Research article

Dominance hierarchies and aggressive behavior among queens of the inquiline ant *Vollenhovia nipponica*

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Abstract. Social parasitism, including temporary parasitism, slave-making, and inquilinism, is one of the most intriguing phenomena in ant societies. Inquiline ants are workerless, completely rely on the worker force of their host ants, and have evolved numerous traits to exploit the host's resources and to increase their own fitness. We examined the inquiline ant *Vollenhovia nipponica*, which is a social parasite of the congeneric species *Vollenhovia emeryi*. Host nests collected in the field usually contained multiple *V. nipponica* queens, suggesting that it is polygynous. However, the average number of queens in a nest decreased from spring to summer, and many old queens were found dead after the eclosion of new sexuals in late summer. *Vollenhovia nipponica* therefore appears to have a short life span as found in other inquiline ants. Laboratory observation revealed that inseminated queens were aggressive towards each other. Queen-queen antagonism led to the formation of dominance hierarchies, in which only a few dominant queens developed their ovaries and laid eggs. Subordinate queens frequently left the nests by themselves. The system is very similar to "functional monogyny".

Keywords: Ants, inquilinism, queens, dominance, functional monogyny.

Introduction

One of the most intriguing phenomena in social Hymenoptera is the occurrence of social parasitism. In ants, more than 200 species are social parasites (Hölldobler and Wilson, 1990). The most extreme form of social parasitism is permanent inquilinism, in which parasites no longer produce any workers themselves and completely rely on the worker force of their hosts to rear their sexual broods. Inquilines have no need to retain many of the characteristics required for independent colony life (Summer et al., 2004). By contrast, they have evolved diverse strategies to exploit the host's resources and to increase their own fitness (Brandt et al., 2005): chemical mimicry or camouflage (*Temnothorax kutteri* Allies et al., 1986; Franks et al., 1990), complete or partial inhibition of the production of host sexuals (Passera et al., 2001), miniaturization of the inquiline sexuals (*Plagiolepis xene*, Aron et al., 1999, 2004), mating in the nest (*Acromyrmex insinuator* Sumner et al., 2004), elimination of host queens (*Myrmoxenus* spp. Buschinger, 1989, 1990), and "a big bang reproduction" (*A. insinuator,* Bekkevold and Boomsma, 2000).

In Japan, only two species of inquiline ants have been reported (Imai et al., 2003). One of them is *Vollenhovia nipponica*, a parasite of the congeneric ant *Vollenhovia emeryi* (Kinomura and Yamauchi, 1992). Preliminary data from field surveys suggested that single host colonies contain multiple *V. nipponica* queens, which exhibited aggressive behavior towards one another. They bit and pulled on the antennae, heads or legs of other queens, and some queens emigrated from the nest chambers. Such aggressive interactions among queens have previously been reported from wasps, bees and both non-parasitic and parasitic ants (Fletcher and Ross, 1985; Keller, 1993; Franks and Scovell, 1983; Bourke and Franks, 1991). Queen-queen aggression presumably arises from conflict over reproduction. By open fighting or ritualized behavior, the conflict is likely to be resolved, leading dominance hierarchies. For instance, in some formicoxenine ants aggression results in "functional monogyny", i.e. only the

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most dominant of several inseminated queens in a colony lays eggs whereas the others remain more or less sterile (Heinze and Buschinger, 1988; Heinze and Smith, 1990; Ito, 2005). It is possible that the aggressive interactions among *V. nipponica* queens serve a similar function.

In the present study, we examined the colony structure and queen interactions of *V. nipponica* and discuss the function of aggressive behavior and its meaning in the life cycle of this inquiline ant.

Material and methods

Vollenhovia nipponica (Kinomura and Yamauchi, 1992) is a small, red ant (body length: 2.5–3.0 mm). Its sexuals are smaller than the sexuals of its host *V. emeryi*, and similar in size to host workers. The host ant *V. emeryi* shows a queen polymorphism with long- and short-wing-queens (Ohkawara et al., 2002, 2006). Short-wing-queen colonies are considerably more frequently parasitized by *V. nipponica* than long-wing-queen colonies (Kinomura and Yamauchi, 1992).

