



# Cooperation and conflict in ant foundress associations: insights from geographical variation

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(Received 14 January 2000; initial acceptance 11 May 2000;  
final acceptance 14 September 2000; MS. number: A8690)

Sociality can promote both cooperation and competition. Although we assume social organisms possess adaptations that allow them to form groups and deal with within-group conflicts, these are often subtle and difficult to detect. Using a simple form of sociality displayed by young ant foundresses of the desert seed-harvester ant, *Messor pergandei*, as a model system, I exploited intraspecific geographic variation in social behaviour to investigate how the social context has altered individual behavioural strategies. I created social groups composed of two normally nonsocial foundresses, normally social foundresses and mixed groups, and compared foundresses' aggression and willingness to invest resources towards colony productivity. Nonsocial foundresses, presumably not adapted to social life, invested significantly more resources into colony growth than normally social foundresses, and experienced reduced survivorship in mixed groups. In contrast, social foundresses displayed two novel competitive behavioural strategies when confronted with nonsocial partners: retaliatory aggression and egg consumption. These results document that the evolution of social behaviour, rather than promoting cooperation, is driven by the evolution of competitive strategies designed to exploit group members and reduce the risk of being exploited by others.

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Sociality promotes both cooperation and competition. Group formation can mitigate stressful ecological factors, in which case individuals have common interests and should cooperate (Strassmann & Queller 1989; Janson & Goldsmith 1995). However, genetic heterogeneity among group members can also cause conflicts over resources, mates, or reproduction that may override group-level benefits (Vehrencamp 1977; Chapuisat et al. 1997).

Although cooperation and competition are both likely to be present in social groups, it is often difficult to identify when these strategies are being employed (Taborsky 1987). One approach to this problem is to measure the extent of cooperation as the cost assumed by an individual in performing actions that benefit the group as a whole (Dugatkin et al. 1992). In general, a cooperative individual should invest more in such actions than one attempting to exploit other group members (e.g. Kukuk et al. 1998). However, in order to identify whether social species have evolved increased or decreased cooperative investment, we must have a measure of the ancestral level of investment against which to compare

the behaviour of socially adapted organisms (Fewell & Page 1999).

Intraspecific variation in behaviour provides a unique opportunity to quantify such investment (Dugatkin & Alfieri 1992). By comparing normally nonsocial and social members of the same species, we can begin to identify the types of behavioural changes that have evolved as a result of the social environment. Geographic variation in social behaviour occurs in several species of ants in the southwestern United States. Newly mated females (foundresses) can either construct new nests solitarily or aggregate with other unrelated foundresses during nest initiation to form temporary multifoundress nests that reduce to a single queen after worker emergence (Hagen et al. 1988). The frequency of group nesting varies among locations, some areas having high levels of foundress sociality while such behaviour never occurs in other areas (Rissing et al., 2000). In at least one of these species, the desert seed-harvester, *Messor pergandei*, this variation is accompanied by intrinsic differences in conspecific tolerance and aggregation behaviour, suggesting that differences in sociality are genetically based (Cahan et al. 1998). Two ecologically similar congeners of *M. pergandei*, *M. julianus* and *M. andrei*, found only solitary nests (Johnson 2000; M. F. Brown, personal communication),

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suggesting that solitary nesting is the ancestral state within the genus.

In this study, I examined how cooperation and competition have shaped social behaviour by comparing behaviour of foundresses that differ in social strategy. I created social groups in the laboratory containing both normally solitary and normally social foundresses and observed their interactions and activities to identify novel behaviours associated with the social form. I measured the extent of cooperation shown by the two forms by comparing levels of aggression towards nestmates and energetic investment into colony growth. Individual investment can be approximated by individual body mass loss because *M. pergandei* foundresses are claustral; that is, they feed the first offspring solely from stored fat and muscle reserves (Rissing & Pollock 1987; Bernasconi & Keller 1996). I investigated the fitness consequences of behavioural differences between foundresses by comparing individual survival and colony productivity associated with different behavioural strategies. To look more closely at behavioural interactions between foundresses of different social strategies, I set up additional observation pairs (experiment 2) to identify the behavioural roles assumed by each foundress and document any aggressive interactions between them.

