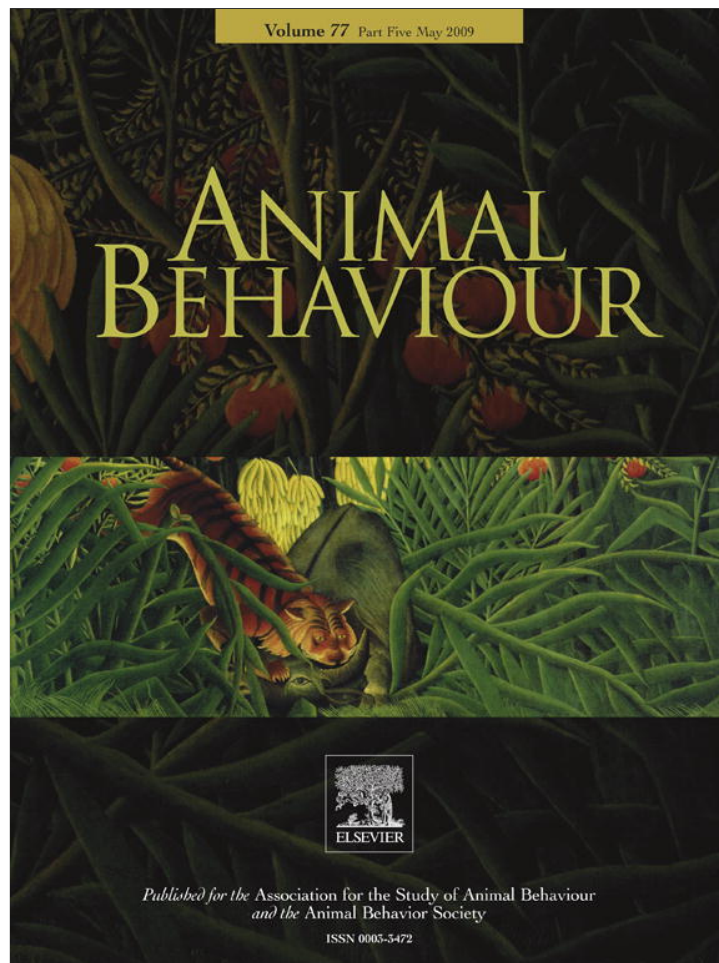


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Influence of queen phenotype, investment and maternity apportionment on the outcome of fights in cooperative foundations of the ant *Lasius niger*

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Cooperative colony founding (pleometrosis) in social insects is an ideal model for investigating how cooperation and competition shape social behaviour among unrelated individuals. In many ant species, foundress associations are more competitive and the colonies survive better compared with single-queen colonies. However, cooperation among queens breaks down at the time of emergence of the first workers, and all but one queen are eliminated. Because no sexuals are produced in incipient colonies, the surviving queen will monopolize the future reproductive success of the colony, while defeated queens will have zero fitness. We examined factors affecting queens' survival prospects during reversion to single-queen colonies in cooperative foundations of the ant *Lasius niger*. By combining phenotypic and genotypic analyses, we determined how queen's size, individual investment and maternity apportionment influence the outcome of fights. Larger queens were more likely to survive fights. However, smaller queens survived up to one-third of the fighting. By contrast, neither weight loss at the time of a fight outbreak, a measure of queens' relative investment in brood production, nor maternity apportionment influenced the outcome of fights. Moreover, investment of cofoundresses and partitioning of reproduction were not adjusted to queen's size, suggesting that reproductive competition among queens does not occur before the emergence of the first workers. These results lead us to consider pleometrotic associations in *L. niger* as a 'best of a bad job', whereby the benefits of joint founding and the probability of surviving the conflict might be sufficient for smaller queens to embark on cooperative foundations.

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The degree to which cooperation and competition shape social behaviour is a major issue of studies on the evolution of sociality. Cooperation is favoured when collective actions improve the animals' abilities to face stressful ecological factors. However, individual-level selection fosters competition over limited resources, mates or reproduction among group members and may override group-level benefits, thereby reducing the incentive for group membership (Hamilton 1964; Vehrencamp 1983; Strassmann & Queller 1989). Conflicts are increased when competition is strong and/or genetic relatedness low within groups. When individuals are unrelated, the benefits associated with inclusive fitness (Hamilton 1964) do not apply. In this context, the evolution of cooperation is driven by the benefits of mutualism, reciprocity or group selection (Mesterton-Gibbons & Dugatkin 1992), three concepts that put forward the conditions under which the combined benefits of group activity outweigh the costs of within-group competition.

