Nest site limitation and colony takeover in the ant *Leptothorax nylanderi*

Susanne Foitzik and Jürgen Heinze

*Zoologisches Institut I, Universität Erlangen-Nürnberg, Staudtstraße 5, D-91058 Erlangen, Germany and LS Verhaltensphysiologie und Soziobiologie, Theodor-Boveri-Institut (Biozentrum der Universität), Am Hubland, D-97074 Würzburg, Germany

Ecological constraints on the success of independent colonies are thought to strongly shape the organization of ant societies. One of the most important factors is probably the availability of suitable empty nest sites. By population censuses, laboratory experiments, and microsatellite analyses, we investigated the colony and population structure of the small, myrmicine ant *Leptothorax (Myrafant) nylanderi* in a deciduous forest near Würzburg, Germany, where nest sites appear to be strongly limited, especially in late summer. Colonies of *L. nylanderi* inhabit cavities in rotting branches, hollow acorns, grass stems, etc. After hibernation, a temporary overabundance of empty nest sites facilitates the fragmentation of larger colonies into smaller buds, which, because the species is monogynous, are in part queenless. Nest sites become scarce in summe due to rapid decay, and both established colonies and young founding queens face a severe shortage of suitable nest sites. This leads to the fusion of established, unrelated colonies, which after initial fighting permanently merge and live together. Typically only one queen survives after fusion. Similarly, young mated queens may seek adoption in alien nests instead of founding their own colonies solitarily, and here again only a single queen survives. This temporary intraspecific parasitism may be an important first step in the evolution of obligatory permanent parasitism, which is widespread in the genus *Leptothorax*. Key words: colony takeover, competition, *Leptothorax*, nest site limitation, population structure, social parasitism.

**METHODS**

**Field site and laboratory culture**

Our study site is an open pine-oak forest with sandy soil on shell-limestone in Sommerhausen, 15 km south of Würzburg, Germany (10°02′-10°03′ E; 49°42′-49°43′ N). The interior part of the forest consists mainly of pine (*Pinus sylvestris*), while at the forest edges oaks (*Quercus petraea*) are dominant. In light areas, shrubs of elder (*Sambucus nigra*) and thickets of rose (*Rosa canina*) and blackthorn (*Prunus spinosa*) occur. Colonies of *L. nylanderi* inhabit small cavities in acorns, acorn stems, grass stems, hazelnuts, and pine cones.

Colonies were discovered either by following foragers back to their nests or by opening potential nest sites. For further investigation, all ants in the nest were collected with an aspirator and transferred to the laboratory, where they were counted and then either frozen for genetic analyses (see below) or cultured in 10 × 10 × 2.5 cm³ plexiglass boxes containing woods of Central Europe are obligatorily monogynous, i.e., their colonies contain only a single queen (Buschinger, 1968), and new colonies are established by solitary foundresses. Sexual mate during nuptial flights (Chauvin, 1947, Plateaux, 1978) and young mated queens therefore cannot easily return to their maternal nests when they fail to find an uninhabited nest site suitable for founding. How do these queens react to habitat saturation, and how does nest site limitation affect the structure of mature colonies of monogynous species?

Previous studies in a dense population of *Leptothorax (Myrafant) nylanderi* near Würzburg, Germany, suggested intense competition for nest sites (Heinze et al., 1996). In this study we present results from population genetic studies and field and laboratory experiments that clearly document that nest site fragility and habitat saturation lead to takeover of nests, the fusion of mature colonies, and temporary intraspecific parasitism, all resulting in a much higher genetic heterogeneity within societies than presumed from the life history of a monogynous and monandrous ant.
sisting of three chambers connected by small passages with a moistened plaster floor (Buschinger, 1974; Heinze and Ortius, 1991). A cavity between a piece of cardboard and a microscope slide, kept apart by a plexiglass frame, served as a nest. Dissections were carried out as described by Buschinger and Alloway (1978).

Field and laboratory experiments

We investigated seasonal fluctuations of colony composition in the Sommerhausen population by collecting and counting the individuals of all colonies found on different 32-m² plots in summer (June–July) and fall (September–October) in 2 consecutive years (1995, 1996). Queens of multiqueen colonies were dissected under a binocular microscope to examine ovarian development. We especially noted the presence of sperm in the spermatheca and also the occurrence of yellow bodies, which indicate that queens have previously produced eggs.