## METHODS

### Experiment 1

I collected *M. pergandei* foundresses from starting nests every 2–3 days during March 1997. Foundresses from two collection sites, Whitewater Canyon and Deep Canyon, California, U.S.A., do not form group nests in the field and are often behaviourally aggressive to one another (Sites 1 and 2, Cahan et al. 1998). I considered foundresses from these sites 'nonsocial'. I collected 'social' foundresses from Frontage Rd., Riverside Co., California and McCartney Rd., Maricopa Co., Arizona. Foundresses from these sites show a high frequency of group nesting and no interfoundress aggression (Pollock & Rissing 1985; Pfennig 1995; site 12, Cahan et al. 1998). I considered foundresses collected from both solitary and group nests at these sites social, as previous behavioural assays showed that foundresses from these sites actively prefer groups regardless of the nest type from which they are collected (Krebs & Rissing 1991; Cahan et al. 1998). It is likely that foundresses had laid some eggs prior to collection; when possible, I excavated foundresses from multiple sites on the same day to minimize differences in egg production before experiments began.

After collection, I provided foundresses with a moist piece of paper towel for at least 8 h to allow them to rehydrate fully and then weighed them to the nearest 0.01 mg. Foundresses were individually marked with acrylic paint on the gaster and assigned to one of five treatments: single nonsocial foundresses (N), single social foundresses (S), pairs of nonsocial foundresses (NN), pairs of social foundresses (SS), or mixed pairs containing one of each foundress type (NS). Foundresses collected from the same field nest were never paired to avoid familiarity

effects on behavioural interactions. Groups were assembled as foundresses became available from field sites over a 2-week period. I placed foundresses into groups no more than one day after collection. Sample sizes per treatment ranged from 13 to 31 pairs. I observed newly introduced pairs for 10 min and noted all instances of biting or grappling. All colonies were housed in capped plastic test tubes containing water-soaked cotton at the far end to maintain 100% humidity throughout the experiment. Colonies were maintained at 25°C for 8 weeks, until the first cohort of workers was at the pupal stage. I noted foundress survival and evidence of injury to dead foundresses, such as loss of body parts, weekly. I compared survival of foundresses across all treatments over the course of the experiment using a Wilcoxon test for right-censored survival data (Pyke & Thompson 1986).

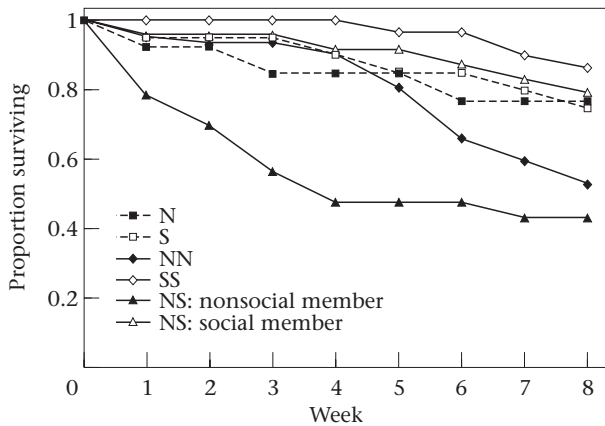
I measured foundress investment and brood production by surveying colonies every 7 days. All foundresses were briefly removed and weighed, and eggs, larvae and pupae were counted under a dissecting microscope. I compared weekly mass changes across treatments with a repeated measures analysis of variance (ANOVA) incorporating foundress strategy type (social, nonsocial) and nest type (solitary, same-type pair or mixed pair) as factors. Initial mass was included as a covariate to control for body size differences. To avoid using nonindependent data from individuals within pairs, I chose a single member of each same-strategy pair randomly to be included in survival and mass-change analysis.

### Experiment 2

To identify behavioural differences between nonsocial and social members of mixed pairs, I set up an additional 10 NS pairs on 14 February 1998 with foundresses collected on 11–12 February 1998. Foundresses were individually marked on the gaster with acrylic paint. I made behavioural scans of foundresses one to four times daily for 26 days. Each pair was observed for approximately 1 min. In each scan, I noted proximity of foundresses to each other and to the brood pile. I then scored each foundress's behaviour as one of the following behavioural classes.

- (1) Inactive: no movement by the foundress.
- (2) Grooming.
- (3) Reproduction: foundress was in an egg-laying posture with the gaster tucked under the thorax.
- (4) Tending brood: foundress was actively touching or manipulating brood with antennae or mandibles.
- (5) Chewing cotton: tearing at the cotton water plug with mandibles. I presumed this to be analogous to excavation behaviour.
- (6) Interacting: foundress was in contact with and actively grooming, antennating or attacking cofoundress.
- (7) Other: walking or antennating nest walls without contacting brood or nestmate.