Colony founding in ants provides an interesting model for studying the interplay between cooperation and conflict in the absence of relatedness and indirect fitness. Founding is the most vulnerable stage in the life of ant colonies because of predation, strong competition among incipient colonies or low resistance to adverse climatic conditions, and less than 1% of founding queens generally survive (Hölldobler & Wilson 1990; Tschinkel 1992a, b; Herbers 1993). In several species, newly mated queens (foundresses) found new colonies independently, that is, without the help of a workforce. Founding is usually claustral, meaning that queens seal themselves into a chamber and rear their first brood solely from stored fat and histolysis of their wing muscles. Foundresses can either start a nest solitarily (haplometrosis) or aggregate with other females during nest initiation (pleometrosis). Queens from pleometrotic foundations are usually unrelated, indicating that they aggregate independently of their kinship (Rissing et al. 1989; Sasaki et al. 1996; Heinze et al. 2001; but see Nonacs 1990). They show cooperative behaviours by sharing nest excavation, caring for the eggs jointly, grooming one another or trophallaxis (Waloff 1957; Hölldobler & Carlin 1985; Sasaki et al. 1996). Several benefits associated with group nesting have been proposed to account for the evolution of pleometrosis (reviewed in

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Strassmann 1989; Bernasconi & Strassmann 1999). First, multiple founding queens have lower mortality rates through the early phase of colony initiation than solitary founding queens (Waloff 1957; Bartz & Hölldobler 1982; Jerome et al. 1998). Second, pleometrotic foundations produce larger initial broods and workforce in a shorter period of time (Bartz & Hölldobler 1982; Tschinkel & Howard 1983; Mintzer 1987; Adams & Tschinkel 1995; Trunzer et al. 1998; Sasaki et al. 2005). High initial worker production enhances the survival rate of the foundations, because colonies with the most workers are more likely (1) to resist intraspecific brood raiding caused by competition among young colonies and to succeed in raiding other foundations (Bartz & Hölldobler 1982; Rissing & Pollock 1991; Adams & Tschinkel 1995; Jerome et al. 1998; but see Pfennig 1995), (2) to prevent usurpation by queens attempting to relocate (Balas & Adams 1997), (3) to increase foraging success (Helms Cahan 2001) or (4) to defend against predation by adult colonies (Jerome et al. 1998). Joint nesting also increases colony fitness in other contexts, for example (5) by improving resistance to adverse abiotic conditions (temperature, precipitation; Tschinkel & Howard 1983; Pfennig 1995; Helms Cahan 2001), (6) by reducing costs associated with nest construction and maintenance (Pfennig 1995; Helms Cahan 2001) or (7) by allowing production of reproductives at an earlier stage (Vargo 1988). Similar benefits have been proposed to account for the evolution of cooperative foundations in other social insects, including termites (Thorne 1982), wasps (Strassmann et al. 1988; Tibbetts & Reeve 2003), bees (Soucy et al. 2003) and thrips (Morris et al. 2002; Bono & Crespi 2006).

However, whereas cofounding increases individual and colony survival, it is also a perilous venture for the individual queen. Cooperation among ant queens breaks down at the time of emergence of the first workers, and all but one foundresses are eliminated, either by direct fighting among the queens (Hölldobler & Carlin 1985; Rissing & Pollock 1987; Heinze 1993; Balas & Adams 1996) or by workers attacking and culling supernumerary queens (Bartz & Hölldobler 1982; Tschinkel & Howard 1983). Because no sexuals are produced in incipient colonies, the surviving queen will monopolize the entire future reproductive success of the colony, while defeated queens will have zero fitness. Foundresses in a group therefore face a trade-off. On the one hand, each queen benefits by increasing investment in the foundation (e.g. by laying eggs or caring for the brood), because a large worker production improves colony survival and growth. On the other hand, increasing investment may be costly to individual queens if it reduces the probability of surviving fights, for instance by decreasing their condition and hence their fighting ability, or by lowering the subsequent fecundity of the surviving queen (Reeve & Ratnieks 1993).

Despite the frequent occurrence of foundress associations, the factors that govern which queen survives are poorly studied in ants and data sometimes remain controversial. Detailed studies have been carried out on the fire ant, *Solenopsis invicta*. Differences in queen phenotype, particularly body weight or size, have been reported as central components of queen survival in this species (Balas & Adams 1996; Bernasconi & Keller 1999). Queens are more likely to survive reduction to monogyny (single-queen colonies) if they are initially heavier than their cofoundresses, or if they lose less weight during brood rearing (Bartz & Hölldobler 1982; Balas & Adams 1996; Bernasconi & Keller 1996). However, Bernasconi & Keller (1998) later showed that survival prospects are affected not only by relative body mass at the time of fights but also by other phenotypic traits such as queen size (i.e. head width), with larger-headed queens being more likely to win the fights. In addition, queens adjust their investment to relative fighting ability. The larger queen of a pair invests less in the foundation (i.e. she loses

relatively less mass) than her unfamiliar nestmate, suggesting that losing less mass and maintaining a better condition than the cofoundress grants direct benefits in fights. Other factors have also been reported to influence queen survival in *S. invicta*, such as increased queen productivity or proximity to the brood (Bernasconi et al. 1997; Adams & Balas 1999), but these results have not been confirmed, since maternity and queen survival were not associated in other experiments (Balas & Adams 1996) and manipulating the queen's share of maternity among the worker brood did not affect survival significantly (Bernasconi & Keller 1996). Finally, the outcome of fights between queens may also be influenced by the workers' genetic interests. Because group nesting usually involves unrelated queens, the inclusive fitness of workers depends directly on which of the queens survives. When workers participate in the elimination of supernumerary queens, there should be strong selection pressure to favour their own mother over unrelated queens. Using brood exchange experiments between queens, Adams & Balas (1999) showed that workers of *S. invicta* are more likely to bite unrelated queens than their mother, supporting kin discrimination. Yet, queens gain no substantial advantage from the outcome of the fight when a preponderance of the workers are their own daughters (Balas & Adams 1996; Bernasconi & Keller 1996).