The durability of nest sites in the field was studied in three 2 m × 1 m observation plots, where all colonies had been located in June 1996 by observing at least five foragers leaving or entering a nest. The condition and type of the nest material was noted, and its location was marked with a small flag. After 47, 62, or 72 days, respectively, all nests were opened, their inhabitants were counted, and the condition of the nest material was examined again. As a measure of size, we crudely estimated the approximate volume, V, of the complete nest site from its diameter, r, and its length, l, assuming that nest sites are cylindrical in shape ($V = \pi r^2 l$). We did not measure the volume of the nest cavity itself because it cannot easily be determined with a large sample size. Furthermore, we observed colonies enlarging the nest cavities (Foitzik S, unpublished data), and nest volume is therefore a constantly changing parameter.

To investigate the immigration rate of colonies into empty areas in the field, we removed all colonies and potential nest sites from 4-m² plots in June and July 1995 (eight plots) and 1996 (eight plots). The colonies were censused to obtain the natural population density of the study sites. The experiment consisted of two treatments in a full-factorial design—leaf litter/no litter and nest site replacement/no replacement. In the first treatment, in half of the plots all leaf litter was removed, and the other plots remained untouched. In the second treatment, all removed inhabited nests were replaced by empty, artificial wood nests (2-3 cm thick and 6-cm long pine wood sticks with a 5-cm long and 5-mm wide hole, partially closed by a wooden splinter) in half of the plots, while in the other plots no artificial nests were added. Two months later, we thoroughly searched the plots and collected and censused all colonies found. The colony composition of the colonies that had immigrated into the plots was analyzed.

The behavior of founding queens was studied with 42 queens, collected in late September 1995, when they had at most laid their first few eggs but had not yet produced larvae or adult workers. On the same day, we collected queenless colonies. The minimum distance between the nests of founding queens and queenless colonies was 5 m. The queenless colonies were transferred into the laboratory and allowed to move into artificial nests as described above. Three hours after the colony had completely moved into the laboratory nest in the left chamber of the plexiglass box, a founding queen was added into the middle chamber. In 15 experiments, only the nest site with the queenless colony was provided; in 27 experiments, the box contained an additional empty nest site in the right chamber. We carefully observed the behavior and location of queens for 30 min per day for 4 days, and after 2 months the final location of the queen was noted.

Colony takeover was investigated in 38 arena experiments. In each test a freshly collected colony was allowed to move into a laboratory nest located in a 50-cm × 30-cm arena. The queen was marked by tying a knot of 30-μm thin copper or tungsten wire between petiole and petiole. A second newly collected colony with a differently marked queen was added into the arena 5 days later without providing a nest. We carefully monitored the arena during the next 2 h and for 50 min over the following 5 days. Aggression in the arena or the nest and the position of the queens was noted. After 7 days we transferred the nests into a three-chambered plexiglass box.

Colony takeover in the field was investigated in the following way. Colonies were collected in mid-August and at least 15 workers from each colony were frozen (−70°C) for genetic analyses. The colonies were standardized by "pruning" in 4 different size classes consisting of 38 colonies each: queenless colonies with 15 (A), 30 (B), and 60 (C) workers, and colonies with a queen and 30 workers (D). We chose colonies in such a way that for standardization at most 25 workers had to be removed. For groups A, B, and C, colonies were used that had already been queenless when collected in the field. All pupae were removed from the colonies to exclude the adoption of a colony's own young queens. The ants were then allowed to move into artificial wood nests and after 10 days in the laboratory these nests were distributed on the forest floor along a 38-m long straight line in 1-m intervals. We marked artificial nests with a flag bearing the colony number. Exactly 2 months later, on 22 October 1996, we collected all artificial nests and counted the inhabiting colonies. All colonies containing a queen were subjected to a genetic analysis (see below): the genotypes of at least 10 workers and the queen from each colony were compared with the genotypes of 2 workers from the colony that originally had moved into the artificial nest site in the laboratory. Where the queen and the 10 workers differed in their genotypes from the two workers from the original colony, additional individuals (up to 25% of all workers) were tested. In some colonies of group D, the genotypes of 10 workers from the original colony were determined.

