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Effect of queen phenotype and social environment on early queen mortality in incipient colonies of the fire ant, *Solenopsis invicta*

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In many ant species, including the fire ant, *Solenopsis invicta*, queens can found their colonies alone or in associations of two or more. Colonies founded by associations produce a larger worker brood, have higher survival and mature earlier than colonies founded by solitary queens. However, cofoundresses almost invariably fight after the eclosion of the first workers. As a result, only one queen survives and monopolizes the colony's future reproductive output. Queen mortality also occurs before worker eclosion, but neither the causes (e.g. starvation, conflict), nor the factors (e.g. social environment) potentially affecting its occurrence, have been investigated. We analysed the effect of social environment and queen body mass on early mortality by keeping queens (1) solitarily, (2) within associations of four queens of the same initial mass, and (3) within associations of four queens of random initial mass. Mortality was higher for queens within associations than for solitary queens. Within associations of equally heavy queens, mortality significantly increased with the queens' body mass. In contrast, mortality of solitary queens did not significantly depend on body mass. Early mortality was significantly more frequent in associations of queens of random initial mass than in associations of equally heavy queens. Altogether these results demonstrate that queen phenotype differentially affects early queen mortality depending on the social environment, and suggest that reproductive competition rather than starvation is the main cause of mortality in multiple-queen associations.

In most ant species, new colonies are established after a mating flight by queens without help from workers (Hölldobler & Wilson 1990; Bourke & Franks 1995). During colony founding, queens generally seal themselves in a burrow and do not forage, and to produce their first workers, they metabolize body reserves that they have stored before the mating flight (Keller & Passera 1989; Wheeler & Buck 1996). In many ant species (13 genera in three families, Choe & Perlman 1997), queens found their colony either solitarily (haplometrosis), or together with other newly mated queens from the same mating flight (pleometrosis; Strassmann 1989; Bourke & Franks 1995). Within associations, queens are generally unrelated (Hagen et al. 1988; Rissing et al. 1989; Sasaki et al. 1996) and all contribute to oviposition and brood care (Rissing & Pollock 1988; Strassmann 1989; Bourke & Franks 1995). Because of the lack of significant relatedness, foundress associations are receiving increasing attention as a model system for investigating the dynamics of cooperation and conflict within groups (Hamilton 1964; Strassmann 1989; Mesterton-Gibbons & Dugatkin 1992; Balas & Adams 1996; Bernasconi & Keller 1996, 1998; Bernasconi et al. 1997; Dugatkin 1997).

Cooperative colony founding provides several benefits. Pleometrotic associations have a larger first worker brood, higher colony survival (Rissing & Pollock 1988), faster colony growth and maturation (Vargo 1988), and are more resistant to nest usurpation (Balas & Adams 1997) than colonies founded by single queens. In particular, the size of the first worker brood crucially affects colony growth and survival in species where there is strong

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competition among neighbouring incipient nests (Rissing & Pollock 1988; Adams & Tschinkel 1995). However, soon after worker eclosion (Sommer & Hölldobler 1995), overt aggression between queens leads to the death or expulsion of all but one queen (Rissing & Pollock 1988). The surviving queen secures for herself the colony's future reproductive output because no sexual progeny are produced during the founding stage (Seger 1993). Thus, after eclosion of the first workers, foundress associations usually develop into monogyne colonies (exceptions: *Iridomyrmex purpureus*, *Acromyrmex versicolor*, *Atta texana*; Bourke & Franks 1995, page 267).

