BEHAVIOURAL ECOLOGY

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Sex-ratio dependent execution of queens in polygynous colonies of the ant *Formica exsecta*

Abstract *Formica exsecta* has become an important model system for studying intraspecific variation in sex ratios. Patterns of sex allocation in polygynous (multiple queen per nest) populations of *F. exsecta* are generally consistent with the queen-replenishment hypothesis. This hypothesis states that colonies produce gynes (reproductive females) in order to increase queen number and enhance colony survival and/or productivity when the number of resident queens is low. However, the small proportion of colonies that raise gynes produce more than necessary for simple queen replenishment. It has been hypothesized that excess production of gynes may occur to reduce the frequency of accepting foreign unrelated gynes into the colony when workers cannot distinguish nestmate from non-nestmate queens. This explanation for excess gynes requires weak or no aggression between non-nestmates and is expected to lead to the selective execution of new queens by colonies that do not invest in the production of gynes. Experimental studies where gynes were introduced into natal and foreign colonies indeed suggested that polygynous populations of *F. exsecta* have a poor nestmate recognition system. Although gynes were significantly more likely to be accepted in their parental colony compared to another foreign female-producing colony, the difference was small. Moreover, encounters between workers from different colonies within the population showed very little aggression and were no more aggressive than encounters between nestmates, again suggesting a weak capacity for nestmate recognition. Our experiment also showed that colonies that produced only males executed most of the gynes that were experimentally introduced into the colony, whereas female-producing colonies accepted most gynes. This is consistent with ants using a simple rule of thumb to decrease parasitism by unrelated queens, whereby colonies selectively destroy gynes whenever gynes are not produced in the colonies.

Keywords Hymenoptera · Nestmate recognition · Polygyny · Sex ratio · Social insects

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Introduction

Sex allocation in social insects has become a general model for tests of inclusive fitness theory, sex-ratio theory and parent-offspring conflict. Sex ratios can show extreme differences between colonies of social insects, and this variation provides an opportunity to study the causes of sex ratio variation within populations (Bourke and Franks 1995; Crozier and Pamilo 1996; Chapuisat and Keller 1999a). Many studies have shown an association between sex ratios and patterns of relatedness within colonies (see Queller and Strassmann 1998), while others have shown associations between sex ratios and other ecological and demographic variables (e.g. Deslippe and Savolainen 1995; Herbers and Banschbach 1998; Passera et al. 2001).

Formica exsecta has become an important model system for studying intraspecific variation in sex ratios (Pamilo and Rosengren 1983; Sundström et al. 1996; Brown and Keller 2000; Brown et al. 2002). The haplodiploid sex determination system of Hymenoptera causes workers to be more closely related to their sisters than to their brothers. This relatedness asymmetry varies with colony structure, such as when queens mate with multiple males. Workers benefit their inclusive fitness by producing the sex to which they are most related relative to the population average (Boomsma and Grafen 1990, 1991). Thus, theory predicts that gyne (here used

synonymously with queen or reproductive female) production should occur in colonies with high relatedness asymmetry and male production should occur in colonies with lower relatedness asymmetry. In a monogynous population of *F. exsecta* in Finland, specialization on the production of males or gynes is associated with colony-level differences in relatedness asymmetry (Sundström et al. 1996; Chapuisat et al. 1997). In contrast, no such association holds in a polygynous population of *F. exsecta* in the Jura Mountains of Switzerland (Brown and Keller 2000). Colonies producing only males have greater effective queen numbers than female-producing colonies, but do not have greater relatedness asymmetry from the perspective of the adult workers that rear the brood.