Genetic analyses and statistics

DNA was isolated by Chelex extraction (Walsh et al., 1991, as modified by Thorén et al., 1995). Frozen ants were homogenized in 100 μl distilled water (dd H_2O) and 7 μl dithiothreitol (DTT) buffer (0.95 g DTT and 20 μl sodium acetate, pH 5.2, diluted in 6 ml distilled water). Thereafter, 10 μl of proteinase K (10 mg/ml) and 100 μl 10% Chelex solution were added, and proteins were digested for at least 1 h at 56°C. After vortexing for 10 s, the homogenate was boiled for 5 min, mixed again thoroughly, and centrifuged at 12000 rpm for 5 min.

The 25-μl reaction mixture for one polymerase chain reaction contained 2.5 μl of the ant DNA extract (approximately 10 ng DNA), 10X Taq polymerase buffer (Goldstar: 20 mM Tris HCl, pH 8.3, 50 mM KCl), 2 mM MgCl₂, 1.25 mM of each dNTP, 0.65 μM of each primer, and 1 unit of Taq polymerase (Goldstar). Polymerase chain reaction was performed with a Perkin Elmer GeneAmp 2400 thermal cycler. Locus L-18 was amplified over 32 cycles with 1 min 93°C, 1 min 54°C, and 1 min 72°C. L-18 is a moderately variable microsatellite marker with at least 11 alleles in the investigated population. Allele frequencies range from 0.022 to 0.269, the observed heterozygosity is 0.746 (Foitzik et al., 1997). Details on the electrophoretic separation and visualization of DNA fragments with Sybr-green have been described by Foitzik et al. (1997).
RESULTS

Population structure

The influence of the season and year on the frequency of colonies with different social organization in the Sommerhausen population was investigated with log-linear analysis. The frequency distribution of founding queens (A), queenless (B), monogynous (C), and multiqueen (D) colonies was strongly affected by the season ($\chi^2 = 57.70, p < .0001$). The distribution differed also, though less strongly, between the years ($\chi^2 = 15.23, p = .01$). In both years, the frequency of queenless colonies was increased in summer (Figure 1; Table 1). Furthermore, though L. nylanderi is considered to be monogynous (Buschinger, 1968; Plateaux, 1978), 20 of 207 colonies collected in fall 1995 (9.0%) and 14 of 212 colonies collected in fall 1996 (6.6%) contained more than a single queen (total

Table 1

<table>
<thead>
<tr>
<th>Factor</th>
<th>df</th>
<th>$\chi^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Social organization</td>
<td>5</td>
<td>727.19</td>
<td>.0000001</td>
</tr>
<tr>
<td>Season</td>
<td>1</td>
<td>1.01</td>
<td>.315</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>1.91</td>
<td>.167</td>
</tr>
<tr>
<td>Social organization + season</td>
<td>5</td>
<td>57.70</td>
<td>.0000001</td>
</tr>
<tr>
<td>Social organization + year</td>
<td>5</td>
<td>15.23</td>
<td>.01</td>
</tr>
<tr>
<td>Season + year</td>
<td>1</td>
<td>-0.00</td>
<td>1.000</td>
</tr>
</tbody>
</table>

Log-linear analysis of the frequency table; $\chi^2$ tests of partial association for different factors.
Table 2
Number of workers, reproductive status of queens, and genotype of workers and queens at microsatellite locus L-18 in 12 multiqueen colonies of *L. nylanderi* collected in fall 1996