Mortality, albeit low, of queens has also been reported before the eclosion of the first workers (*Lasius pallitarsis*: Nonacs 1990; *Solenopsis invicta*: Adams & Tschinkel 1995; Bernasconi & Keller 1996, 1998), but the causes underlying this mortality have not yet been investigated. Early queen death may stem from starvation, as queens do not forage during the founding stage (Bourke & Franks 1995; Wheeler & Buck 1996) and lose up to 50% of their body mass between the mating flight and worker eclosion (Tschinkel 1993; Bernasconi & Keller 1996). Alternatively, early queen death may be caused by conflicts between queens. The starvation and conflict hypotheses both predict lower risk of death for queens that are heavier. Heavier queens are likely to be better provisioned with energy stores used during colony founding (fat: Keller & Passera 1989; storage proteins: Voss & Blum 1987; Wheeler & Buck 1995, 1996) and thus to be at lower starvation risk. Heavier queens are also likely to have higher relative fighting ability, and thus higher survival if mortality is due to conflict. Indeed, the relative body mass of *S. invicta* queens within a two-queen association correlates with the probability of winning the fights that occur after worker eclosion, with the heavier queen being more likely to survive (Balas & Adams 1996; Bernasconi & Keller 1996). By contrast, the predictions of the starvation and conflict hypotheses diverge for the effect of social environment. If starvation is responsible for early queen death, mortality should be lower within associations than for solitary queens, because queens within associations lose less mass than solitary queens (Markin et al. 1972; Tschinkel 1993; Bernasconi & Keller 1998). The lower mass loss of queens in pleometrotic associations stems either from a lower investment in brood feeding, and/or from egg cannibalism. Egg cannibalism occurs only within associations (Voss & Blum 1987; Tschinkel 1993) with the effect that the number of larvae per queen is lower in associations than for solitary queens (Tschinkel 1993), thus possibly reducing the brood care demands on the queens. By contrast, if early queen death stems from conflicts between queens, mortality should be higher in associations than for solitary queens.

In this study, we address the question of whether the occurrence of early queen mortality within colonies of the ant *Solenopsis invicta* is affected by (1) the presence of cofoundresses, (2) the queens' absolute body mass after the mating flight, and (3) the variance in initial mass of queens within associations.

METHODS

Queens were collected after the mating flight of a monogyne population (i.e. mature colonies contain only one queen, Ross & Fletcher 1985; Ross & Keller 1995) in Walton County, Georgia, U.S.A. on 18 July 1995. They were immediately shipped to the laboratory, first on surface to Atlanta, Georgia, and from there by flight through a company specialized in animal shipping (Jacky Maeder Ltd, Zurich, Switzerland and Circle International, College Park, Georgia, U.S.A.) under controlled temperature (15 ± 5°C) and pressure conditions. They were shipped within two large plastic bottles with a meshed lid for air circulation, each filled with wet filter paper to provide moisture and structure. This procedure did not lead to any increase in the level of mortality of queens compared with experiments where queens were set up in experimental colonies immediately after collection (L. Keller & G. Bernasconi, unpublished data).

We started the experiments within 48 h of field collection. The first day of the experiment is referred to as day 1. The natural onset of oviposition is 2–3 days after the mating flight (Markin et al. 1972; Voss & Blum 1987) and workers eclose as a cohort after day 21 (Voss & Blum 1987). The colonies were kept in a dark, ventilated chamber (28 ± 2°C, 70 ± 10% RH) in artificial nests as described in Bernasconi & Keller (1996). Assignment procedures were randomized, and replicates assigned to the different treatments were randomly distributed within the rearing room. Queens were not fed.

Effect of Absolute Queen Body Mass

To compare the effect of body mass on the occurrence of early queen mortality across social environments, we weighed 612 queens (Mettler AE 100; nearest 0.1 mg) on day 1 and placed them within nests either singly (haplometrotic treatment, N=252) or in associations of four queens of the same initial mass (± 0.1 mg; pleometrotic treatment, N=360 queens). We assigned more queens to the pleometrotic treatment because there is a higher probability that diploid males will be produced in colonies containing several queens. In Hymenoptera males are usually haploid, but diploid eggs may also give rise to males if homozygous at the sex-determining locus or loci (Crozier 1971). The frequency of diploid males is particularly high in the U.S. population of *S. invicta* because of the recent genetic bottleneck (Ross et al. 1993). Because the presence of diploid males decreases colony survival during the founding stage in monogyne *S. invicta* (Ross & Fletcher 1986), we considered whether or not colonies produced diploid males in our analysis.