Data suggest that sex ratio specialization in this population can be explained by the queen-replenishment hypothesis (Brown and Keller 2000; Brown et al. 2002). Nestmate queens in our study population are related (Liautard and Keller 2001). In polygynous ants, queens frequently remain in their mother nest after mating and eventually disperse on foot with workers to initiate new colonies nearby (Bourke and Franks 1995; Keller 1995). This mode of reproduction may lead to intense local resource competition and is often associated with dramatically male-biased sex ratios (reviewed in Bourke and Franks 1995; Crozier and Pamilo 1996). In such species, the production of new queens should occur preferentially or only in colonies that contain relatively few queens because these are the colonies that benefit most from recruiting new queens (Brown and Keller 2000). Queen lifespan is typically limited in polygynous ants (Keller and Genoud 1997) and as queen numbers decrease, local resource competition between queens is reduced. As a result there is a premium on recruiting new queens to enhance colony survival and productivity below a certain threshold of queen number (Elmes and Keller 1993). As predicted by the queen-replenishment hypothesis, colonies that produce gynes increase their effective queen number and are significantly more likely to specialize in male production the following year (Brown and Keller 2002).

Although current data support the queen-replenishment hypothesis, female-producing colonies appear to produce too many gynes to be explained solely by the need to raise queen numbers to the point of optimum productivity and survivorship (Brown et al. 2002). We previously proposed that overproduction of gynes occurs in order to dilute the effect of potentially accepting foreign gynes during the period of queen replenishment (Brown and Keller 2000). This hypothesis assumes weak or no capacity for nestmate recognition to reject foreign gynes. If colonies are unable to distinguish between foreign and natal gynes, then colonies engaged in queen replenishment may be subject to being parasitized by gynes of foreign colonies. These colonies may thus benefit from overproducing gynes as a means to decrease the cost associated with the infiltration of foreign unrelated queens.

The first aim of this study was to determine whether the key assumption of the dilution hypothesis, namely that colonies possess poor nestmate recognition, is fulfilled in polygynous populations of *F. exsecta*. The second aim of this study was to determine whether other secondary mechanisms may have evolved to prevent or decrease the level of inter-colony parasitism in species with poor nestmate recognition. It has been proposed that such a simple mechanism would be for colonies producing no gynes to selectively destroy gynes and newly mated queens that they encounter (Rosengren et al. 1993; Brown and Keller 2000). This simple rule of thumb would provide an efficient mechanism to prevent parasitism by unrelated queens in years when colonies produce no gynes. To test whether colonies producing no gynes are more likely to discriminate against gynes, we introduced gynes into foreign colonies producing males only and those producing both males and gynes and compared the probability of accepting gynes.

Materials and methods

The experiments were carried out in populations of *F. exsecta* at Les Chenevières, Les Orgères, and Pré Nouveau in the Swiss Jura Mountains. The distance between populations ranged from 1.25 to 3.83 km. Our previous work on these populations (Brown and Keller 2000; Brown et al. 2002; C. Liautard, W.D. Brown and L. Keller unpublished data) showed that each population consistently produces extremely male-biased population sex ratios with about 90% of nests producing only male reproductives, about 10% producing reproductive gynes often along with males, and a small fraction producing only workers. Therefore, as in previous work (Brown and Keller 2000; Brown et al. 2002), we categorized colonies as being either male producing (males only) or female producing (gynes and usually males as well) based on samples of pupae and observations of the developing brood within the nests. Reproductive brood are the first to emerge in mid to late July and their gender is easily distinguished owing to discrete size classes (Fortelius et al. 1987; Brown and Keller 2000) and clear morphological differences.

Queen execution

For each population, we chose 10 male- and 10 female-producing colonies for the experimental introduction of gynes. Alate gynes were collected on the surface of their natal nests as they emerged generally between 0730 and 1100 hours. We used only emergent, alate gynes to standardize condition. Generally, gynes were collected along with ca. 20 workers and 200 ml of nest material and taken to the laboratory where we provided them with water and stored them in fluon lined, 6-l plastic boxes at 25°C and a 12:12 h light cycle. Gynes were normally used the following day and none were used after more than 3 days. We also occasionally used gynes on the same day that they were collected.