Field collection and laboratory breeding of parasitized colonies

Vollenhovia emeryi nests in the soil and in decayed logs and branches in open coniferous or mixed forests. From April to September 2004 and 2006, parasitized colonies were collected in a secondary forest near the coast in Kanazawa of central Japan (36°35′S, 136°35′N). All collected colonies were brought to the laboratory, and their contents were censused by counting the number of *V. nipponica* sexuals and brood. The colony composition of the host was also checked.

To observe the behavior of parasite queens, five colonies were transferred into artificial nests made of plaster (16 cm×8 cm×3 cm) and kept at a constant temperature (23.5°C and humidity on a diet of mealworms.

Determination of colony structure by dissection

In 24 colonies collected in summer (N = 7) and autumn (N = 17) of 2004 and 2005, all winged (N = 183) and wingless *V. nipponica* queens (N = 152) were killed by crushing the heads and dissected under a binocular microscope to examine their ovarian development and insemination. Ovary development was quantified by counting the number of ovarioles and yolky oocytes and checking for the presence of yellow bodies.

Observation of aggressive behavior among V. nipponica queens

From April to June 2005, interactions among *V. nipponica* queens were observed in five laboratory colonies (colony No. 509-1 (A), 509-5 (B), 509-2 (C), 427-8 (D), 427-1 (E)). All colonies had been collected in April 2005 after the end of hibernation. All queens, including winged female sexuals were individually marked with a colored dot on the thorax. For the presentation of data in this paper, queens are named by a combination of colony No. and a number indicating their rank in the dominance hierarchy. To some individuals, in particular winged female sexuals, no rank could be assigned, probably because they did not mate with males yet and not attend the dominance interactions. These were omitted from the analysis or referred with a lower case letter instead of a number. The colonies were observed for 480 to 540 min. each under a binocular microscope by focal and opportunistic sampling. We focused on individual queens for 20 to 30 min., but simultaneously recorded all interactions involving queens in that particular colony.

The behavior of queens during encounters with different nestmates suggested the existence of dominance hierarchies. Rank orders were determined by arranging individuals in an order that minimized reverse interactions. If the ratio of initiated attacks to received attacks differed significantly from a random probability of 0.5 (binominal test, one-tailed, P < 0.05), the more aggressive queen was regarded as dominant to the less aggressive ones. If no queen was significantly dominant, either due to frequent reversals or to a low number of observed interactions, the relationship was considered unknown. Furthermore, linearity of the dominance was tested by the method of De Vries (1995). As the number of interacting queens in colony A and B was small and incomplete information was available for colony E, linearity was investigated only in colonies C and D.

After the observations, all queens were dissected to determine their ovary development and insemination status. Some queens in colony E died during observation and were dissected soon after their death, whereas some of the queens that died could not be dissected. The condition of ovaries was rated as follows, I: without oocytes and yellow bodies; II: with one or two oocytes and no yellow bodies; III: with more than three oocytes and yellow bodies.

Results

Colony structure and life cycle in V. nipponica

A total of 129 *V. emeryi* colonies parasitized by *V. nipponica* were collected during the three years of our study. The colony size of the host ant *V. emeryi* was on average $113.4 \pm SD$ 161.6 workers (range: 5–979), and the queen number was 3.4 ± 3.8 queens (range: 0–23). A single colony contained on average 6.3 ± 8.8 dealate queens of *V. nipponica* (range: 1–76), 14.2 ± 25.6 winged female sexuals (range: 0–153), and 8.3 ± 15.7 males (range: 0–86). Dissections of queens in 24 colonies of 2004 and 2005 showed that only two (0.9%, N = 183) winged female sexuals were inseminated, and that their ovaries were not developed. In contrast, 133 dealate queens (87.5%, N = 152) were inseminated, and 37 (27.8%) had developed ovaries that contained one or more yolky oocytes and yellow bodies. Of the 129 parasitized colonies from 2004 to 2006, 98 (75.9%) contained multiple inseminated queens (average 8.0 ± 9.5 queens, range: 2–76).