The initial masses of queens kept singly ($\overline{X} \pm \mathrm{SD}$=14.96 ± 0.86 mg, N=252) and of queens assigned to four-queen associations (15.01 ± 0.83 mg, N=360) did not differ significantly (independent t test: t_{610}=0.73, P=0.47). Half of the colonies in each treatment were observed until day 10, and the other half until day 20. We compared mortality after 10 and 20 days to test whether mortality schedule correlates with changes in investment patterns. Queens' investment up to day 10 encompasses mainly egg laying and feeding of young larvae (the first larvae emerge on day 7), while up to day 20 it also includes feeding of older larvae and laying numerous trophic eggs (Voss & Blum 1987).

We tested whether a queen's probability of dying within pleometrotic associations was independent of the occurrence of the death of other queens in the same colony, by comparing the observed distribution of deaths with the expected distribution if deaths occur randomly among colonies (binomial distribution with intrinsic hypothesis; Zar 1996). The observed distribution departed significantly from random expectation (likelihood ratio test: $G_1=5.29$, $P<0.02$), with multiple deaths within the same colony being more frequent than expected. This indicates that deaths within the same association did not occur independently of each other. Therefore, the multivariate analysis of mortality was carried out at the colony level (see below).

We analysed the effect of initial body mass, treatment, duration of observation period, presence of diploid males and their interactions on the occurrence of within-colony mortality using multiple logistic regression (GLMstat 1.5). Multiple logistic regression examines the influence of regressor variables on a dichotomous response (Hosmer & Lemeshow 1989). Model simplification was carried out with backward elimination (Crawley 1993). In each step we removed the least significant parameter (highest P value in the Wald test), starting with interaction terms. Model simplification aims at the simplest, most parsimonious model to explain the data. The minimal adequate model retains the subset of regressor variables whose elimination from the model would cause a significantly worse fit to the data, as measured by deviance difference. To avoid pseudoreplication we used 'colony-based mortality' as a response variable, taking values of either one or zero in both treatments. For haplometrotic colonies, colony-based mortality codes whether the queen died (this event occurs with probability P) or survived $(1-P)$, and in four-queen associations it codes whether all queens survived or at least one queen died. Assuming that queens within the same association die independently of each other (see below), colony-based mortality would take values of $[(1-P)^4]$ for colonies where all queens survived and of $[1-(1-P)^4]$ if at least one queen died, where P is the probability of mortality for solitary queens. Are these probabilities comparable? By applying binomial expansion one obtains $[1-(1-P)^4]=4P-6P^2+4P^3-P^4\approx 4P$ (because P is small, and thus all higher terms can be neglected). After logistic transformation, the response variable becomes logit(P) for haplometrotic colonies and $\text{logit}[1-(1-P)^4]\approx\log(4)+\text{logit}(P)$ for pleometrotic colonies. Thus the difference in how survival probabilities are coded to obtain colony-based mortality can be corrected for in the regression analysis by using an 'offset' (McCullagh & Nelder 1983, page 138) of $\log_e(4)$ for four-queen colonies and of zero (i.e. $\log_e(1)$) for one-queen colonies. Because the assumption of independence was violated, we also estimated the offset value directly from the data (McCullagh & Nelder 1983, page 138). The theoretical value ($\log_e(4)=1.38$) that assumes independence did not differ significantly from the value estimated from empirical data (2.2, SE=0.53, 95% confidence interval 1.1–3.4) suggesting that the offset value chosen is a suitable correction. The suitability of the logistic model with colony-based mortality as a response was further supported by estimating a smooth function (smoothing splines) from the data, in an augmented additive model (all nonlinear parts of the smooth functions were not significant; all P values >0.20; K. Halvorsen, personal communication).

