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# Reproductive competition and colony fragmentation in the guest-ant, *Formicoxenus provancheri*

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*Abstract.* Aggressive reproductive conflicts and dominance interactions among queens are involved in establishing functional monogyny in the ant, *Formicoxenus provancheri*. Competition among potential reproductives may lead to the founding of new societies by budding or colony fragmentation.

*Key words. Formicoxenus*; Formicidae; reproductive competition; dominance; colony founding; budding.

Colony-founding strategies of ants are remarkably diverse: after mating, ant queens either found new colonies on their own, solitarily or in groups, or they are adopted into an established colony, which may subsequently split or bud[1]. The behavioral mechanisms that lead to colony fission or budding are poorly understood, but it has been suggested that aggressive interactions within the colonies might occasionally be involved[2]. During the past years, numerous studies have revealed a remarkable degree of antagonism among reproductives in many ant species. By overt aggression or stereotyped domination, queens may form hierarchies in which only one or a few high-ranking individuals lay eggs[3–7]. Subordinates either stay in the nest without reproducing or leave and attempt to found their own colonies. Emigration of subordinate queens following dominance interactions has been observed in several *Leptothorax* species[2,8]. We here report observations which show that aggressive interactions among queens may also precede colony fragmentation in the North American ant, *Formicoxenus provancheri*.

*F. provancheri* is a guest-ant which lives in the nests of the ant *Myrmica incompleta*. The workers spend much time sitting on top of their hosts, which they lick ('shampooing') and from which they also obtain food. The *Formicoxenus* nurse their brood themselves, however, and they are also capable of surviving for months without their hosts[9,10]. In contrast to most other species of ants, in *Formicoxenus* reproductive and non-reproductive females are morphologically not clearly distinct. Intergrades (intermorphs) exist between females with a fully developed thorax (gynomorphs) and females which externally resemble the typical ant workers of related species (ergatomorphs)[11,12]. Regardless of morphology, all individuals may have fully developed ovaries and a spermatheca, they may be capable of mating and may thus function as fully fertile queens. Single colonies of *F. provancheri* frequently contain several inseminated females; however, it has been shown by dissection that only one of them is fertile ('functional monogyny'[13]).

## *Materials and methods*

Colonies of *Formicoxenus* were collected for behavioral studies in Quebec, Canada[10]. Budding and aggressive interactions were observed in a colony from Mégantic (Co. de Frontenac) which during the observation period consisted of approximately 40 *Myrmica* host workers, 18 *Formicoxenus* (4 workers with spermatheca, *IJLM* in the tables; 3 workers without spermatheca, *PQR*; 8 intermorphs, *ABCDEFGK*; 3 not closely examined, *HNO*), 20 *Myrmica* larvae, and 5 *Formicoxenus* larvae. The number of hosts decreased over the observation period. All adult *Formicoxenus* were individually marked with knots of 0.025 mm copper and steel wires tied in different combinations around the neck and between propodeum, petiole, postpetiole, and gaster[14]. The behavioral data were obtained in individual sessions of 30 to 90 min per day for a total of 32 h during an eight week period following the end of hibernation. Activities of all individuals were noted at random intervals (scan sampling[15]).

## *Results and discussion*

As in other functionally monogynous ants[2,8], functional monogyny in *Formicoxenus provancheri* is established by ritualized and openly aggressive interactions among potential reproductives. The first antagonistic interactions, such as antennation bouts, grabbing, and gentle pulling on the opponent's antennae and legs, were observed 14 d after the end of hibernation (table 1). Interactions between intermorphs *A* and *B* became more and more violent until *B* first temporarily, then permanently settled in another part of the *Myrmica* nest 10 d after the first fights were observed. Rather than emigrating solitarily, individual *B* was joined by two workers, one

Table 1. Number of aggressive interactions (antennation bouts, grabbing and pulling legs and antennae, and stinging attempts) observed among nestmates in a colony of the guest-ant *Formicoxenus provancheri* (8.2 h total observation time). *A*, *B*, and *C* fought for dominance in the colony. Note that *B* is attacked repeatedly by *A* and frequently dominates other nest-mates herself.