Figure 1 shows seasonal changes in the number of dealate queens and female and male sexuals. The number was significantly different among seasons (One-way ANOVA: dealate queen: $F5$, $112 = 2.3$, $p = 0.04$; female sexuals: $F5$, $112 = 3.5$, $p = 0.006$; male: $F5$, $112 = 7.3$, $p < 0.0001$). In April, colonies contain on average more dealate queens (April: 6.4 ± 4.1 queens). In this period, males mating with winged female sexuals were observed in the nests. From May to July, the number of dealate queens in a colony decreased (May: 5.8 ± 5.2 queens, June: 4.1 ± 4.1 queens, July: 3.0 ± 1.8 queens) (Fig. 1a). The number of dealate queens from May to July was significantly different from that in April ($t = 2.0$, $\alpha \leq 0.05$, Student t-test). In the host ant, *V. emeryi*, colony budding frequently occurred during this period (Ohkawara et al., 2002), and inseminated queens of *V. nipponica* probably disperse to the new nests of the host colony with budding. The number of winged females and males also decreased from April to June (Fig. 1b). The number was different between the periods from April to May, and from June to

July (winged female: $t = 2.0$, $\alpha \leq 0.05$, male: $t = 1.9$, $\alpha \leq 0.05$, Student t-test). They disappeared from the colonies in July; probably having conducted dispersal flight to invade into new host colonies. From August to September, new adults of both the host and the parasite eclosed. New sexuals of the parasite tended to eclose earlier than those of the host. In September, males mating with winged females were observed again. The increase of dealate queen number in September results from this mating behavior and subsequent dealation (Fig. 1a).
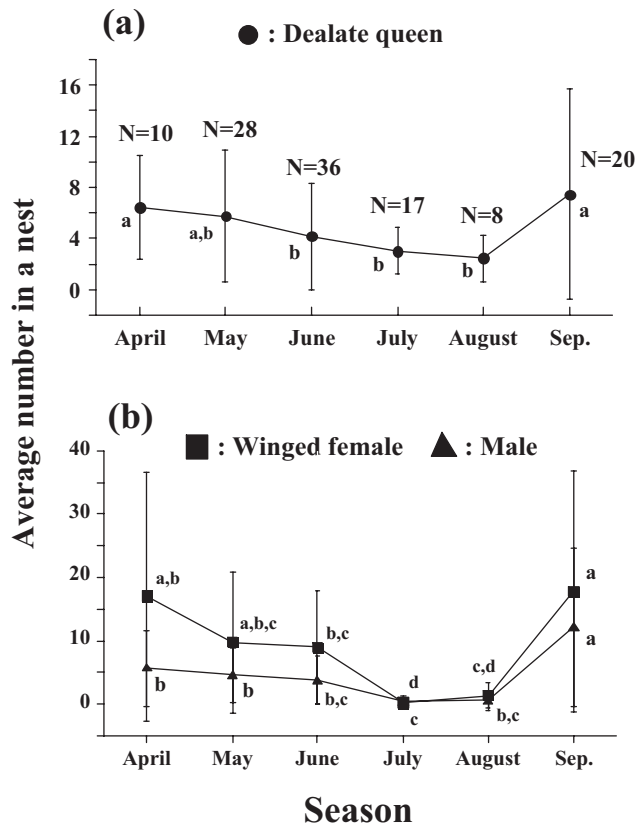

Figure 1. Seasonal change of the number of individuals of *V. nipponica* per host nest in the field from 2004 to 2006: (a) dealate queen, and (b) new sexuals (winged female sexuals and males). N means the total number of collected host colonies. Letters represent the number that differ significantly at $\alpha \leq 0.05$ based on Student t-test.

In August, the number of dealate queens reaches its lowest point (2.4 ± 1.8 queens) (Fig. 1a). Moreover dissections of queens in autumn of 2004 and 2005 showed that all dealate queens in the period had no developed ovaries and yellow bodies, and they were new adults eclosed from August to September. They suggest that most fertile queens which started to lay eggs in April die in this period, as was observed in the colonies kept in laboratory. The queens dispersed by flight in July also might start their egg production in the next spring after hibernation. Consequently *V. nipponica* queens could have a short life span.