In this study, we examined how queen phenotype, individual investment and maternity apportionment influence the outcome of fights during reversion to monogyny in cooperative foundations of the black garden ant, *Lasius niger*. Foundress associations may account for 18% of newly founded colonies in some populations (Sommer & Hölldobler 1995). However, mature nests of *L. niger* are strictly monogynous. Reversion to monogyny is initiated by the queens, which start fighting with one another soon after emergence of the first workers. Queens of *L. niger* live up to 29 years (Kutter & Stumper 1969) and mature colonies can reach 50 000 workers (Fjerdingstad et al. 2003). Production of the first sexuals (males and new queens) starts a few years after foundation; thus, the surviving queen monopolizes the entire future reproductive success of the colony. Because of these life history characteristics, foundresses of *L. niger* are probably under strong survival selection, making this species an interesting model to study the relationship between phenotype, cooperative investment and success in fights.

We considered three factors that have been proposed to influence survival prospects of queens in ants. For this purpose, we used queens of the same initial weight at the time of foundation. First, we investigated whether investment of individual queens during foundation and, hence, queen weight at the time of emergence of the first workers affect the outcome of fights. If survival is positively associated with queen weight, then heavier queens are predicted to have a higher chance of winning the competition. The extent of cooperative investment in brood production was estimated as queen mass loss; differential investment may indeed translate into differential loss of mass during colony founding (Bernasconi et al. 1997). We tested whether individual investment is associated with the queen's size (head width), and whether differential mass loss within queen pairs reflects the number of worker offspring produced by each queen. Second, we examined whether queen size affects the probability of surviving fights. If queen head size has a positive effect on survival, then larger queens are expected to have a higher chance of winning the conflict. Third, we determined whether relative maternity is associated with queen survival. If workers are able to favour their mother selectively through preferential feeding or during fights, then the queen that produced the most workers is expected to have higher survival prospects. Queen maternity at the time of a fight was assessed for adult workers and worker larvae, using microsatellite markers.

METHODS

Study Species and Sampling

Males and female sexuals of *L. niger* take part in large mating flights involving many colonies. After mating, queens initiate new colonies in small burrows in the ground, either alone or in association. Cofounding queens are presumably unrelated. Previous studies showed that joint nesting translates into an advantage in survival and colony growth (Sommer & Hölldobler 1992, 1995). Queens in two-foundress nests outlive solitary founding queens, and survival rates of multiple-foundress colonies exceed survival rates of single-foundress colonies. Moreover, pleometrosis has a positive effect on early colony growth and competition, since it confers higher worker production rates, and larger colonies are more successful in brood raids. Direct queen–queen aggression plays the major role in determining which queen will survive reversion to monogyny. Workers may join the fights later, without showing any particular preference for a queen. Nevertheless, they could influence the outcome of fights indirectly, by preferentially feeding the most fecund queen, which in turn will have a greater chance of winning contests owing to a substantial weight gain (Sommer & Hölldobler 1995).

Freshly mated and dealated queens of *L. niger* were collected on the ground in Brussels, Belgium, within a few hours of a large mating flight on 17 June 2006. They were weighed (± 0.1 mg) immediately after the nuptial flight (Mettler AT261 Delta Range balance). We assigned 312 queens to pairs ($N = 156$) of the same (± 0.1 mg) initial weight ($\bar{X} \pm SD = 26.28 \pm 2.02$ mg; range 20.6–30.9 mg), and housed them in moist glass tube nests closed with a cotton plug without food. Queens were paired randomly with regard to the collection place, so that females associated in the same foundation were almost certainly not related. Foundations were kept at 25 °C in the dark until the first workers completed development. After emergence of the first workers, the queens were weighed again. They were marked with a small dot of paint on the thorax (enamel, Humbrol) to identify the individual foundresses of an association, and put back in their nest. The nests were opened by removal of the cotton plug, and ants were fed diluted sugar and insect fragments every other day. They were reared under a 12:12 h light:dark cycle. Handling of foundresses had no weight- or size-related consequences for subsequent queen survival (Pearson correlations on survival versus queen weight and size during 1 week following foundation and emergence: all $P > 0.10$).