<table>
<thead>
<tr>
<th>Colony</th>
<th>Queens present</th>
<th>Yellow bodies in queen(s)</th>
<th>No. of workers</th>
<th>Genotypes of queens</th>
<th>Genotypes of workers (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IX 2</td>
<td>a, b</td>
<td>a</td>
<td>40</td>
<td>HH</td>
<td>HH (12)</td>
</tr>
<tr>
<td>IX 11</td>
<td>a, b</td>
<td>b</td>
<td>55</td>
<td>GG</td>
<td>EE (12)</td>
</tr>
<tr>
<td>X 27</td>
<td>a, b</td>
<td>a</td>
<td>90</td>
<td>HH</td>
<td>DD (12)</td>
</tr>
<tr>
<td>XIV 21</td>
<td>a, b</td>
<td>a</td>
<td>69</td>
<td>EE</td>
<td>BB (12)</td>
</tr>
<tr>
<td>XVI 20</td>
<td>a, b</td>
<td>c</td>
<td>76</td>
<td>EF</td>
<td>HH (7), EE (5)</td>
</tr>
<tr>
<td>IX 23</td>
<td>a, b, c</td>
<td>b</td>
<td>15</td>
<td>DF</td>
<td>DE II (5), GG (9)</td>
</tr>
<tr>
<td>X 28</td>
<td>a, b</td>
<td>b</td>
<td>14</td>
<td>FJ</td>
<td>EE (7)</td>
</tr>
<tr>
<td>XII 8</td>
<td>a, b</td>
<td>a, b</td>
<td>52</td>
<td>II</td>
<td>GG (10), GG (2)</td>
</tr>
<tr>
<td>XIII 11</td>
<td>a, b</td>
<td>a, b</td>
<td>58</td>
<td>DL</td>
<td>FF (5)</td>
</tr>
<tr>
<td>XV 18</td>
<td>a, b</td>
<td>a, b</td>
<td>9</td>
<td>DK</td>
<td>JJ (5)</td>
</tr>
<tr>
<td>XVI 5</td>
<td>a, b</td>
<td>a</td>
<td>98</td>
<td>HH</td>
<td>LF (4), FF (5)</td>
</tr>
</tbody>
</table>

All queens and approximately 11 to 12 workers per colony were analyzed.

numbers of colonies excluding founding queens). Multiqueen colonies were considerably more frequent in fall than in summer. Two or more queens were found to be inseminated in 33 of a sample of 34 multiqueen colonies, where all queens were dissected. In some cases, the ovaries of both queens contained yellow bodies, suggesting that both queens had previously been laying eggs (Table 2). According to microsatellite analyses in 12 multiqueen colonies, nest-mate queens typically did not share alleles at locus L18 and therefore were considered not to be first-degree relatives (they could, however, be cousins, aunts, and nieces, etc.). Only in one colony were two of three queens possibly first-degree relatives. Six of the analyzed 12 colonies contained workers that appeared to be offspring of both queens; in one colony, in addition to progeny of 1 of the 3 present queens, workers were found whose genotypes did not match those of any queen (Table 2).

Nest site fragility and colony movements
Of 18, 15, and 14 nest sites found to be inhabited by *L. nylanderi* in June 1996, only 10, 9, and 6 (50, 55.5, and 42.9%) still contained ants when opened after 47, 62, and 72 days, respectively. The calculated half-life of nest sites therefore does not exceed 10 weeks in summer. Larger nest sites (overall volume, not the volume of the nest cavity) were more durable and less frequently abandoned than small nest sites (Mann-Whitney U test, U = 81.0, p < .0001, n1 = 25, n2 = 22; Figure 2). In a larger sample of colonies, size of nest sites was correlated with colony size (Spearman rank test, 300 colonies, r = .63, p < .001, Figure 3).

Colony movement was directly observed in the field during four occasions. The rapid immigration of colonies into areas from which we removed all colonies also suggests frequent colony migrations. Colonies were collected from sixteen 4-m² plots, which each had initially contained an average of 32.4±5.1 (SD) nests (i.e., more than 8 nests/m²). Resettlement of these areas was generally high: in 1 plot, 30 new colonies were found after 2 months. The immigration rate depended strongly on the availability of nest sites (two-way ANOVA: influence of nesting sites: df = 1, F = 42.52, p < .0001; influence of leaf litter: df = 1, F = 6.78, p < .05; Figure 4). In plots where no artificial nest sites were provided, on aver-
age, 4.1±3.0 (n = 8) colonies were found, in contrast to 19.6±8.5 (n = 8), where a nest site had been added for each removed colony. Colony composition differed strongly between treatments (log-linear analysis: χ² = 88.82, p < .0001). In plots with nest site replacement, fewer founding colonies (7% versus 33%) and more queenless colonies (42% versus 24%) were found compared to the plots where no nest sites had been added.

Behavior of founding queens

Two months after founding queens had been given the choice to either join a queenless colony or found solitarily without a nest site in the laboratory, 15 of 15 queens were present in the originally queenless colonies. Similarly, when queens were given the choice between a nest site inhabited by a queenless colony and an empty nest, 19 of 27 queens had entered the queenless colony. Aggression between workers and the founding queens were observed only during the first 4 days after the experiment began. Queens reacted to worker antagonism by retreating or crouching. Five queens were observed to leave the nest after being attacked by workers but reentered later and were eventually accepted by the workers. In four cases the queens were violently attacked and killed by the workers. Thirty of those colonies that had adopted founding queens were kept in the laboratory for more than a year, and all queens were still alive after this period and laid eggs, which were tended by the unrelated workers.