| Attacker | Attacked *A* | *B* | *C* | *D* | *E* | *F* | *G* | *H* | *I* | *J* | *K* | *L* | *M* | *N* | *O* | *P* | *Q* | *R* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *A* | - | 8 | 2 | | | 5 | 1 | 3 | 4 | 3 | 3 | | 2 | 1 | 1 | 4 | 3 | 1 |
| *B* | | - | | | 1 | 7 | 2 | 3 | 2 | 9 | 6 | 2 | 2 | | 1 | 2 | 2 | |
| *C* | | 1 | - | | | | | 4 | 1 | 1 | | | | | 1 | 2 | 1 | 2 |
| *D* | | | | - | | | | 1 | 1 | | | | | | 1 | | | |
| *E* | | | | | - | | | | | | 1 | | | | | | | 2 |
| *F* | | | | | | - | | | | | | | | 1 | | | | |
| *G* | | | | | | | - | 1 | | | | | | | | | | |
| *H* | | | | | | | | - | 1 | | | | | | | | | |
| *I* | | | | | | | | | - | | | | | | | | | |
| *J* | | | | | | | | | | - | | | | | | | | |
| *K* | | | | | | | | | | | - | | | | | | | |
| *L* | | | | | | | | | | 1 | | - | | | | | | |
| *M* | | | 1 | | | | 2 | | | | | 1 | 1 | - | - | 1 | 1 | |
| *N* | | | | | | 1 | | | | | | | | | | - | 1 | |
| *O* | | | | | | | | | 1 | | | | | | | | - | |
| *P* | | | | | | | | | | | 1 | | | | 2 | 1 | | - |
| *Q* | | 1 | | | | 2 | 1 | 2 | | 1 | | | | | | | | |
| *R* | | | | | | | | | | | | | | | | | | |

with spermatheca (*L*) and the other without spermatheca (*R*). Why exactly these two individuals left the main colony is not clear. Prior to budding, *R* had been the ant most frequently observed grooming the *Formicoxenus* brood (19 observations in 22.5 h vs 0 to 9 observations, average 2.4, in all other *Formicoxenus*) and it had also groomed adult *Formicoxenus* at a comparatively high rate. *L*, on the other hand, had been observed 61 times outside the *Formicoxenus* nest, 'shampooing' *Myrmica* workers (vs 1 to 53 observations, average 18.1, in all other *Formicoxenus*).

Budding seemed to ease tension within the main colony: intermorph *A* had apparently consolidated its dominant position and only rarely engaged in aggressive interactions (table 2). This parallels observations in other leptothoracine ants that in the presence of high-ranking rivals, dominant ant queens may randomly launch attacks on other nest-mates, but become less agressive once the hierarchy is firmly established[2,16]. Three days after separation, the first eggs appeared in the main colony, most probably laid by *A*, which was observed depositing an egg 5 d after separation. Unfortunately, *A*

Table 2. Number of aggressive interactions observed in the same colony after colony fragmentation (7.5 h total observation time). *B*, *L*, and *R* had emigrated from the *Formicoxenus* nest and settled in another part of the *Myrmica* host colony, thus the tension between *A* and *B* was eased. However, *B* repeatedly fought with foragers from the main colony. *A* had apparently consolidated its dominant position among the remaining nest-mates and began to lay eggs. Why *F*, *G*, *J*, and *R* became heavily involved in aggressive interactions with other ants is not known. The condition of the ovaries is categorized as follows; −, completely undeveloped ovaries; ±, slightly elongated ovarioles; +, strongly elongated ovarioles with developing oocytes. The presence of sperm in the spermatheca is indicated by brackets ([+] and [±]).