We tested the behavior of workers towards these newly emerged alate gynes by placing the gynes into nests. We followed a protocol similar to Fortelius et al. (1993) except that we used only one gyne (rather than multiple gynes) per tube to avoid the possibility of worker induced aggression between gynes (e.g. Bernasconi and Keller 1996). Single gynes were placed into 50-ml Falcon tubes. To allow circulation of air, these tubes had been cut open approximately 0.5 cm from their tapered end, with fine fiberglass screening glued over the opening. To allow workers to enter the tubes while trapping the larger gynes within, we created approximately 50, 2.5-

mm diameter holes in each tube. These holes were smaller than the diameter of the gyne's abdomen but preliminary trials in the laboratory showed that workers could easily enter the tube. Between 0730 and 1200 hours, tubes containing gynes were inserted into the upper part of the mound, 5–10 cm deep, and left for approximately 24 h. We then collected the tubes, recorded whether the gyne was alive or dead, and whether the gyne was obviously physically damaged (e.g., decapitated or de-limbed) or de-alated. Experiments were not initiated during days of heavy rain.

We applied three experimental treatments. Gynes were inserted into (1) their natal colony, (2) a foreign female-producing colony, or (3) a foreign male-producing colony. Because only about 10% of colonies in these populations are female producing, most of these were used for both of the first two treatments. Sample sizes per source colony were up to 10 gynes per treatment, though these numbers were occasionally smaller (mean±SE, 8.92±0.24). Gynes were used only once.

Because results of the first experiment were suggestive of nestmate recognition of gynes by workers, we performed a second experiment designed to accentuate possible differences in cues of nestmate recognition. We employed a similar experimental design but introduced gynes collected from foreign colonies located in either (1) their own population or (2) a different population. The previous experiment allowed us to compare worker response to queens from foreign and natal colonies within populations; here the experiment allows us to compare worker response based on the source population of gynes.

At the end of each trial, all gynes were collected into 1.5-ml centrifuge tubes with the date, source colony and treatment colony recorded. These gynes were then frozen at –20°C and the spermathecae of a sample were later dissected to assess whether they had mated prior to use in the experiment. This allowed us to assess the mating frequency of gynes prior to possible dispersal and to examine whether the execution of queens by workers is related to prior mating.

We analyzed our data using repeated-measures ANOVA with arcsine-transformed mortality, under each of the three treatments, treated as repeated measures for queens collected from a common source colony. Population was treated as a factorial variable with three states, corresponding to the three study populations. We used orthogonal contrasts to determine which treatments differed significantly in queen mortality, given the a priori predictions of mortality of gynes increasing from natal colony, to foreign female-producing colonies, to male-producing colonies. Differences between populations in gyne mortality were analyzed using Fisher's LSD post hoc tests with no a priori predictions. In the second experiment, sample sizes were too small to allow analysis of the effects of specific population on queen execution. Therefore, we performed a paired t-test with one-sided probability based on the prediction that queens from outside the population would have lower survivorship.

Nestmate recognition

We tested for nestmate recognition of workers by assaying the aggressive behavior of workers when encountering colony mates versus ants from colonies of differing geographic separation. We used a paired design with three experimental treatments, replicated for 15 focal colonies. Forty workers were collected from each of 15 focal colonies. We assayed aggression for each focal colony by placing 10 workers together in a 2-l plastic box with fluon-lined walls to prevent escape. An additional 10 workers were added to the box from either (1) the same colony, (2) the nearest neighboring colony, or (3) a colony separated by at least 20 m. All ants were marked on the thorax with non-toxic colored paint to identify their colony of origin and all observations were performed blind with respect to the treatment. Ants were observed for 5 min and all instances of mandibular flaring and biting were considered to be aggressive acts and were recorded. Counts of aggressive behavior were square-root transformed and analyzed using repeated measures ANOVA. After supporting our prediction of no significant

effects, we calculated one-sided estimates of the statistical power of the analysis (the probability of rejecting a false null hypothesis) based on the prediction of greater aggression between non-nestmates.