Competition for nest sites and colony fusion

In all experiments, where a colony without a nest was placed into an arena with a single, already inhabited nest, workers of the newly added colony discovered the nest within 15 min and entered through the nest entrance. Nest defense by resident workers was generally inefficient: the nest entrance was typically left unguarded, and fighting between alien and resident workers started only after direct physical contact. Fighting between workers did not elicit aggressive reactions by workers close by, suggesting that the resident workers do not use an alarm pheromone to recruit nest mates for the defense of their nest. Resident workers unsuccessfully tried to remove the foreign workers by carrying them away for distances of 15–30 cm. More and more alien workers entered the nest, and if the resident colony was considerably smaller, they started to carry brood into the nest within 10 min. In 8 of 38 experiments, the workers of the intruding colony could not successfully enter the nest. In 7 of these 8 cases, the resident colony was notably larger than the intruding colony; in the remaining case the resident colony contained 120 and the intruding colony 140 workers (binomial test, p = .03).

In the 30 cases where alien workers could enter the nest, they sooner or later began to attack the resident queen. In some experiments, the queen of the intruding colony was carried into the nest within the first 50 min of the experiment. In most cases, both queens were attacked by the workers of the alien colony. The queens tried to escape by crouching and generally did not leave the nest. In seven cases, queens carried
out of the nest by workers tried to reenter, even if still attacked by workers.

Aggression between workers from the resident and the intruder colony became less intense during the first 5 days of the experiment, and no fighting could be observed after 5 days. In 30 of 38 cases, the two colonies finally merged and coexisted in the same nest. In no case did the resident colony emigrate from the nest or carry out brood. Workers from both original colonies were still interacting peacefully in six additional mixed colonies after approximately 180 days.

After fusion, most colonies quickly became monogynous. In 14 of the 30 fusions, 1 of the 2 queens was killed during the process of colony merging or was escaped and remained alone or with 2 or 3 workers in the arena, where she eventually died. In 16 cases, 2 queens and workers from both colonies lived alongside in the same nest for 1 to more than 64 days. In 5 multiqueen nests, we observed aggression among the queens leading to the death of 1 queen. Here, 1 queen was already injured, but it is unknown whether injuries were inflicted by workers or by the attacking queen.

In 6 of the 30 merged nests, both queens died, and in 6 both were still alive at the end of the experiment. In 11 of the remaining 18 single-queen colonies, the queen of the larger colony survived, whereas the queen of the smaller colony survived in 7 colonies ($\chi^2 = 0.45$, ns). In five of the merged colonies, the resident queen survived ($\chi^2 = 1.87$, ns).

The occurrence of fusion of colonies and the adoption of founding queens in the field was investigated by placing 152 artificial nests inhabited by L. nylanderi colonies in the field. Two months later, 87 nests (57.2%) were still inhabited, though most of the nest sites had decayed to a certain degree. The presence of queens in nests that had been queenless at the beginning of the experiment and a strong increase in the number of workers in some nests suggested that alien queens and/or workers had invaded some of the nests and either replaced or merged with their original inhabitants. Especially those nests that had initially contained only a small group of workers and brood now were inhabited by often large, monogynous colonies (Table 3). In four colonies, belonging to groups C and D, two inseminated queens were present 2 months later. To identify whether nest sites had been completely taken over by alien colonies with a queen or whether queenless worker groups had adopted founding queens, we compared the genotypes at microsatellite locus L18 of workers taken from the colonies before the experiment and workers and queens found in the nests 2 months later. Nests either contained (1) a mixture of original and alien workers and an alien queen, (2) the original queen and workers and alien workers, (3) only an alien queen and alien workers, or (4) only individuals from the original colony (Table 4). The frequency of nest takeover did not differ significantly between colonies of similar size with and without queens (groups B and D, $\chi^2 = 0.06$, df = 1, $p = .81$). Microsatellite analysis also showed that at least 5 of the 11 examined colonies from group D had contained 2 or more matrilines before the experiment started, suggesting that colony takeover or fusion indeed occur in the field without any experimental manipulation. Note that because of the possibility that alien workers by chance had the same genotypes at L18 as the workers originally inhabiting the colony, our results give only a lower bound on colony fusion and takeover.