If foundresses were interacting, I scored the behaviours of each foundress as antennation, standing on the second foundress, or biting. All foundress deaths were noted and surviving members of pairs were excluded from analysis in all subsequent observations.



**Figure 1.** Proportional survival over time of *Messor pergandei* foundresses across nest treatments. Filled symbols indicate nonsocial foundresses; open symbols indicate social foundresses. Solitary nest treatments are indicated with dotted lines and grouped treatments are indicated with solid lines.

**RESULTS**

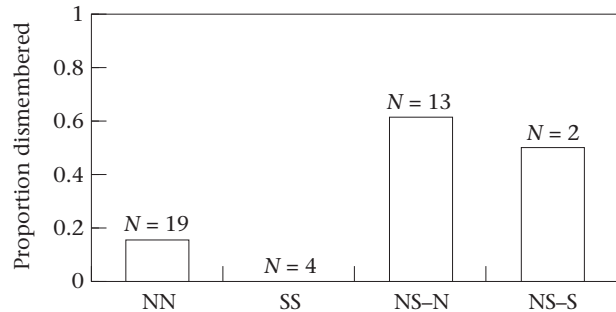
**Experiment 1**

Foundresses from different behavioural regions differed significantly in their likelihood of initiating aggressive behaviours in the first 10 min of pair formation ( $G_2=8.59$ ,  $P<0.02$ ). NN foundresses initiated aggression in 11 of 25 observed pairs. Fewer SS pairs (3 of 18) displayed aggression, although this difference was not significant ( $G_2=3.75$ , NS). Sixteen of 27 NS pairs were aggressive, significantly more than SS pairs but not different from NN pairs (mixed versus social:  $G_2=8.57$ ,  $P<0.02$ ; mixed versus nonsocial:  $G_2=1.21$ ,  $P=0.54$ ). Aggressive encounters in NS nests were significantly more likely to be initiated by the nonsocial member ( $G_1=4.27$ ,  $P<0.04$ ).

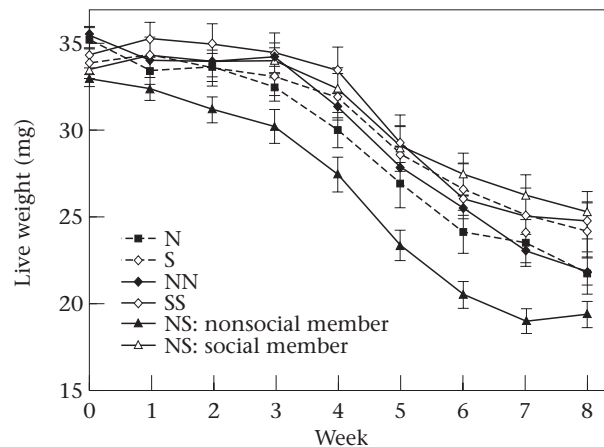
Nonsocial members of NS pairs experienced significantly lower survival than social foundresses from all treatments ( $\chi^2_5=21.33$ ,  $P<0.001$ ; Fig. 1). Mortality risk for these foundresses was highest during the first 4 weeks. Social foundress survival was high (81.2% overall) and not significantly affected by nest treatment. Nonsocial foundress survival did not differ from social foundresses when kept alone. Nonsocial foundress survival in NN pairs was intermediate to, and not significantly different from, nonsocial members of NS pairs and social foundresses. Mortality risk for NN foundresses was highest during the last 4 weeks of the experiment.

Of all individuals that died while members of pairs, 31.6% (12/38) were found at least partially dismembered. Dismemberment was not distributed equally across nest types (Fig. 2). A logistic regression revealed that dead individuals from mixed pairs were significantly more likely to be dismembered ( $t_{36}=2.83$ ,  $P<0.01$ ).