Results

Queen introductions within populations

The proportion of alate queens killed by workers differed significantly between treatments (repeated measures ANOVA: $F_{2, 52}=72.74$, $P<0.0001$; Fig. 1). Orthogonal con-
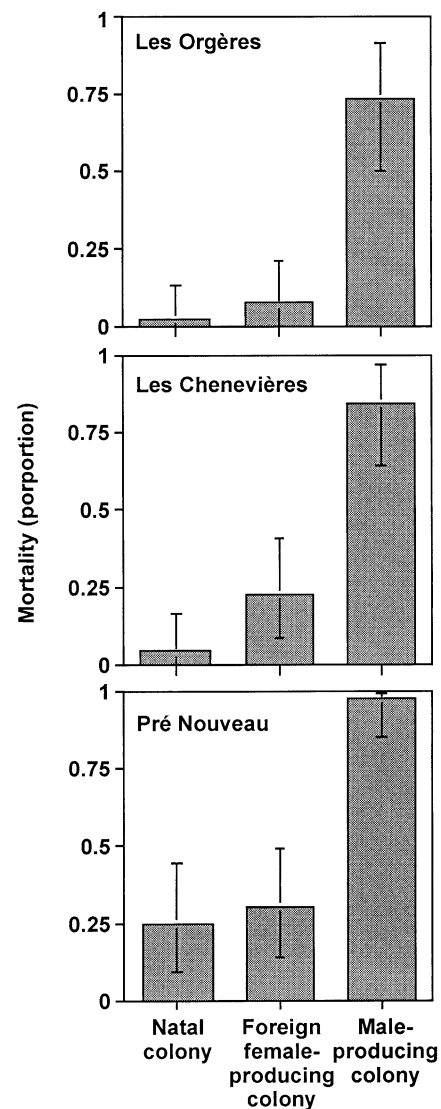

Fig. 1 Proportion of alate queens killed by workers when introduced to their natal colony, a foreign female-producing colony, and a male-producing colony within each of three populations. Means are back-transformations of angular transformed data. *Error bars* are back-transformations of 95% CI which yield slightly asymmetric values. Note that these error bars incorporate variation among colonies that did not contribute to error variation in the (pair-wise) repeated measures ANOVA

trasts yielded significant differences among all three combinations. Queens introduced into male-producing colonies had mortality ranging from 73.3% at Les Orgères to 97.6% at Pré Nouveau. In contrast, mortality of queens introduced into their natal colony was much lower, ranging from only 2.5% to 25.0% among populations ($F_{1, 26}$=115.59, $P<0.0001$). Mortality of gynes introduced into foreign female-producing colonies was also much lower than mortality in foreign male-producing colonies (7.5–30.5% among populations: $F_{1, 26}$=70.15, $P<0.0001$) but was greater than that of queens re-introduced to their natal colony ($F_{1, 26}$=5.70, $P=0.025$). Gyne execution was associated with clear bodily damage in 28 of 51 (55%) cases. Twenty-three of 51 (45%) of executed gynes were decapitated, 8 of 51 (15.7%) both decapitated and de-alated, and 5 of 51 (9.8%) were de-alated. None of 82 surviving gynes was physically damaged and only one (1.2%) was de-alated.

The effect of treatment did not differ significantly between populations (i.e., there was no significant treatment by population interaction: $F_{4, 52}$=0.38, $P=0.82$) but there was a significant difference among populations in gyne mortality ($F_{2, 26}$=10.13, $P=0.0006$; Fig. 1). Post hoc tests showed that gyne mortality was significantly greater at Pré Nouveau than both Les Chenevières ($P=0.01$) and Les Orgères ($P<0.0005$). The difference in gyne mortality between Les Chenevières and Les Orgères was not significant ($P=0.10$).

Queen introductions between populations

Mortality of queens introduced from a foreign population (12.0%) was greater, but not significantly so (paired t-test: $t=1.59$, $df=18$, $P=0.064$) than that of queens introduced into non-natal colonies within their own population (3.7%) (Fig. 2).

Mating status

Fourteen of 156 queens (9.0%) had mated prior to being collected, as indicated by sperm presence in the spermatheca. All 14 mated females retained their wings, though 4 mated females had mature ovarioles (from 1 to 4) in their ovaries. There was no significant effect of prior mating on the frequency of queen mortality (r^2=0.01, $P=0.91$) based on a log-linear analysis that accounted for the effect of treatment on queen mortality (r^2=21.18, $P<0.0001$). Only 2 of 10 mated gynes died after being introduced into female-producing colonies (0 of 5 introduced into their natal colony and 2 of 5 introduced into a foreign colony). This is comparable to the overall rate of mortality of queens introduced into female-producing colonies (Fig. 1).