Effect of Variance in Queen Body Mass

To test the effect of heterogeneity in initial queen mass within associations on the occurrence of mortality, we randomly placed another 160 queens from the same mating flight in four-queen colonies ($N=40$) on day 1. Thus, in this treatment queens within the same association are expected to vary randomly in initial mass. Queens in this treatment were not weighed. Mortality in these associations was compared to mortality in associations with queens of the same initial mass (see above). Because mortality for this group was recorded until day 18, they were compared to the subgroup of $N=45$ colonies with equally heavy queens that had been observed until day 20 (considering only the first 18 days). Because the presence of diploid males did not significantly affect patterns of mortality (see Results), colonies with diploid males were included in this analysis.

Unless specified, data are given as mean ± SD; P values are two-tailed.

RESULTS

Twenty-four (6.7%) of the 360 queens kept pleometrotically died; these deaths were distributed among 18 of the 90 pleometrotic colonies. In haplometrotic colonies, 8 (3.2%) queens out of 252 died. On an individual basis, mortality was significantly higher for queens kept pleometrotically than for queens kept singly (likelihood ratio: $\chi^2_1=3.87$, $P<0.05$).

Diploid males were detected in 14 out of 252 one-queen colonies (5.5%) and 22 out of the 90 (24%) four-queen colonies. There was no significant association between the presence of diploid males and the occurrence of mortality in haplometrotic colonies (Table 1). In particular, the queen survived in all the haplometrotic colonies where diploid males were recorded, suggesting that diploid males are not yet negatively affecting queen fitness at this early stage of colony founding. Similarly, in pleometrotic colonies the presence of diploid males was not significantly associated with the occurrence of mortality, either with 'colony-based mortality' (Table 1), or with the distribution of multiple queen deaths within associations (likelihood ratio test: $G_2=1.50$, $P=0.47$).

The minimal adequate model resulting from logistic regression analysis of mortality contained the treatment (haplometrosis versus pleometrosis), initial mass, and their interaction; it also included duration of observation period (Table 2). This model explained the data significantly better than the null model (Table 2, test I-II).

Table 1. Diploid male presence and occurrence of mortality

	One-queen colonies		Four-queen associations	
	Survived	Died	All survived	At least one queen died
Normal brood	230	8	56	12
Brood containing diploid males	14	0	16	6
Fisher's exact test	P=1.00		P=0.36	

Table 2. Results of multiple logistic regression for colony-based mortality in 252 one-queen colonies and 90 four-queen associations

Model		Deviance	*df*	Deviance difference	Likelihood ratio test
Maximal model (III)	Constant+duration+treatment+mass+ diploid male presence+ all two-way interactions	141.8	331	II–III: 4.2	$P(\chi^2_6>4.2)>0.50$
Minimal adequate model (II)	Constant+duration+treatment+ mass+treatment×mass	146.0	337	I–II: 17.2	$P(\chi^2_4>17.2)<0.005$
Null model (I)	Constant only	163.2	341		

Treatment refers to haplometrotic versus pleometrotic conditions.

Predicted values generated by the minimal adequate model did not depart significantly from observed values (Table 2: goodness-of-fit test: $\chi^2_{337}=146.0$, $P>0.90$), indicating that the model accurately described the data. Adding the effect of diploid male presence and all remaining interactions did not significantly improve model fit (Table 2, test II-III). The interaction term (treatment × mass) was significant (deviance difference for removing the interaction from the model=7.6, $P(\chi^2_1>7.6)<0.01$; Fig. 1) indicating that the effect of initial mass on mortality differed between the treatment groups. Therefore we estimated the slope coefficient for the effect of initial mass on mortality separately for each treatment, by fitting nonparallel lines for the covariate (mass) for the different treatment levels (haplometrosis versus pleometrosis; Crawley 1993). This analysis revealed that initial queen mass significantly affected occurrence of mortality within pleometrotic associations but not in haplometrotic colonies. For pleometrotic associations, the slope coefficient was significantly positive (estimated coefficient ± SE=0.79 ± 0.35; Wald test: $Z=2.23$, $P=0.02$) indicating that mortality was higher in associations of heavier queens. Consistent with this finding, the mass of queens in associations where mortality occurred (15.40 ± 0.81 mg, $N=18$) was significantly higher than in associations where all queens survived (14.92 ± 0.85 mg, $N=72$, unpaired t test: $t_{88}=2.24$, $P<0.03$). By contrast, mortality was not significantly dependent on initial mass for solitary queens, as indicated by the slope coefficient being not significantly different from zero in this treatment group (deviance difference resulting from the replacement of the slope with one of zero: $\chi^2_1=2.9$, NS; Crawley 1993, page 284). Accordingly, there was no significant difference in queen body mass between colonies where mortality occurred