Colonies were observed daily until queen execution (see below). They were followed for a maximum of 28 days after worker emergence. We chose this period for two reasons. First, it corresponds to the mean time reported for the elimination of all but one queen as a result of fights (Sommer & Hölldobler 1995). Second, increasing the period of observation between emergence (thus, weighing) and fighting may bias the data because of natural variation in queen weight over time, and an increased effect of cofounding factors on queen mortality not linked with queen fights. Brood production at the time of execution, that is, the number of larvae, pupae and workers in each foundation, was counted. Individuals (brood and workers) were stored in EtOH 98% for subsequent genetic analyses.

We considered only healthy colonies in which a single queen survived. We excluded colonies in which one or both queens died before workers completed development ($N = 61$) and where foundations produced brood that did not give rise to adult workers ($N = 3$). There was no significant difference in the initial weight of queens that survived and successfully produced workers and queens that failed to do so (mean initial weight \pm SD: successful:

26.88 ± 1.86 mg, $N = 92$; failures: 26.43 ± 2.26 mg, $N = 64$; t test, $t_{154} = 1.28$, $P = 0.20$). In addition, 45 successful foundations had not returned to monogyny 28 days after worker emergence. Overall, our sample consisted of 47 two-queen foundations.

Queen–Queen and Worker–Queen Interactions

Once the first adult workers had emerged, we examined colonies at least twice a day for instances of threats, fighting or queen deaths. When they occurred, agonistic interactions between queens and/or between queens and workers were recorded using a digital camera (Panasonic WV-CL920). Video recordings were analysed during repeated playbacks to observe the behaviour of the queens and the workers during execution of the supernumerary queen.

Early Individual and Combined Investment

Because queens do not forage, individual investment in producing and feeding the brood can be estimated as weight loss before worker emergence. Previous studies indeed showed that the amount of the first worker brood is positively correlated with weight loss of solitary founding queens in *L. niger* ($F_{1,63} = 15.71$, $r^2 = 0.20$, $P < 0.001$; S. Aron & L. Passera, unpublished data). Weight loss is given as the proportion of the initial weight at the time of the nuptial flight. Combined weight loss corresponds to the total weight loss of both queens as a proportion of their total initial weight.

Morphometrics

We used head width as an estimate of queen size, because of its high correlation with other body measurements in ants (Schwander et al. 2005; Fournier et al. 2008). Moreover, differences in head width are associated with relative weight loss of cofoundresses and with queen survival in at least one other ant, *S. invicta* (Bernasconi & Keller 1998). The maximum head width (between the eyes) of the queens was measured at a magnification of $\times 50$ (± 0.1 mm) using a MZ6 stereomicroscope (Leica Microsystems, Wetzlar, Germany). To test for repeatability, measures were taken twice on 20 queens randomly selected in our study population. Repeated measures differed on average by only 0.02 mm and were highly correlated (Pearson correlation: $r_{18} = 0.98$, $P < 0.001$).

Genetic Analyses

Kinship analyses were carried out for 20 two-queen foundations using microsatellite DNA. For each colony, we genotyped both queens and a sample of workers ($\bar{X} \pm SD = 16.29 \pm 5.38$). DNA was extracted from body parts of individual ants (one leg of queens and the thorax of workers) using a standard proteinase K/SDS and phenol/chloroform protocol (Sambrook & Russell 2001). We genotyped individuals at four microsatellite loci previously developed for *L. niger*: Ln1-5, Ln10-53, Ln10-174 and Ln10-282 (Fjerdingsstad et al. 2003). In our sample, these markers are independent and have 18, 15, 17 and 16 alleles, respectively, and a level of observed heterozygosity ranging from 0.56 to 0.93. Genotypes were obtained by polymerase chain reaction (PCR) amplification. Reactions were performed in 10 μ l volumes containing 2 μ l of DNA (10 ng of template DNA), 1 μ l of 10 \times PCR buffer (Qiagen Inc., Valencia, CA, U.S.A.), 0.2 μ l of 10 mM dNTP, 0.3 μ l of 10 μ M of each primer (the forward primer was 5' end fluorescent dye-labelled, the reverse primer was unlabelled), 0.05 μ l of Taq DNA polymerase (Qiagen) and double-distilled water. Loci Ln10-53 and Ln10-282 were multiplexed. Amplifications were performed on a Peltier Thermal

Cycler (MJ Research PTC-200) using the cycling profile: 94 °C for 3 min; 35 cycles at 94 °C for 45 s, 55 °C for 45 s, and 72 °C for 60 s; and a final extension at 72 °C for 30 min. PCR products were analysed on an ABI 3100 capillary sequencer and alleles were analysed using ABI GeneMapper version 3.0 software (Applied Biosystems Inc., Foster City, CA, U.S.A.). Paternal genotypes and queen mating frequency were inferred through microsatellite analyses of the sperm in the queen's spermatheca. Queen abdomens were dissected in the extraction solution. Intact spermathecae were opened with forceps and the sperm was removed with a micropipette. The spermathecal content was amplified at all four loci as described above.

Sibship was inferred using Colony version 1.3 (Applied Biosystems, Foster City, CA, U.S.A.) to identify groups of full and half sib offspring using a maximum-likelihood approach for relationship estimation (Wang 2004). This procedure was straightforward because queens' and fathers' genotypes were known and because of the haploidy of males since, for each locus, a male gives the same allele to all his offspring.