Only 1 of 82 surviving gynes (1.2%) lost her wings during the experiment and she had no sperm in her spermatheca. Similarly, none of the 13 queens that became de-alate and were executed by workers had
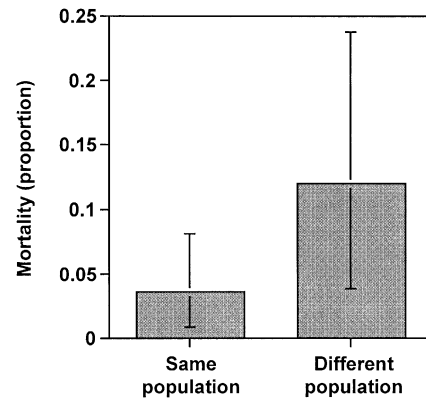

Fig. 2 Mortality of alate queens introduced into female-producing colonies from either the same population or a different population. Means are back-transformations of angular transformed data. *Error bars* are back-transformations of 95% CI which yield slightly asymmetric values. Note that these error bars incorporate variation among colonies that did not contribute to error variation in the paired *t*-test

sperm in their spermatheca. Thus there is no evidence that the wing loss that we observed was stimulated by mating.

Nestmate recognition

Aggressive acts among workers were rare during the trials, ranging from 0 to 4 occurrences of biting or mandibular flaring per 5 min. There was no significant difference in aggression among ants from colonies of varying geographic distance within the population (repeated measures ANOVA: $F_{2, 28}$=1.33, $P=0.28$). Workers directed an average of 1.80 (back-transformed; 95% CI: 1.12–2.62) aggressive acts towards nestmates, 1.44 (0.51–2.69) aggressive acts towards workers form the nearest colony, and 0.94 (0.35–1.70) aggressive acts towards workers from a distant colony. Statistical power (the probability of rejecting a false null hypothesis) was very high ($1–\beta>80\%$) given that mean aggression was slightly higher for nestmates. Aggression between non-nestmates was not greater than aggression between nestmates and in all cases levels of aggression were extremely low.

Discussion

Our data indicate that nestmate discrimination in polygynous populations of *F. exsecta* is not well developed. Although the mortality of introduced queens was significantly greater in foreign colonies than within the natal colony, the difference was not very pronounced. In particular, we found that about 80% of the gynes were accepted by foreign female-producing colonies. We also found that the rejection rate was not much higher when gynes were introduced in a foreign nest from another populations compared to foreign nests of the same

population, indicating relatively weak nestmate recognition both within and between populations.

Our behavioral observations of aggression between workers also support the idea of a poorly developed level of nestmate recognition in *F. exsecta* populations. Workers are extremely aggressive towards foreign species (W. D. Brown, personal observation) but are extremely benign towards conspecific workers from other colonies within their own population. Colonies within populations appear to originate often from the same gyne lineage, based on the observation that mitochondrial haplotypes are often uniform within populations but different between populations in the Swiss Jura Mountains (Liautard and Keller 2001). This suggests that the absence of nestmate recognition may be caused by a lack of genetic diversity at recognition loci. However, there is substantial variation at nuclear microsatellite loci (Brown and Keller 2000), possibly due to male dispersal. In contrast to the general lack of aggression that we observed, Cherix et al. (1980) reported intense aggression between workers from a peripheral colony of polygynous *F. exsecta* and workers from more centrally located nests within a population in the Swiss Jura Mountains. Rosengren et al. (1986) also reported inconsistent patterns of nestmate discrimination for polygynous *F. exsecta* on islets in the Gulf of Finland. In one case workers introduced into foreign colonies of the same islet were rejected while ants from an islet 7 km away were accepted. Comparatively, polygynous *F. truncorum* colonies accepted workers transferred from nests on nearby islets (Rosengren et al. 1985), whereas *F. uralensis* accepted introduced workers from the same population but rejected workers from two foreign populations (Rosengren and Pamilo 1983).