Foundress body mass declined significantly over the course of the experiment (repeated measures ANOVA:  $F_{8,600}=5.34$ ,  $P<0.001$ ; Fig. 3). Overall, S foundresses had a lower rate of mass loss than N foundresses ( $F_{8,600}=11.76$ ,  $P<0.001$ ). Neither treatment type nor initial mass had an overall effect on foundress mass loss trajectories



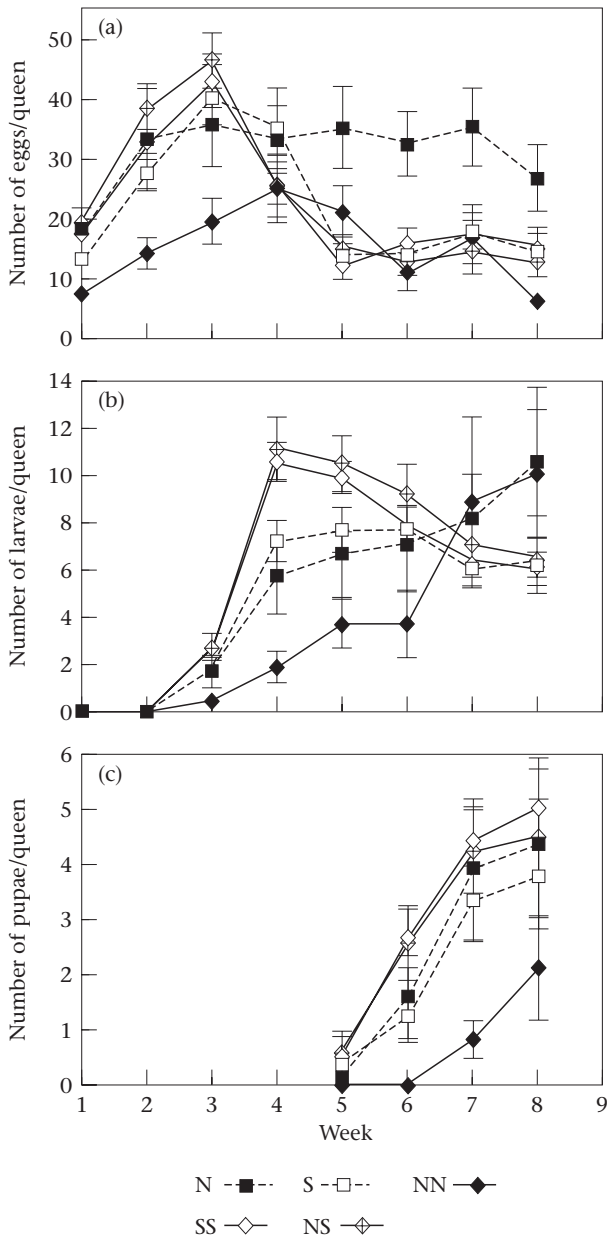
**Figure 2.** Proportion of *M. pergandei* foundresses found dismembered in nests across nest treatments. Data for nonsocial (NS-N) and social (NS-S) members of mixed pairs are presented separately.



**Figure 3.** Average  $\pm$  SE weekly live weights of *M. pergandei* foundresses across nest treatments. Filled symbols indicate nonsocial foundresses; open symbols indicate social foundresses. Solitary nest treatments are indicated with dotted lines and grouped treatments are indicated with solid lines.

(treatment:  $F_{16,600}=1.37$ ,  $P=0.15$ ; weight:  $F_{8,600}=1.53$ ,  $P=0.14$ ); however, there was a significant interaction effect between foundress identity and treatment ( $F_{16,600}=2.38$ ,  $P=0.002$ ). This effect was due to a greater difference in mass loss between N and S members of NS groups when compared to mass losses of N and S foundresses in solitary nests or in same-type pairs.

Foundresses began to produce eggs within 24 h of being placed in experimental nests. Eggs were maintained in a single pile within the nest tube in all treatments except NN nests. In these nests, eggs were more scattered throughout the nest, and began to show bacterial and fungal growth after 6 weeks in 61% of nests. Nests were excluded from subsequent analysis of offspring production when all brood were completely covered in pathogens. Egg production peaked at week 3, and all treatments except NN showed similar per-foundress egg production at this time. Egg numbers declined to approximately one-third of week 3 levels over all subsequent weeks in all treatments containing at least one S foundress (Fig. 4a). N and NN treatments had significantly different egg production trajectories from S treatments, showing no decline in egg number over time (repeated measures



**Figure 4.** Average number of eggs (a), larvae (b) and pupae (c) produced over time in *M. pergandei* laboratory nests. Solitary nest treatments are indicated with dotted lines and grouped treatments are indicated with solid lines.