DISCUSSION

Nest site limitation is a common trait in populations of cavity-dwelling ants in boreal and temperate forests and strongly affects the structure of their populations. In Nearctic Leptothorax longispinosus, for example, the availability of empty nest sites influences the number of queens per nest and the number of nests inhabited by individual colonies (Herbers, 1986). Our study suggests that in its monogynous, monandrous congener Leptothorax nylanderi, nest site limitation leads to nest usurpation and temporary intraspecific parasitism.

Our study population in a pine-oak forest near Würzburg is extraordinarily dense—nest density is the highest ever recorded for Leptothorax. The abundance of nest sites apparently changes tremendously during the year. Nest sites, such as grass stems, acorns and dead twigs, are not very durable and become rare in spring and summer due to decay; half of the nest sites had become uninhabitable within 10 weeks of summer. On the other hand, few new natural nest sites had become available during this period, whereas in fall and winter new nest sites presumably are added through storms and seed production by oaks, pines, and hazelnuts.

The high percentage of queenless colonies found in early summer suggests that large colonies split into several subunits early in spring when nest sites are available. Later in the year, nest fragility and high colony density lead to strong competition for empty nests. Small colonies and founding queens appear to be affected most because, according to the positive correlation between the volume of the nest site and colony size (number of workers), they are restricted to the most ephemeral, smallest nest sites. Because of the rapid decay of their nests, small colonies probably have to move to new nests several times per year. Frequent colony movement was evident in the field from the fast resettlement of areas experimentally freed of all colonies. In experimental plots where we added an artificial nest site for each removed colony, between 52% and 96% of the original colony density of more than 8 colonies/m² was reached within 2 months in summer by immigration of colonies from neighboring areas. In these plots many colonies were queenless, once more indicating that colonies split when nest sites are available. Areas where no artificial nest sites had been provided after colony removal were repopulated to a much lower degree and especially by founding queens. Removal of leaf litter had a weaker effect on resettlement rate.
According to the presence of unrelated workers in some colonies, it appears that they do the same in the field. Queens co-occupying a nest site, and some were evidently invaded by a colony from another species. This invasion was likely from a colony fusion or from the presence of unrelated queens that were not daughters or sisters. Queens co-occupying a nest site, and some were evidently invaded by a colony from another species. This invasion was likely from a colony fusion or from the presence of unrelated queens that were not daughters or sisters.

Colonies collected in fall that contained two or more queens most likely originated from colony fusion or from the adoption of young founding queens and thus also reflect nest site limitation. In arena experiments, homeless colonies began to move into occupied nest sites if no other nest sites were available. Contrary to our expectations, both colonies stayed together after initial fighting, though after a few weeks typically only one of the two queens was still alive. According to the presence of unrelated workers in some colonies in the field, nest takeover and colony fusion also occur under natural conditions. Furthermore, 2 months after artificial nest sites with colonies of _L. nylanderi_ were placed in the field, more than one-third of these nest sites contained an alien queen, and some were evidently invaded by a complete alien colony. Larger colonies were usurped to a lower degree than smaller colonies, but the presence of a resident queen apparently did not influence takeover rate.

Founding queens readily invaded laboratory colonies, and it appears that they do the same in the field. Queens co-occupying a nest site were not closely related, suggesting that supernumerary queens were not daughters or sisters of the resident queens. Both nest takeover and colony fusion are easily understood as adaptations to habitat saturation and nest site lim-
ination in monogynous ants and might considerably increase the fitness of homeless colonies or founding queens. It is surprising, however, that resident workers do not defend their nests more vigorously against intruders and that workers from two different monogynous colonies eventually merge to form a single, stable society.

In the case of queenless colonies, one could argue that workers might benefit from their nest being usurped by a founding queen from fusion with a colony containing an unrelated queen. Both circumstances would ensure that sexual brood still present in the queenless colony will be raised to adulthood long after all related workers have died of old age. However, it first appears that most queenless nests of L. nylanderi in the Sommerhausen population are fragments of polydromous colonies, which will move together in fall (Heinze et al., 1996). Second, workers of L. nylanderi are quite long-lived (Plateaux, 1978) and will typically be able to raise all female sexual offspring still present in the colony once the queen has died. In addition, workers in queenless colonies produce their own sons from haploid eggs (Heinze et al., 1997), but can no longer do so after adopting an alien queen. Hence, we doubt that the adoption of an unrelated queen is adaptive for workers in queenless colonies.