Aggressive behavior among V. nipponica queens

In all five colonies, *V. nipponica* queens showed aggressive interactions. The behavior was directed exclusively towards each other. The attacker bit thorax, head or mandibles of the opponent after initial antennation (biting). Through biting or pulling on an antenna or leg, the attacker immobilized an opponent for several minutes (immobilization). In some cases, the attacker climbed on top of the opponent and tapped its body with its antennae (mounting) for a few seconds, while the subordinate crouched and froze. Moreover, the attacker removed the opponent from the nest by biting its postpetiole, lifting or turning it over (lifting), and carrying it to another part of the nest. During the observation, 93–301 occurrences of antagonistic behavior were recorded (0.17–0.63 times/min.) (Table 1). Of the four types of antagonistic behavior, 57.9% (N=894) were biting (Table 1). A bite was brief in duration (less than 1 min.) whereas other behaviors lasted longer. However the effect of time budget in each behavior on antagonism was unclear. Aggression continued until the subordinate queens left the nests. Egg cannibalism or proctodeal trophallaxis among the queens was not observed. Furthermore, the aggressive interactions were never directed towards host workers or queens. Because the antagonistic behavior was usually unilateral, we interpreted the attacker and opponent as dominant and subordinate.

Inseminated queens showed higher frequencies both of attacking and being attacked than uninseminated queens (Wilcoxon test: attack: $Z = -4.21$, $p < 0.01$; attacked: $Z = -4.39$, $p < 0.01$,). The behavior of individual inseminated queens during encounters with other queens indicates the existence of hierarchies with a few dominant queens in the colonies (Table 2). In colonies C and D, there were linear hierarchies among inseminated queens (Index of linearity: colony C: $h' = 0.90$, $p < 0.05$; colony D: $h' = 0.67$, $p < 0.05$) (Table 2c, d). In all colonies, one or two inseminated queens exhibited a major part of the aggressive behaviors (i.e., A1 and A2, 93.0%; B1, 69.0%; C1 55.0%; D1 and D2, 56.0%; E1 and E2, 92.0%), and can be considered "alpha queens". In colonies B and C, B1 and C1 were significantly dominant over all other queens (binominal test one tailed: $p < 0.05$). In colony D, D1 was significantly dominant over all others except D2 and D3 (binominal test one tailed: $p < 0.05$). Dissection showed that, A1, A2, B1, C1, D1, D2 and E2 had developed ovaries, yellow bodies, and more than three maturing eggs (development class: III). E1 died during the observation and could not be dissected. In contrast, the development class of 26 subordinate queens was II (4 queens, 15.4%) and I (22 queens, 84.6%). The ovaries of high-ranking queens contained significantly more oocytes than those of subordinate queens (Mann-Whitney U-test: $U = 132$, $p < 0.05$) (Fig. 2).

In all colonies, subordinate queens frequently left the nests. In colony B and C, the subordinates (B2, B3, B4, C2, C3, C6, and C7) left the nest chambers two to 25 times for

Table 1. Composition and frequency of aggressive interactions in five colonies.

	Colony				
	A	**B**	**C**	**D**	**E**
Host					
Queen	5	3	5	4	2
Worker	40	94	65	51	76
Parasite					
Inseminated queen	3	5	8	9	10
Uninseminated queen	7	3	0	3	3
Male	6	1	3	2	5
Observation time (min.)	540	540	540	480	540
Frequency of aggressive behavior (%)					
Biting	54 (58.1)	60 (54.5)	119 (49.4)	185 (61.5)	100 (67.1)
Immobilization	23 (24.7)	30 (27.2)	72 (29.9)	82 (27.1)	35 (23.5)
Lifting	15 (16.1)	17 (15.5)	43 (17.8)	28 (9.3)	14 (9.4)
Mounting	1 (1.1)	3 (2.7)	7 (2.9)	6 (2.0)	0 (0)
Total	93	110	241	301	149

Table 2. Matrices of aggressive behavior among parasite queens in five colonies: A, B, C, D, and E. Behavior was observed for 480–540 min. and the figure shows the number of aggressive acts during the observation. In colony E, two queens (E1, E3) died without interacting with others. The ovary development in each queen was classified as follows, I : without oocytes and yellow bodies; II : with one or two oocytes and no yellow bodies; III : with more than three oocytes and yellow bodies.

