons for lower-ranked queens to stay in functionally monogynous colonies.

Queen behaviour in the population of northern Japan is remarkably different from that in the population of central Europe studied by BOURKE (1991). The most striking difference is the occurrence of queen antagonism as mentioned above. In both populations, oophagy was frequently observed; however, behavioural characteristics of oophagy are very different between the European and the Japanese populations. In the European population, the queens ate mostly old eggs piled on the nest floor (BOURKE, 1991) and freshly-laid eggs were rarely eaten by queens who showed random egg eating without discrimination between nest mate eggs and their own eggs (BOURKE, 1994). In the case of the Japanese population, oophagy always occurred directly after oviposition and eggs piled on the nest floor were never eaten. Queens and workers ate eggs preferentially. The frequency of oophagy was also greatly different: in the European population, the number of eggs eaten / number of eggs laid during observation was 0.75 (calculated from BOURKE (1991)) while in the Japanese population it was just 0.22. Furthermore, workers also showed oophagy of reproductive eggs laid by supernumerary queens in the Japanese population while this was rare in the European population. The remarkable behavioural differences in oophagy seem to be a consequence of the difference in reproductive structure: strong selection for functional monogyny may lead to preferential oophagy by functional queens and workers in Japanese colonies. As shown by BOURKE (1994), queens of *L. acervorum* could not discriminate own eggs from the other's eggs. Thus, selection would favor oophagy directly after oviposition when the egg-layer could be identified. Such oophagy directly after oviposition is also shown in the ponerine ants *Diacamma* sp., *Pachycondyla villosa* Fabricius, 1804, and *Dinoponera quadriciceps*, and the myrmicine ant *Acanthomyrmex ferox* Emery, 1893 (PEETERS & TSUJI, 1993; HEINZE, et al., 1996, MONNIN & PEETERS, 1997; GOBIN & ITO, 2000).

Dissection of *L. acervorum* queens collected in the field (ITO, 1990) and behavioural observations shown in

this paper indicated that some supernumerary queens laid eggs at a low rate under the presence of a functional queen. The results shown here suggest that these eggs could not survive under the occurrence of preferential egg cannibalism by functional queens and workers. Therefore, functional monogyny in Japanese *L. acervorum* is completed by preferential egg cannibalism in addition to queen antagonism.

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