ANOVA: N versus all S treatments:  $F_{7,413}=4.19$ ,  $<0.001$ ; NN versus all S treatments:  $F_{7,392}=2.65$ ,  $P<0.02$ ). Larvae appeared in colonies after 3 weeks. Numbers of larvae differed significantly across treatments ( $F_{20,175}=2.419$ ,  $P=0.001$ ; Fig. 4b). SS and NS nests tended to produce more larvae per foundress than other treatments, while NN nests tended to produce fewer. The number of pupae produced per foundress did not differ across treatments ( $F_{12,195}=0.924$ ,  $P=0.52$ ; Fig. 4c). The small number of NN nests without complete offspring mortality by the pupal stage ( $N=4$ ) reduced the power to detect potential differences statistically for this treatment group.

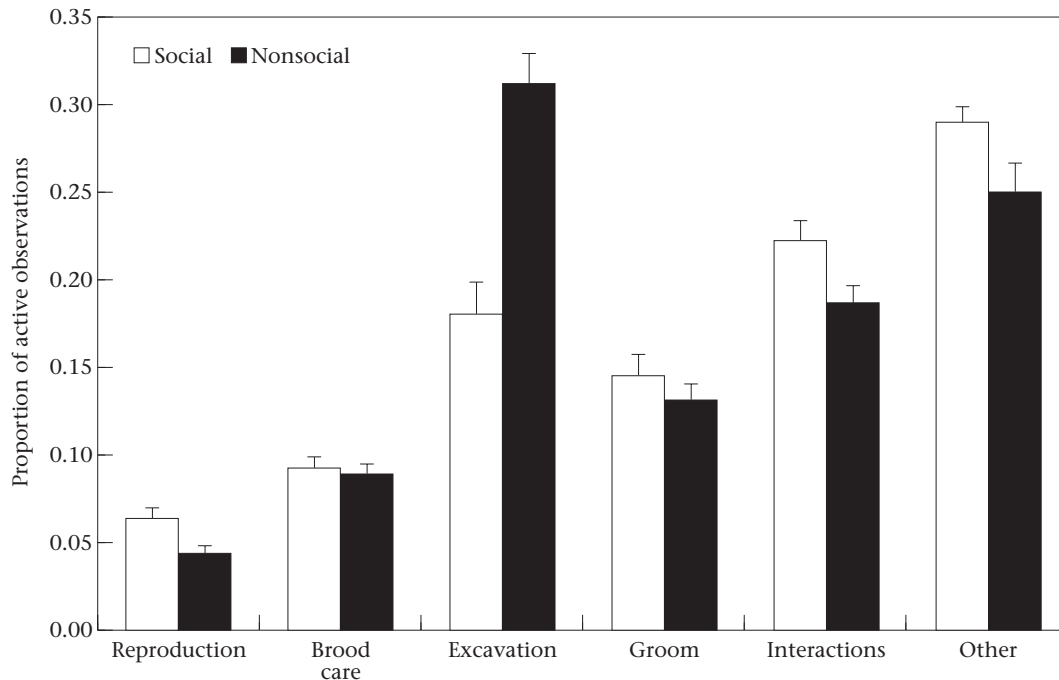
## Experiment 2

N foundresses were significantly more active within nests than S foundresses (paired  $t$  test:  $t_9=3.19$ ,  $P=0.01$ ). However, N and S foundresses showed no significant differences in either proximity to or contact with the brood (proximity:  $t_9=0.928$ ,  $P=0.38$ ; contact:  $t_9=1.098$ ,  $P=0.30$ ). At least one foundress was in contact with the brood in 54.1% of observation periods. When active, nonsocial and social foundresses distributed their time among activities similarly ( $G$ -test of independence:  $G_5=5.52$ ,  $P=0.36$ ; Fig. 5). Aggressive interactions were observed in two pairs. In pair 9, the S foundress was seen standing on the N foundress for two observation periods on days 4 and 5. The N foundress was subsequently observed lying on her side and back for two observation periods, after which she was found dead on day 6. In pair 10, the N foundress was observed standing on the S foundress during five observation periods throughout the duration of the experiment. No obvious sign of injury to the S foundress resulted from these interactions.