Table 2a) Matrices of aggressive behavior in colony A.

Attacker	Attacked			Total times attacking	Ovary development
	A1	A2	A3		
A1	–	22	21	43	III
A2	18	–	21	39	III
A3	3	3	–	6	II
Total times attacked by other queens	21	25	42	88	

Table 2b) Matrices of aggressive behavior in colony B.

Attacker	Attacked					Total times attacking	Ovary development
	B1	B2	B3	B4	B5′		
B1	–	25	23	16	6	70	III
B2	2	–	6	8		16	I
B3	1	2	–	6		9	I
B4	1	2	1	–	2	6	I
B′	1				–	1	I
Total times attacked by other queens	5	29	30	30	8	102	

Table 2c) Matrices of aggressive behavior in colony C.

Attacker	Attacked								Total times attacking	Ovary development
	C1	C2	C3	C4	C5	C6	C7	C8		
C1	–	16	17	40	17	9	11	23	133	III
C2	6	–	10	6	7	7	8	6	50	I
C3	5	3	–	3	6	2	4	3	26	II
C4	5	2	2	–	3	2	2	4	20	I
C5	2		1	3	–	1	1		8	I
C6			1	1		–			2	I
C7					1		–		1	I
C8			1					–	1	I
Total times attacked by other queens	18	21	32	53	34	21	26	36	241	

Table 2d) Matrices of aggressive behavior in colony D.

Attacker	Attacked									Total times attacking	Ovary development
	D1	D2	D3	D4	D5	D6	D7	D8	D9		
D1	–	11	9	19	12	10	13	11	9	94	III
D2	11	–	14	7	9	12	5		7	65	III
D3	3	5	–	7	2	1	9	2	2	31	I
D4	6	2	3	–	5	4	3	4	1	28	I
D5	2	5		3	–	3	4	3	4	24	II
D6	2	2	1	7	3	–	2		3	20	I
D7			3	4	1	3	–	1	1	13	I
D8	3		1		3		1	–		8	II
D9				1					–	1	I
Total times attacked by other queens	27	25	31	48	35	33	37	21	27	284	

Table 2e) Matrices of aggressive behavior in colony E.

Attacker	Attacked										Total times attacking	Ovary development
	E1′	E2	E3′	E4	E5	E6	E7′	E8	E9	E10		
E1′	–	11		6	4	8	9	2	11	10	61	no data
E2	7	–		8	4	1		6	1	7	34	III
E3′		2	–	2							4	no data
E4			1	–				1			2	I
E5				1	–						1	I
E6						–		1			1	I
E7′							–				0	I
E8								–			0	I
E9									–		0	I
E10										–	0	I
Total times attacked by other queens	7	13	1	17	8	9	9	9	13	17	103	

540 min. during the observation period (average: 0.02 ± 0.01 times / queen / min.). They might have tried to emigrate to new nests, but in the laboratory were frequently carried back into the nest chambers by foraging host workers.
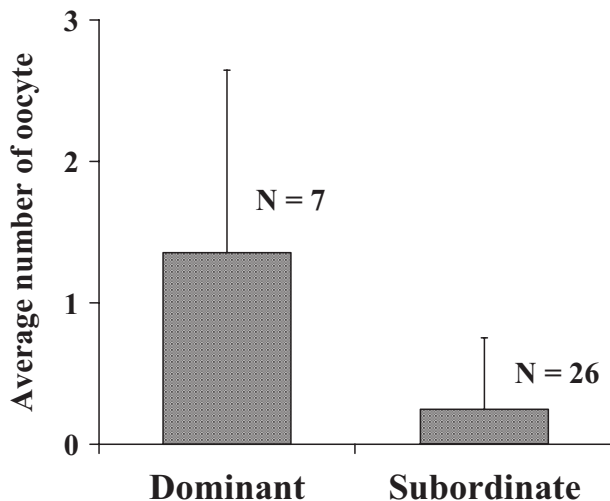

Figure 2. Average number of oocytes in the ovarioles of dominant and subordinate queens. Dominant queens had more oocytes into their ovarioles than subordinate queens (Mann-Whitney U-test: $U=132$, $p < 0.05$).