Statistical Analyses

The unequal contribution of each queen to worker production (i.e. the reproductive skew B) and the associated probability level for each group and across all groups were calculated using the program Skew Calculator 2003 developed by P. Nonacs (<http://www.eeb.ucla.edu/Faculty/Nonacs/skew%20calculator%202003.htm>). This index is equal to zero for randomly distributed reproduction, positive when skew is higher than random and negative when more evenly distributed than random.

Parametric standard tests were used on data showing normality and homoscedasticity; in other cases, nonparametric procedures were applied. Unless otherwise specified, means are presented \pm SD. All statistical tests were two-tailed; they were carried out with the computer program SPSS 13.0 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Forty-seven pleometrotic foundations were reduced to a single queen within 28 days of worker emergence. Agonistic interactions between queens and/or between queens and workers were recorded for five colonies. As previously reported in *L. niger* (Sommer & Hölldobler 1995), queens started fighting with one another. They engaged in fierce contests; injuries were often severe, including loss of legs and antennae. Worker attacks also occurred; they bit a single queen, usually the more injured one. No worker aggression was observed following the death of one queen.

Queen Weight Loss, Size and Brood Production

The mean time to emergence of the first workers \pm SD was 55.55 ± 6.30 days; it was not associated with the initial average weight of queens (standardized regression: $F_{1,45} = 0.10$, $r^2 = 0.002$, $P = 0.75$). Weight loss of queens (estimated as the proportion of the initial mass) at emergence of the first workers was positively associated with their initial weight at foundation. Heavier queen pairs lost a significantly higher combined weight than lighter queen pairs ($F_{1,45} = 9.11$, $r^2 = 0.17$, $P = 0.004$). Similarly, queen head size was positively associated with relative weight loss; the larger the queens, the more they invested in colony foundation ($F_{1,90} = 4.56$, $r^2 = 0.05$, $P = 0.035$). The absolute loss of mass combined for the two nestmate queens was positively associated with total brood production (workers, pupae and larvae; $\bar{X} \pm \text{SD} = 92.68 \pm 49.98$); the more they produced brood, the more they lost weight ($F_{1,45} = 6.33$, $r^2 = 0.12$, $P = 0.016$). Consistent with these results,

colonies headed by initially heavier queens produced more brood than colonies with initially lighter queens ($F_{1,45} = 6.63$, $r^2 = 0.13$, $P = 0.013$).

However, within each association cooperative queens lost significantly different amounts of weight between the nuptial flight and the emergence of the first workers. The mean relative weight loss was equal to $30.05 \pm 9.15\%$ and $18.03 \pm 9.33\%$ for the lighter and heavier queens, respectively (paired t test: $t_{46} = -9.36$, $P < 0.001$). Individual weight loss was not associated with the relative head width of queens within the same association ($t_{45} = -0.09$, $P = 0.93$).

Survival prospects were not associated with the queen's relative body weight (lighter or heavier) at the time of emergence of the workers (Fisher's exact test: $P = 0.84$; Fig. 1). The surviving queens had lost on average $23.70 \pm 8.95\%$ of their initial body mass, while the losing queens had lost $24.53 \pm 12.85\%$ (paired t test, $t_{45} = -0.37$, $P = 0.71$). In addition, the heavier queen's probability of survival did not increase with the magnitude of her weight advantage (logistic regression: $\chi^2_1 = 0.21$, $P = 0.65$).

Queen Relative Maternity

The distribution of genotypes in parent-offspring combinations was consistent with queens being mated with one to four males ($\bar{X} \pm \text{SD} = 1.83 \pm 0.95$). The number of mates per queen was not associated with either initial body weight (Spearman correlation: $r_s = -0.01$, $N = 30$, $P = 0.95$) or head size ($r_s = -0.09$, $N = 30$, $P = 0.65$). The same result was found when queens were divided into singly and multiply mated queens (independent t tests on initial body weight or head size: both $P > 0.59$).

Queen maternity was assigned unambiguously in 17 associations. Genetic analyses showed that queens did not share maternity equally. In eight associations (47%), one queen produced significantly more offspring than the other (mean B index \pm SD = 0.13 ± 0.35 ; range -0.06 – 0.37). Over the 17 pairs, the contribution of the queens to the production of descendants was, however, independent of queen weight loss; the queens losing more weight did not mother a larger proportion of the brood (paired t tests on relative weight loss: $t_{16} = 0.16$, $P = 0.88$). Similarly, apportionment of maternity was independent of queen size; larger queens did not mother a larger proportion of the brood (paired t tests on relative size difference between queens:

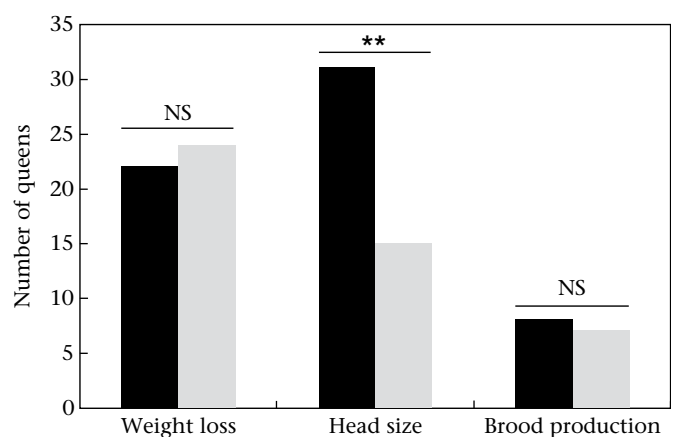


Figure 1. Number of queens surviving reversion to monogyny according to their relative weight loss (i.e. a measure of individual investment), head size and contribution to the brood in two-queen foundations of the ant *Lasius niger*. Black bars: number of winning queens that were the heaviest, the largest or the most productive of the association; grey bars: number of winning queens that were the lightest, smallest or less productive of the association. Fisher's exact tests: ** $P < 0.01$.

$t_{16} = 0.21$, $P = 0.83$). The same results were obtained when we considered only the eight associations with significant reproductive skew (Wilcoxon signed-ranks tests on relative weight loss: $Z = 0$, $P = 1$; on relative size difference between queens: $Z = -0.43$, $P = 0.67$). By contrast, over all colonies the relative contribution of queens to brood production was positively and significantly associated with queen mating frequency ($r_s = 0.45$, $N = 30$, $P = 0.013$), but no association occurred between the number of males and the relative weight loss of queens ($r_s = 0.23$, $N = 30$, $P = 0.22$).

Survival prospects within each association were not associated with the mating status of queens (higher or lower mating frequency; Fisher's exact test: $P = 0.71$) and were independent of their relative contribution (greater or lower) to the brood ($P = 1$; Fig. 1). Surviving queens contributed on average $50.37 \pm 32.13\%$ to the brood and were the most productive ones in 53% of the two-queen colonies, while losing queens contributed $49.62 \pm 32.13\%$ (paired t test: $t_{16} = -0.05$, $P = 0.96$).

Queen Size

Queen's head size had a significant effect on survival probability, with larger queens winning the conflict twice as often as smaller queens (Fisher's exact test: $P = 0.002$; Fig. 1). Larger queens (mean head size \pm SD = 1.32 ± 0.05 mm) survived in 31 of 46 associations (67%) and smaller queens (1.31 ± 0.04 mm) survived in 15 foundations (33%). The magnitude of the size advantage did not influence the survival probability (logistic regression: $\chi^2_1 = 0.08$, $P = 0.07$; range of size 1.13–1.42 mm).

DISCUSSION

In *L. niger*, larger queens were more likely to survive fights after worker emergence in two-queen colonies. Neither weight at the time of a fight outbreak nor weight loss, a measure of the queens' relative investment in brood production, had a significant effect on the survival probability of queens. Moreover, genetic analyses showed that there was no advantage for the queen that had more daughters present at the time of the fight. Head width difference between queens, or other phenotypic traits associated with head width, has also been reported to influence the survival probability of cofounding queens in *S. invicta* (Bernasconi & Keller 1998), with the larger-headed queen of an association more frequently surviving the fighting period.

Our results show that heavier pairs lost more weight during the founding stage, and that increased investment resulted in higher offspring productivity. However, cooperative queens of an association lost different amounts of weight between the nuptial flight and the emergence of the first workers. Weight loss difference between queens of a pair reached up to 47% of the initial weight in some colonies, and was on average 12% over all colonies sampled. Reduced individual investment might be explained if queens losing less weight are heavier at the time of the fight and this increases their chance of survival. Yet, our study showed that differential weight loss during colony foundation did not directly influence survival. Mass loss was also independent of queen size, indicating that queens do not adjust their investment according to the difference in head width between the nestmates. Because queens draw on their own body reserves to produce workers, the queen within an association that loses most mass is expected to have a larger share of maternity among larval and adult workers. A previous study of laying behaviour indeed showed that egg production is not equally distributed among founding queens in *L. niger*, with some females contributing considerably more eggs than others (Sommer & Hölldobler 1995). In line with these observations, our genetic analyses showed that queens did not share

maternity equally, with a significant reproductive skew in about half the colonies. However, contrary to expectation, we found no association between an individual queen's weight loss and her maternity share. This may stem from at least three different sources. First, one queen may contribute a larger proportion of viable eggs. Second, there might be differential cannibalism of the eggs laid by both queens. Oophagy is indeed a common phenomenon during the founding phase in *L. niger* (Sommer & Hölldobler 1992). Third, one queen may regurgitate more and/or contribute disproportionately to brood care. The proximate causes of differential weight loss between the queens of an association in *L. niger* remain enigmatic and certainly merit further studies, especially since individual investment was not a predictor of survival prospects.