Our data also support the hypothesis that the rate of acceptance of foreign gynes was influenced by whether or not recipient colonies produced gynes. With weak nestmate recognition this simple rule of thumb prevents parasitism by foreign gynes. Colonies producing no gynes are expected to selectively destroy all gynes entering the colony. Accordingly, our data showed a significant difference in response to foreign gynes by male- and female-producing colonies. Mortality of queens introduced into male-producing colonies averaged over 87% compared to only 20% in female-producing colonies. Alate queens may thus have a good chance of successfully entering foreign female-producing colonies but very little chance to enter successfully the majority of the colonies, which are male-producing. This is the first demonstration of sex-ratio dependent execution of foreign queens. Fortelius et al. (1990) reported similar patterns of queen execution in *F. lugubris* (now classified as *F. paralugubris*) but small sample sizes apparently precluded statistical analyses.

Poor nestmate recognition may therefore explain why we see levels of gyne production far beyond what is necessary to replenish queen number with the colony. Alate queens that enter foreign colonies and take over a share of reproduction contribute nothing to the inclusive fitness of other individuals in the colony, and thus there will be strong selection to stop these foreign queens from reproducing. For male-producing colonies, the solution is for workers to simply kill all alate queens. For female-producing colonies with poor nestmate recognition, the solution may be to flood the colony with daughter queens during the period of queen dispersal to out compete foreign queens numerically for limited opportunities to become reproductives. Queen number can then be pared down prior to the next breeding season, as occurs in the Argentine ant *Iridomyrmex humilis* (Keller et al. 1989). This is similar to the "competition model" of Rosengren et al. (1993), which holds that polygynous colonies may accept related queens in order to decrease the proportional reproductive output of foreign queens when there is a high risk of foreign queens entering the nest. Production of excess queens may then achieve the secondary benefit of dispersing daughters into foreign colonies, further escalating investment in gyne production. Nevertheless, the decision of whether to produce gynes must ultimately depend on the need for queen replenishment within the colony, otherwise all colonies with sufficient resources would be selected to produce gynes for dispersal into foreign nests.

Currently, it is difficult to determine whether a similar phenomenon of overproduction of gynes in female producing nests also occurs in other *Formica* species or ants of other genera. Foreign gynes have been introduced in several species of *Formica*, with variable patterns of acceptance. Workers of polygynous *F. polyctena* colonies killed mated queens introduced from neighboring nests (Rosengren and Pamilo 1983, cited in Rosengren et al. 1986). In contrast, Rosengren et al. (1986) found that both mated and virgin queens were accepted into all of seven "semi-natural" *F. truncorum* nests (large numbers of workers within natural nest material from their original nest), two of which already possessed queens and five of which were orphaned. Both experiments were performed outside the period of the production of reproductive brood, making the results difficult to interpret. Fortelius et al. (1993) found that *F. paralugubris* gynes experimentally introduced into nests specializing in gyne production are tolerated only during the active production of sexual brood. Execution of gynes increased as production of sexual brood began to wane and alate gynes were no longer present in the nest. They did not introduce gynes into male-producing nests.

About 9.0% of *F. exsecta* queens had mated prior to the experiment. These gynes had most likely mated within the nest prior to dispersing by flight or on foot to an adjacent colony. Occasional mating within the nest has been reported for *F. rufa* (Escherich 1906, cited in Fortelius et al. 1993) and Chapuisat and Keller (1999b) report a very high rate of local mating in *F. paralugubris*. Fortelius et al. (1993) found that unmated gynes were accepted at about twice the frequency of mated gynes by polygynous nests of *F. paralugubris*, although mating status may have been confounded with female age. We found no effect of mating status on queen mortality in *F.*

exsecta, though subtle effects cannot be ruled out without a larger sample size.

In conclusion, colony sex-ratio dependent execution of queens is consistent with a rule of thumb strategy to dilute the effect of accepting foreign, unrelated gynes given a poor capacity for nestmate recognition in polygynous populations of *F. exsecta*. In female-producing colonies needing to replenish queen numbers, colonies may be driven to excessive production of gynes to numerically out compete foreign gynes that may attempt to enter the colony.

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