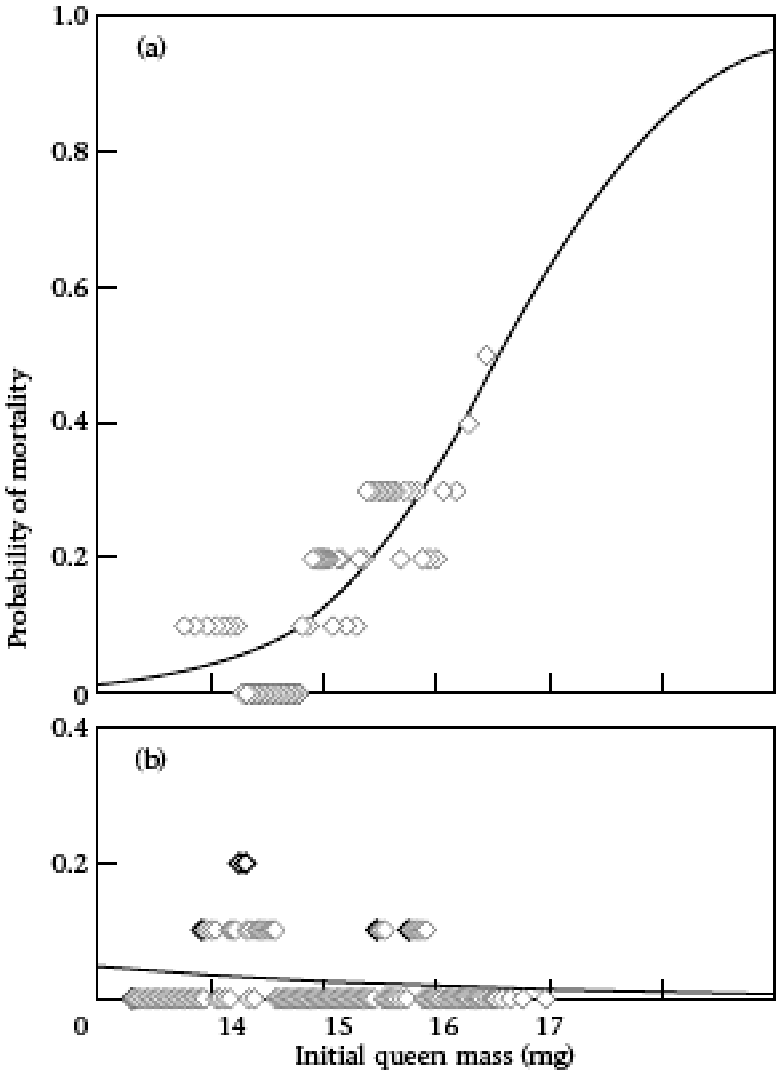

Figure 1. Probability of occurrence of colony-level mortality in response to initial queen mass. Each point is the moving average of 10 colonies of increasing initial mass. The curves give the expected probability (logistic regression). (a) Pleometrotic colonies; (b) haplometrotic colonies.