Patterns of cooperation and competition between queens during the crucial stage of colony founding in *L. niger* contrasts with that reported in the well-studied fire ant *S. invicta*. In the latter species, queens gain an advantage (1) from losing less weight during the association, (2) from being heavier and (3) from being larger (i.e. having a bigger head) at the time of the fight (Balas & Adams 1996; Bernasconi & Keller 1998, 1999; Adams & Balas 1999). Bernasconi & Keller (1996, 1998) claimed that cofoundresses adjust their investment to head width difference, which in turn is associated with relative fighting ability. In agreement with this, larger-headed queens lose less weight during the founding phase and have a significant advantage in the later competition. The greater the size difference, the less mass the larger queen loses. In addition, the queen losing less weight achieves a larger share of maternity among larvae and adult workers than her nestmate (Bernasconi et al. 1997). Finally, queens in pleometrotic associations invest less energy in rearing the brood than solitary queens (Tschinkel 1993; Bernasconi & Keller 1998). Alternatively, M.T. Balas (personal communication) proposed that both queens of an association reduce their investment in the brood in anticipation of the fight, but that a large difference in size may result in larger queens retaining more weight in the presence of a smaller rival. Whatever the causes of differential weight loss, conflicts among fire ant queens within associations occur before the outbreak of overt aggression, indicating selfish interactions among cofoundresses consistent with individual selection.

Our behavioural, morphological and genetic results on *L. niger* do not reveal a conflict, if any, among individual queens within associations before the fighting. Queens did not adjust their investment strategy to relative fighting ability. We found no association between queen size and weight loss during colony founding, and the queen losing less mass did not have a higher survival probability. In addition, we found no advantage for the queen that had more daughters present at the time of the fight. Rather, queens of an association probably cooperate until worker emergence. Consistent with this hypothesis, multiple-foundress colonies of *L. niger* have a higher worker production rate than single-foundress colonies (Sommer & Hölldobler 1995), enhancing the survival rate of pleometrotic foundations.

In social insects, the magnitude of pleometrotic advantage may be a function of local colony density. When colony densities are high, brood raiding by other colonies is a significant mortality factor and success in competition between young colonies is likely to be a major benefit of pleometrosis (Tschinkel 2006). By increasing initial worker brood production, pleometrosis has indeed been shown to enhance the competitive ability of incipient colonies in various ants (e.g. *Myrmecocystus mimicus*: Bartz & Hölldobler 1982; *S. invicta*: Tschinkel & Howard 1983; *Veromessor pergandei*: Rissing & Pollock 1987), including *L. niger* (Sommer & Hölldobler 1995). However, the benefits of cooperative founding might not be consistently high in this species, because the foundresses do not seem to aggregate themselves preferentially (Sommer & Hölldobler

1995). When queens are given a choice between establishing a nest alone or in cooperation, they show neither preference for nor avoidance of pleometrosis. Thus, foundress association in *L. niger* might be primarily promoted by crowding. Young mated queens of the species indeed occur in very high densities on the ground after the nuptial flight. Local queen density and nest site limitation could then be causal factors regulating pleometrosis, as is the case for other ant species where group size increases with increasing foundress density (*S. invicta*: Tschinkel & Howard 1983; *Leptothorax longispinosus*: Herbers 1986; *Lasius pallitarsis*: Nonacs 1992; Gunnels et al. 2008). Given that the size difference between founding queens significantly affects survival probability at the time of the fight, why do queens with lower fighting ability embark on a temporal cooperation with superior fighters? In most ant species founding by pleometrosis, including *L. niger*, kinship is not a factor influencing queen association because the chance of encountering relatives is low. Nonacs (1989, 1992) proposed that variance in competitive ability should favour conditional joining behaviour. In agreement with this prediction, laboratory experiments on *L. pallitarsis* showed that the joining decision of queens depends on the phenotype of potential cofoundresses, with queens preferentially joining lighter residents and lighter queens being more likely to leave nest sites when joined by others (Nonacs 1992). Foundresses of *L. niger* do not join others in a manner consistent with increasing their competitive advantage. In choice tests, queens show neither avoidance of nor preference for joining heavier or lighter nestmate queens (Sommer & Hölldobler 1995). Larger queens (as measured by weight or size) represent valuable mutualistic partners for the short term, because queen size is positively associated with weight loss and total brood production. On the other hand, larger queens have a higher probability of winning the fight. However, smaller queens of *L. niger* survive up to one-third of the fighting. This indicates that other factors besides larger size influence survival probability. This might be a necessary condition to maintain cooperation between cofoundresses because if winning was consistently associated with a given trait (e.g. size), an inferior competitor would have no chance of surviving. Hence, faced with zero fitness, queens should never enter into pleometrotic associations with nonrelatives (Strassmann 1989). Another causal explanation for the association of foundresses with superior fighters is that queens are under strong selection to leave the soil surface, to escape desiccation and predation (Tschinkel 1998). They can do so by entering any available holes. Once in a site, they may not leave it because they are unlikely to survive predation while searching for another suitable nest site and/or because another site may not be better than the one left.