| Attacker | Attacked *B* | *L* | *R* | *A* | *C* | *D* | *E* | *F* | *G* | *H* | *I* | *J* | *K* | *N* | *N* | *O* | *P* | *Q* | Ovary |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *B* | - | 6 | | | | | | | 3 | | | 1 | | | 2 | | 3 | 5 | [+] |
| *L* | | - | | | | | | 39 | 2 | 3 | | | | | | | 4 | | − |
| *R* | | | - | | | | | 4 | | | | | | | | 2 | 1 | | − |
| *A* | 1 | | | - | | | | 2 | | | | | | | | | | | +/[+]? |
| *C* | | | | | - | | | | | | | | | | | | | | ? |
| *D* | | | | | | - | | | | | | | | | | | | | [±] |
| *E* | | | | | | | - | | 16 | | | 21 | | | | | 3 | | [±] |
| *F* | | | 12 | | | | | - | - | | | | 3 | | | | | | ± |
| *G* | | | | | | | | | | - | | | | | | | | | ? |
| *H* | | | | | | | | | | | - | | | | | | | | − |
| *I* | | | | | | 1 | | | | | | - | 2 | | | | | | − |
| *J* | | | | | | | | | 2 | | | | - | | | | | | − |
| *K* | | | | | | | | | | | | | | - | | | | | − |
| *M* | | | | | | | | | | | | | | | | - | | | ? |
| *N* | 6 | | | | | | | | | | | | | | | - | | | ? |
| *O* | | | | | | | | | | | | | | | | | - | | − |
| *P* | 7 | | | 2 | | | | | | | | | | | | | | - | − |
| *Q* | 8 | | | | | | | | | | | | | | | | | | |

was accidentally lost after 8 weeks and thus could not be dissected. However, from its external morphology and the observed egg laying it is likely that it had had completely developed ovaries with a spermatheca and elongated ovarioles. In the colony bud, which settled near the *Myrmica* brood about 8 cm from the main *Formicoxenus* nest, the first eggs were observed four weeks after budding had occurred.

Intermorph *B* was observed returning into the main colony on the first day after its emigration, where it was immediately attacked and expelled by *A*. It also engaged in heavy fighting, including bites and stinging attempts, with foragers from the main colony, such as *N*, *P*, and *Q*, Similarly, it was shown in *Leptothorax* that though workers typically do not interfere in dominance interactions among queens they may start to attack subordinates which develop eggs once a dominant queen has begun to reproduce[8,17]. Our artificial nest was probably too small to contain two separate *Formicoxenus* colonies, hence foragers from the main nest began to attack *B*. Natural colonies of *Myrmica incompleta* may cover areas of more than one square meter and several colonies of *F. provancheri*, each with its own reproductive individual, have regularly been found within single *Myrmica* nests[9,10,13].

Though preliminary, our observations document for the first time dominance interactions among nest-mate ant queens in the genus *Formicoxenus*. In addition, they are of special interest as they indicate the involvement of aggressive interactions in colony fragmentation in *F. provancheri*. As yet, aggressive reproductive competition as cause of colony fragmentation has been reported only from a primitively eusocial wasp, *Ropalidia cyathiformis*, in which, following a period of high aggression, a group of individuals left the parent nest and founded a new colony nearby[18]. Similarly, in the Australian meat ant, *Iridomyrmex purpureus*, aggressive interactions among queens may not only lead to their spatial separation in different parts of the nest (oligogyny[19]), but may also be involved in budding (B. Hölldobler, unpubl.).

Though certainly not all cases of swarming, fission, or budding in ant colonies can be explained by reproductive conflicts among nestmates, it is likely that some aggression precedes colony fragmentation in those ant species in which the social organization is shaped by antagonism among reproductives, i.e., some *Leptothorax* species, several ponerines, and oligogynous ants. In species in which workers aggressively compete for the production of males but are dominated by fertile queens, e.g. the slave-making ant, *Protomognathus americanus*[20], budding might enable high-ranking workers to reproduce; aggressive interactions might facilitate colony fragmentation in this case, too.

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