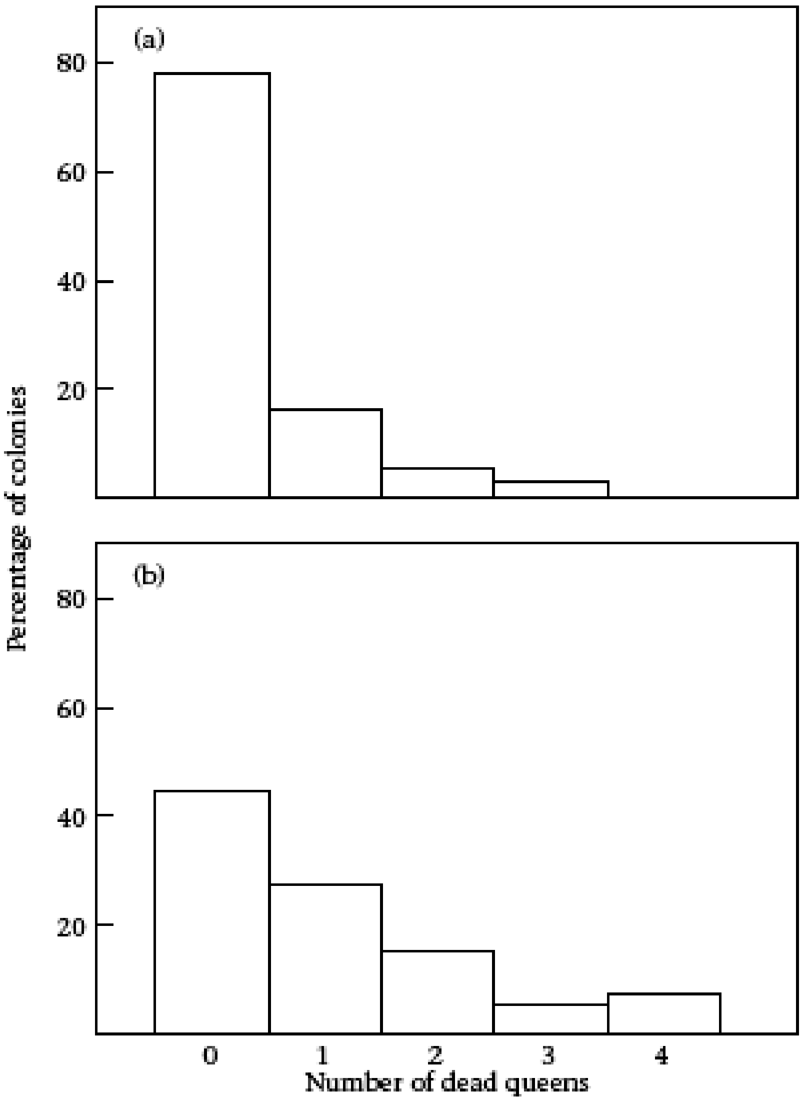

Figure 2. Queen mortality before worker eclosion in four-queen associations with queens of the same initial mass (a; N=45), and of random initial mass (b; N=40).

(14.46 ± 0.85 mg, N=8) and colonies where it did not occur (14.98 ± 0.78 mg, N=244; unpaired t test: t_{250}=1.68, P=0.095) in the haplometrotic treatment (note that here the mass of queens in colonies where mortality occurred tended to be lower than in colonies where mortality did not occur, i.e. the direction of difference is opposite than for the pleometrotic treatment).

Mortality increased with the duration of observation (10 or 20 days; significant main effect, Table 2; estimated coefficient ± SE: 1.23 ± 0.49; Wald test: Z=2.52, P=0.01), in both the haplometrotic and pleometrotic treatment, as indicated by the non-significant interaction term (treatment × duration), eliminated by backward selection (deviance difference caused by removing this term = −0.35, df=1, P>0.50).

At the colony level, there was a significant difference in the distribution of number of queens dying in each colony between associations with queens of random initial mass and associations containing queens of the same initial mass (Kolmogorov–Smirnov two-sample test: D=0.33, N_1=45, N_2=40, P<0.001; Fig. 2). Queen mortality was significantly higher within associations of queens of random initial mass (26%, 41 out of 160 queens) than within associations of queens of the same initial mass (8%, 14 out of 180 queens; likelihood ratio test: G_1=20.4, P<0.0001).