## DISCUSSION

Group-nesting ants have often been referred to as 'co-operative' colony founders, because individuals appear to cohabit nests peacefully and invest equally in colony growth (Rissing & Pollock 1988). However, recent studies of foundress interactions, especially in the imported fire ant, *Solenopsis invicta*, suggest that individuals within these social groups are competitive, although conflict is often subtle and difficult to detect when all individuals employ similar competitive strategies (Bernasconi & Keller 1996, 1998; Bernasconi & Strassmann 1999). The results of this study suggest that although a reduction in conspecific aggression is a necessary precursor to successful social life, interfoundress conflict has produced a number of adaptive shifts in foundress behaviour in *M. pergandei*. Normally nonsocial foundresses behave more cooperatively than social foundresses in their investment decisions when placed in a social context. In contrast, social foundresses show novel competitive strategies in both their interactions and investment patterns that allow them to exploit such cooperative behaviour within group nests successfully.

Nonsocial and social foundresses showed marked differences in levels of initial aggression, which reflect differences in founding patterns in the field. Nonsocial foundresses generally behaved aggressively when forced into nests with conspecifics. Such aggression most likely serves a territorial function in a field context, although the rarity of obvious injury or foundress death despite sustained foundress contact suggests that potential nest sites in the field may be relatively common and not a resource subject to intense foundress competition. Although not physically dangerous, foundress aggression may have interfered with parental behaviour. Nonsocial pairs suffered from high rates of egg rot and few pairs successfully produced workers. Clearly, successful social grouping requires a significant reduction in intraspecific aggression, even when such aggression is



**Figure 5.** Distribution of activities performed (mean+SE) during observation periods by nonsocial and social foundresses within mixed nests of *M. pergandei*.

largely ritualized as appears to be the case in nonsocial *M. pergandei*.

Although nonsocial foundresses were initially more aggressive, they were also more likely to suffer negative fitness consequences from such interactions. Initial aggression in NN pairs rarely escalated to more serious injuries. In mixed groups, however, the nonsocial member of the pair was significantly more likely to die than her social counterpart (Fig. 1). The majority of these deaths were early on in the experiment and dead foundresses were often dismembered. Dead foundresses in same-type paired treatments were usually intact, suggesting that dismemberment was not simply a general result of postmortem cannibalism by protein-starved nestmates (Tschinkel 1993). Instead, dismemberment of these foundresses probably reflects injuries sustained before death from particularly aggressive interactions in mixed nests. Such fatal injuries were significantly skewed towards the nonsocial member of these pairs, indicating that social foundresses, when provoked by initially aggressive foundresses, were more successful at escalated fighting than their opponents (Fig. 2). Such conditional aggressive behaviour in social foundresses suggests that the lack of overt aggression in SS pairs should not be interpreted as unconditional intraspecific tolerance. Social *M. pergandei* foundresses in natural nests do become aggressive after workers begin to forage (Rissing & Pollock 1987). The high value of the colony at this stage increases the risks that individuals will incur to win, and social foundress fighting inevitably leads to the death of all but one foundress (Rissing & Pollock 1987). The high proportion of nonsocial foundresses killed in mixed nests suggests that social foundresses assess their nestmates' intentions even outside of the colony context in which aggression is

normally expressed and respond to aggressive signals with a novel level of intensity. Thus, the social context appears to have selected for an escalation of retaliatory behaviour that is only visible when aggression is initiated by socially naïve individuals.

When kept alone, nonsocial and social foundresses were equally successful at starting colonies and produced the same number of pupae (Figs 1, 4c), but social foundresses used fewer resources to produce these offspring than their nonsocial counterparts (Fig. 3). This suggests that sociality has caused a reduction in individual investment. Foundresses may benefit from withholding their body reserves when in groups, as higher body mass can increase subsequent fighting ability and/or reduce starvation risk relative to other foundresses while the young colony is ergonomically stressed (Rissing & Pollock 1987; Bernasconi & Keller 1998). Because the starting colony is a closed system, however, reducing levels of investment must remove resources from brood production. Although initial worker numbers were not affected, the significant difference in egg numbers later in the second half of the colony founding period suggests that fewer workers may be produced in the second cohort in social foundress colonies. Such an effect could be a significant fitness cost of social foundress behaviour, as young colonies are particularly vulnerable to starvation and predation in the first few months after worker eclosion. On the other hand, however, reducing investment from the second cohort, which merely enlarges a pre-existing workforce, is considerably less damaging to colony survival than reducing investment into the first cohort, upon which foundresses depend entirely for initial nutritional input. By delaying investment reduction until the first cohort is produced, the group-level fitness costs of withholding

body resources may be minimally compromised by individual-level fitness gains.