Discussion

The present study is the first time that a dominance hierarchy with antagonistic interactions has been documented in inquiline ant. Antagonistic interactions among inseminated queens of the inquiline ant *V. nipponica* led to a dominance hierarchy, and only a few dominant queens became fertile and laid eggs in the nest. The system is similar to functional monogyny known in a few myrmicine and ponerine ants (Buschinger and Winter, 1976; Buschinger, 1986; Heinze and Smith, 1990; Heinze et al., 1992; Ito, 1990, 1993, 2005).

Dominance hierarchies in social animals regulate conflicts among reproductives and stabilize social groups (Wilson, 1975). In functionally monogynous ants, subordinate queens have the option of leaving the nest to found a new society alone or with groups of workers through colony budding (Heinze and Smith, 1990; Heinze, 1993a) or of becoming a future egg-layer by queen replacement. Because *V. nipponica* appears to have a short life span, it is hardly that subordinate queens replace the dominant egg-layer in their original nests. Dominance interactions in this ant probably serve to regulate the number of egg-layers in a nest and to encourage emigration to other nests. In the laboratory, many subordinate queens left the original nests by themselves, but later were carried back into the nest

chamber by host workers. Perhaps subordinates wandering outside the nests are taken by host foragers into other host nests, and thereby emigrate to a new host colony. This encouragement of emigration provides reproductive opportunities to subordinate queens. Furthermore it may be advantageous for dominant queens to increase inclusive fitness, if they are genetically related.

The mechanisms of domination in *V. nippponica* show some unique aspects. In *Leptothorax* ants, the aggressive interactions are frequent directly after hibernation and become less once the dominant queen has started to reproduce, perhaps because then a chemical fertility signal of the alpha queen has become more important than direct physical aggression (Heinze et al., 1992; Ortius and Heinze, 1999; Ito, 2005). Dominance interactions in *V. nipponica* were also more frequent after hibernation. However, the dominant queens remained aggressive toward subordinates and other fertile queens throughout the whole reproductive season and did not cease aggression until they died. This suggests that alpha queens of *V. nipponica* do not have an inhibitive fertility signal or that the inhibition by such a chemical signal is not strong. Chemical inhibition is considered to be an evolutionary strategy to regulate conflict among reproductive individuals (Keller and Nonacs, 1993). Because of its short life span, *V. nipponica* does not need to maintain a stable dominance hierarchy for a long time and it therefore seems reasonable that it does not use chemical inhibition of subordinates. However this hypothesis should be tested by chemical analysis in future.

Why has the dominance hierarchy evolved in *V. nipponica?* Functional monogyny is likely to evolve in habitats consisting of small, scattered patches (Heinze and Buschinger, 1987, 1989; Heinze, 1992, 1993a,b). Bourke and Heinze (1994) explained this with a model of reproductive skew and severe ecological constraints; a patchy habitat should promote multiple queening with a dispersal strategy with more non-dispersers, high relatedness, high reproductive skew, and high within-colony aggression. In the case of *V. nipponica*, short-wing-queens of the host *V. emeryi* never conduct dispersal flights and found new colonies by budding. Consequently, host colonies are likely to be patchily distributed, which makes long-range dispersal difficult. In fact, the field collection data showed that the nests of *V. emeryi* were patchily distributed in the area of this study site (Ohkawara, unpubl. data). The distribution pattern of host colonies also should induce a lack of dispersal flight and within nest mating in *V. nipponica*.

Acknowledgements

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