DISCUSSION

Our study shows that, before worker eclosion, individual mortality is higher in pleometrotic than in haplometrotic colonies. Moreover, the occurrence of within-colony mortality significantly increased with higher initial mass of queens in pleometrotic associations, whereas there was no significant effect of initial queen mass on mortality in haplometrotic colonies.

These results are not consistent with the hypothesis that starvation is the prime cause of mortality of queens before worker eclosion. In fact, the starvation hypothesis makes the opposite predictions, namely that mortality should be (1) higher in haplometrotic colonies than in pleometrotic associations and (2) lower in associations of heavier queens than in associations of lighter queens with less body reserves. The former prediction stems from the fact that queens lose more mass in haplometrotic than pleometrotic associations (Markin et al. 1972; Tschinkel 1993; Bernasconi & Keller 1998) and thus should suffer higher mortality from starvation.

The observed higher mortality in pleometrotic than haplometrotic colonies is consistent with the hypothesis that competitive and aggressive interactions already break out during early colony founding in pleometrotic associations of *S. invicta*. Interestingly, mortality significantly increased with the queens' body mass within associations of equally heavy queens. This pattern may be explained if heavier individuals are intrinsically more likely to fight to attain a higher reproductive status. Fights have been occasionally observed within laboratory colonies before worker eclosion, sometimes followed by the death of one queen. Unfortunately, insufficient fights were observed to test whether there is a statistical association between mass of queens and probability of fights occurring before worker eclosion, thus to provide direct evidence that aggression is responsible for the observed mortality patterns. Similar effects of body mass have been found in the context of fighting in other arthropod species. In pairwise contests of male spiders *Argyrodes antipodiana*, escalation is more likely to occur if pairs consist of absolutely larger males (Whitehouse 1997).

Our study also revealed a greater mortality within pleometrotic associations with queens of random mass than within associations containing queens of equal mass. This result is unlikely to be accounted for by differences in average queen mass between the two types of colonies because assignment of queens to either treatment group was randomized. Therefore the explanation must lie in the different distribution of mass within colonies (equal versus random). For example, it may be that aggressive interactions are less common in associations with queens of equal mass because no queen benefits from challenging evenly matched competitors. In contrast, larger queens may benefit from challenging their smaller nestmates in associations of random mass, thus leading to higher mortality in these colonies.

Ross & Fletcher (1986) showed that queens producing diploid males experience increased mortality as early as 9–10 weeks after eclosion of the first workers. In contrast, our experiments showed no significant effect of the presence of diploid males on queen survival before worker eclosion (i.e. in the first 3 weeks of colony founding). This suggests that the negative effect on queen survival resulting from the production of diploid males primarily occurs after the eclosion of the workers.

In conclusion, this study provides evidence that social environment and queen phenotype affect the pattern of early queen mortality. We propose that the most parsimonious explanation is that reproductive competition among queens within pleometrotic associations of fire ants can occur before the eclosion of the first workers. Previous studies indeed showed that queens behave selfishly prior to worker eclosion. Queens in pleometrotic associations invest less energy in rearing the brood than solitary queens (Markin et al. 1972; Tschinkel 1993; Bernasconi & Keller 1998). Moreover investment of cofoundresses is adjusted to head width difference, a phenotypic trait associated with fighting ability. Queens with larger heads both invest less energy in rearing the brood and are more likely to survive fights occurring after worker eclosion (Bernasconi & Keller 1998). Genetic analyses also showed that the queen that invests the least energy in brood production achieves a greater share of maternity in the first worker brood and is most likely to survive, and that this effect is produced by competitive interactions among cofoundresses (Bernasconi et al. 1997). Together, these studies suggest that there is strong reproductive competition among queens long before the eclosion of the first workers. The increased death rate observed in pleometrotic associations may thus arise from physical aggression serving as retaliation against attempts at cheating by some queens, for example through reduced energy investment or egg cannibalism. The results of this and our previous studies on fire ants challenge the often proposed view that conflicts within foundress associations are completely absent before worker eclosion.

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