When placed in same-type pairs, both nonsocial and social strategy foundresses maintained the investment patterns they displayed in a solitary context. This differs from investment patterns in the fire ant *Solenopsis invicta*, in which foundresses facultatively reduce energetic investment in the presence of conspecifics (Bernasconi & Keller 1998). However, individual flexibility should be more important for *S. invicta* because the incidence of group founding in this species is often lower than for social *M. pergandei*, where over 90% of foundresses join groups (Markin et al. 1972; Cahan et al. 1998; Bernasconi & Strassmann 1999).

When placed into a social context, normally nonsocial foundresses were more 'cooperative' than normally social foundresses, investing more resources into colony growth at the expense of their nutritional condition. This high level of investment had strong potential fitness costs when exposed to a social foundress strategy. Nonsocial foundresses were effectively exploited in mixed nests, investing significantly more resources than when alone while social foundresses invested even fewer. Differences in female investment could be generated by several mechanisms: social foundresses may lay fewer eggs, they may perform less work within the nest or perform only less energetically costly tasks, or they may consume excess eggs within the nest. It is likely that both foundresses are participating in initial egg laying, as per-foundress productivity was similar across treatments during the first 3 weeks. Social foundresses in mixed nests did spend significantly more time inactive, which may reduce the metabolic costs associated with colony founding. It is unclear, however, whether this difference can explain overall differences in energetic investment. Nonsocial foundresses may be particularly active in an unfamiliar social context and not show higher levels in their normal solitary nest environment. There was no evidence that social and nonsocial foundresses differ in the distribution of tasks performed (Fig. 5). The most likely mechanism of reproductive investment differences across nest treatments suggested by this study is egg consumption, especially during later stages of colony founding.

All colonies produced far more eggs than workers (Fig. 4). High egg production and subsequent reduction in brood number is often attributed to consumption of eggs by larvae (Baroni Urbani 1991). All colonies containing at least one social foundress showed this pattern, including mixed colonies; however, both single and paired nonsocial foundress colonies did not show a decline in egg number even when larvae were present in their nests. This raises the possibility that social foundresses may be consuming eggs. Oophagy is a common component of reproductive competition in other Hymenoptera, including ants (Sinha et al. 1993; Nakata & Tsuji 1996; Bernasconi & Strassmann 1999). If nonsocial foundresses are stimulated by declining egg number to produce more eggs, they would tend to increase their investment while providing a continuing source of eggs for social foundresses to consume. Thus, even if social foundresses cooperate fully during the egg-laying phase

of colony development, they can recoup some of those resources later through competitive egg consumption.

This study demonstrates that there are two distinct stages to social evolution that involve different behavioural changes. In order for sociality to evolve, there must be selective advantages to grouping that outweigh the costs of sharing a nest. Such fitness benefits would favour the loss of territorial aggressive behaviour to permit successful nest cohabitation. Once grouping evolves, however, individuals should attempt to skew those benefits towards themselves, even at the cost of group productivity, until the point where the reduction in group benefits would put the actor below the fitness level of a solitary individual. This creates a tight balance between cooperative and selfish behaviours within social groups, as the costs and benefits of each change over time. In *M. pergandei*, social foundresses retain full levels of reproductive investment at the beginning of colony founding, when the potential impacts on colony survival are greatest. As the founding period progresses, social foundresses begin to reveal their competitive tendencies by progressively reducing their investment, culminating in the fatal fighting and group dissolution that occur when workers emerge. The magnitude of this shift away from cooperation, and the fitness advantages associated with within-group exploitative strategies, become clearly evident only when viewed in comparison with individuals not adapted to social life.

### Acknowledgments

I would like to thank Steven Rissing for valuable discussions and advice on experimental design and interpretation. Thanks also to Ken Helms, who helped extensively with field collections. Jennifer Fewell, Patricia Gowaty, Jennifer Gee, Glennis Julian and two anonymous referees provided helpful comments on the manuscript. Allen Muth generously provided laboratory space and equipment at the Boyd Deep Canyon Reserve in Palm Desert, California. This work was supported by National Science Foundation grant DEB-9623487 to S. Cahan and S. W. Rissing.

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