Similarly, the adoption of colonies with queens only one queen will survive for more than a few weeks and the queens are not closely related, the workers from one colony will serve an alien queen and tend brood to which they are not closely related without further increasing their inclusive fitness. They thus suffer the fate of "intraspecific slavery" similar to those workers that are pillaged as pupae from colonies defeated in territorial contests in honeypot ants (Hölldobler, 1976, 1981) and other species, including North American Lepothorax (Alloway, 1980). In the intraspecific raids of slave-making ants (Buschinger, 1970, 1986), typically only brood is pillaged, whereas adult workers flee or are killed, probably because larvae or pupae more easily imprint to an alien colony odor (Carlin, 1988; Hölldobler and Wilson, 1990). We have previously shown that nest material has a strong influence on colony odor in L. nylanderi (Heinze et al., 1996), which probably proximately explains the easy fusion of genetically distinct colonies in this species.

Founding queens may similarly invade the nests of established, alien colonies when facing a severe shortage of nest sites. In several polynygous Lepothorax, queens mate in the vicinity of their maternal nests and thus can easily seek adoption in their original colonies (e.g., Heinze et al., 1995; Herbers and Grieco, 1994; Sülle et al., 1991; Stuart et al., 1993.). Sexually L. nylanderi mate during a nuptial flight (Chauvin, 1947; Plateaux, 1978) and their return into the maternal nests is therefore unlikely. On average about 58 young queens are produced per square meter, and most of these probably attempt to found their own colonies solitary. About 21% of the queens found cooperatively with other foundresses in a polymorphic association (Foitzik S, unpublished data). Our data show that some queen seeks adoption into alien queenless colonies, where once they are adopted they exploit the present workers to rear their own young and thus strongly increase the growth of their own colonies. Others invade colonies containing a resident queen, and as polynygyn L. nylanderi is a temporary phenomenon, only one queen will survive. Whereas resident queens of L. nylanderi typically stop to produce eggs in the fall, young adopted queens develop their ovaries and attempt to lay eggs (Foitzik S, unpublished data). As fertility presumably is important if workers take part in the decision about which queen survives (e.g., Fletcher and Blum, 1983), egg laying in fall may be a tactic of founding queens to increase their chances of replacing resident queens.

The invasion of established colonies by founding queens can be seen as temporary intraspecific social parasitism. The use of the term "parasitism" in this context is somewhat controversial. In a strict sense, "parasitism" means a "symbiosis in which members of one species exist at the expense of members of another species" (Wilson, 1971). Here we follow a less restricted usage that includes cases where one of several reproductive tactics in a species is to reproduce or rear young at the expense of conspecific individuals. The term "intraspecific parasitism" has widely been used to describe the phenomenon of birds laying their eggs in nests of other members of the same species (e.g., Andersson, 1984; Birkhead et al., 1990; Moller, 1987), of wasps and bees usurping nests built by conspecifics (Cervo and Dani, 1996; Field, 1992; MacDonald and Matthews, 1975; Makino, 1989; Taylor, 1939), and to refer to the reproduction of ant queens reducing the inclusive fitness of all other resident colony members (Elmes, 1973; Rosenberg et al., 1993). "Facultative intraspecific parasitism" has been seen as a first step toward obligatory interspecific parasitism in wasps (Taylor, 1939). In ants, interspecific parasitism is especially common in the genus Lepothorax and related taxa. Intraspecific parasitism, where foundress queens invade unrelated orphaned colonies, has hitherto only been reported from the red imported fire ant, Solenopsis invicta, where a small queen morph is thought to invade alien colonies and has apparently lost the capability of founding solitary (Tschinkel, 1996). In L. nylanderi, all foundresses, even those provided with an empty nest site, chose to invade queenless colony fragments over nesting solitarily, suggesting that intraspecific parasitism in this ant is an option open to all young queens.

We thank two anonymous reviewers for helpful comments on the manuscript. The studies were supported by the Deutsche Forschungsgemeinschaft (Heisenberg grant He 1625/6-1 to J.F., He 1625/7-1), Graduiertenkolleg "Grundlagen des Arthropodenverhaltens," University of Würzburg.

REFERENCES