Reeve & Ratnieks (1993) suggested that reversion to monogyny could stem from a dramatic change in the cost to benefit ratio associated with the presence of several foundresses. Claustal foundations have no food input and females should conserve their energy. Once the first workers emerge, having young nests open to food input and elimination of supernumerary queens allow both reduction in food competition and monopoly of reproduction. In *L. niger*, queens start to fight violently soon after worker emergence (Sommer & Hölldobler 1995; this study). Workers may take part in the fights afterwards. Selection should favour preference for the most productive queen, who should be the mother of most workers. Yet, analysis of matriline frequencies shows that this was not always the case. The queen that was eliminated was often the mother of the majority of workers. Rather, worker attacks were frequently directed against the most injured and mutilated queen. From the workers' perspective, rapid execution of the most injured queen may be adaptive. It reduces the risk of both queens being hurt and eventually dying, which may greatly impair colony survival, and allows workers to save the less wounded queen.

Consistent with this hypothesis, recent theoretical models showed that when workers do not reliably discriminate their relatedness to cofoundresses, they are selected to choose the queen that will increase the colony's chance of survival at the expense of potentially beneficial nepotistic interactions within the colony (Balas 2005).

Our genetic analyses are consistent with previous studies showing that *L. niger* queens can mate with up to four males during large-scale mating flights (Boomsma & van der Have 1998; Fjerdingstad et al. 2002; Fjerdingstad & Keller 2004). We found a positive association between queen mating frequency and apportionment of maternity at the time of emergence. There are at least two hypotheses for this association. The first is that multiple mating improves brood survival because the resultant increase in genetic variation among offspring enhances resistance to environmental conditions (e.g. parasites, pathogens). Increasing genetic diversity within colonies has been shown to enhance productivity and fitness in social insects (ants: Cole & Wiernasz 1999; Wiernasz et al. 2004; honeybee, *Apis mellifera*: Tarpy 2003; Mattila & Seeley 2007; bumblebees: Baer & Schmid-Hempel 1999; see also Rueppell et al. 2008). This hypothesis, however, seems, unlikely to account for the relationship between the number of mates and the contribution of queens to the brood. In an extensive study of the relationship between queen mating frequency, within-colony genetic variability and colony fitness in *L. niger*, Fjerdingstad et al. (2003) failed to find any consistent benefit of multiple mating on colony performance. First, colonies headed by singly or multiply mated queens did not differ in their size or overall sexual productivity. Second, there was no difference in productivity between incipient colonies headed by singly and multiply mated queens. Finally, the frequency of multiple mating by queens at the time of the mating flight was lower than among queens of mature colonies. Although this result was consistent with a survival advantage for multiple-paternity colonies, the trend was not repeated in other populations or in successive years on the same populations (Fjerdingstad et al. 2003). A second possible explanation is that polyandry boosts queen fecundity. That mating triggers an increase in egg laying has been reported in some species (Manning 1962; Thornhill & Alcock 1983). For instance, during copulation males of *Drosophila melanogaster* transfer a protein in the seminal fluid that increases female egg-laying rates (Herndon & Wolfner 1995). Females mated to male flies that lack the protein lay fewer eggs than mates of normal males do. Similarly, females of the ant *Cardiocondyla obscurior* mated with fertile males have increased fecundity (Schrempf et al. 2005). To our knowledge, whether egg-laying rate is positively associated with queen mating frequency has not been studied in social insects. The finding that mating status of queens was not associated with head size or initial body weight contrasts with the results of Fjerdingstad & Keller (2004), who reported a positive relationship between queen phenotype and mating behaviour. In their study, heavier queens of *L. niger* at the time of mating flights were more likely to mate with several males. The reasons for such a difference are unclear. According to these authors, multiple mating in *L. niger* would stem from queens being coerced to mate with several males, because the operational sex ratio is highly male biased and heavier queens could be less likely to prevent additional males from mating with them. Under this scenario, one may not exclude the possibility that ecological and/or demographic differences between populations regarding, for example, colony density or productivity, or population-level sex ratio, could influence the relationship between queen phenotype and queen mating frequency.

In conclusion, this study shows that queen phenotype influences the pattern of early queen mortality during reversion to monogyny in cooperative foundations of the black garden ant,

L. niger. Larger queens were more likely to survive the fighting. By contrast, neither the queen's weight nor individual investment in brood production (differential mass loss) and maternity apportionment affected the queens' survival prospects. Ultimately, queens should enter pleometrosis and cooperate with unrelated, superior (larger) queens if this strategy increases the probability of survival and production of reproductive offspring. Conversely, if the chances of surviving the conflict and becoming the sole reproductive are smaller than the chance of success by haplometrosis, it would be to the queen's advantage not to join another foundress. Pleometrosis in *L. niger* confers a higher survival rate of incipient colonies, because it improves the competitive ability of young colonies and success in brood raids (Sommer & Hölldobler 1995). The benefits of pleometrosis and the fact that smaller queens of an association can survive up to one-third of the conflicts might be sufficient for young queens to embark on cooperative foundations, especially when local colony density is high. This would characterize a best of a bad situation for smaller queens.

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