

Effects of Foundress Number on Brood Raids and Queen Survival in the Fire Ant *Solenopsis invicta*

Author(s): Eldridge S. Adams and Walter R. Tschinkel

Source: *Behavioral Ecology and Sociobiology*, Vol. 37, No. 4 (1995), pp. 233-242

Published by: [Springer](#)

Stable URL: <http://www.jstor.org/stable/4601133>

Accessed: 03-11-2015 17:34 UTC

REFERENCES

Linked references are available on JSTOR for this article:

http://www.jstor.org/stable/4601133?seq=1&cid=pdf-reference#references_tab_contents

You may need to log in to JSTOR to access the linked references.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Springer is collaborating with JSTOR to digitize, preserve and extend access to *Behavioral Ecology and Sociobiology*.

<http://www.jstor.org>

Eldridge S. Adams · Walter R. Tschinkel

Effects of foundress number on brood raids and queen survival in the fire ant *Solenopsis invicta*

Received: 9 December 1994 / Accepted after revision: 14 May 1995

Abstract In several ant species, colonies are founded by small groups of queens (pleometrosis), which coexist until the first workers eclose, after which all but one queen is killed. It has been hypothesized that, by producing a larger cohort of workers, cooperating queens may increase colony success during brood raids, a form of competition in which brood and workers from losing nests are absorbed into winning colonies. To test whether this benefit is sufficient to favor pleometrosis, newly mated queens of the fire ant *Solenopsis invicta* were assembled in groups of one, two, three, or four, reared in the laboratory until the first workers eclosed, then planted in the field in replicated assemblages. The proportion of colonies engaging in brood raids increased with average foundress number per nest and with colony density but was unaffected by variance in foundress number among interacting colonies. Within mixed assemblages of single-queen and multiple-queen colonies, queen number had no effect on the likelihood of engaging in raids or the probability of nest survival through the brood raiding period. However, following nearly 30% of raids, queens moved to new nests and displaced the resident queens. When queen relocation and subsequent mortality were accounted for, it was found that the survival of queens from four-queen groups was substantially higher than that of solitary queens. By contrast, the survival of queens from two-queen colonies was no greater than that of solitary queens. These results show that the competitive advantages of multiple-queen colonies are sufficient to counterbalance the increased mortality of queens within groups only when the number of foundresses is greater than two and when colonies are founded at high den-

sity. When colonies lose brood raids, the workers appear to abandon their mothers to join surviving colonies. However, in laboratory experiments, queens attempting to enter foreign nests were significantly more likely to displace the resident queen if their own daughters were present within the invaded nest. Thus, workers may be able to bias the probability that their mother rejoins them and displaces competing queens.

Key words *Solenopsis invicta* · Brood raids · Population dynamics · Pleometrosis · Cooperation

Introduction

Nest founding by multiple queens, or pleometrosis, occurs in several species of ants in which mated queens cluster at high densities following nuptial flights (reviewed by Rissing and Pollock 1988; Heinze 1993; Herbers 1993; Roisin 1993). These queens initially cooperate, sharing in nest excavation and brood-care, grooming one another, and depositing their eggs in a common pile. However, in several well-studied species, queen fighting or executions by workers eliminate all but one queen soon after the first workers emerge (Bartz and Hölldobler 1982; Tschinkel and Howard 1983; Rissing and Pollock 1986; Peeters and Andersen 1989; for exceptions see Hölldobler and Carlin 1985; Mintzer 1987). Since co-founding queens in these species are usually unrelated (Hagen et al. 1988; Nonacs 1989) and probably cannot distinguish which queen is most likely to survive (Roisin 1993), pleometrosis appears to be an instance of cooperation driven by mutualism (Rissing and Pollock 1988; Nonacs 1992; Roisin 1993) or group selection (Mesterton-Gibbons and Dugatkin 1992). Studies on this phenomenon have sought to understand the conditions under which the advantages of group formation outweigh the disadvantages of competition among queens within groups.

E. S. Adams (✉)
Department of Biology, University of Rochester, Rochester,
NY 14627, USA

W. R. Tschinkel
Department of Biological Science, Florida State University,
Tallahassee, FL 32306 USA

Empirical studies on pleometrotic ants have revealed several possible advantages of increased foundress number. During the initial stages of colony founding, pleometrosis lowers the mortality rates of queens in some species (Waloff 1957; Bartz and Hölldobler 1982), but not in others (Tschinkel and Howard 1983; Tschinkel 1993). The total number of workers reared by the colony during the claustral phase of nest founding rises with foundress number up to a maximum, then declines with additional queens (e.g., Bartz and Hölldobler 1982; Tschinkel and Howard 1983; Tschinkel 1993). In *S. invicta*, the total number of workers produced reaches a maximum between four and seven queens (Tschinkel 1993). However, there are no consistent economies of scale: the rate of worker production per queen may increase (Bartz and Hölldobler 1982), remain the same (Rissing and Pollock 1991), or decline (Tschinkel 1993) with increasing foundress number. High initial rates of worker production may benefit colonies in many ways: by improving the probability of successful nest construction (Peeters and Andersen 1989), by increasing survival through the first winter (Tschinkel and Howard 1983), by allowing reproduction at an earlier age (Tschinkel and Howard 1983), by allowing earlier production of replete workers (Bartz and Hölldobler 1982), or by improving the colony's competitive ability in struggles with other incipient colonies (Bartz and Hölldobler 1982; Rissing and Pollock 1987, 1991; Tschinkel 1992b). This study focusses on the effects of foundress number on interactions among young colonies.

The hypothesis that competition among colonies favors pleometrosis is partially supported by laboratory and field studies. Competition among colonies at the incipient stages is often severe (Pollock and Rissing 1989; Tschinkel 1992a) and the probability of victory in pairwise laboratory contests increases with worker number (Bartz and Hölldobler 1982; Rissing and Pollock 1987, 1991; Tschinkel 1992b). However, to support this hypothesis, it is not enough to show that larger colonies are more likely to outcompete small ones. Since only one queen per association will survive to produce reproductive offspring, competition among colonies is sufficient to favor pleometrosis only if the probability of victory of colonies founded by n queens is more than n times greater than that of colonies founded by solitary queens. If this condition does not hold, then the average survival of solitary queens will exceed that of cooperating queens and competition among colonies by itself will not favor pleometrosis. In addition, this hypothesis requires that competitive encounters among incipient colonies be frequent or else this advantage of pleometrosis cannot be manifested. At present, the ecological variables affecting competition among young ant colonies are poorly known. The decision by queens to found colonies in groups alters both the density and sizes of incipient colonies, which may in turn affect the intensity of com-

petition. Furthermore, the competitive performance of single- and multiple-queen colonies are best compared in the field since encounters staged in small laboratory containers may alter the behavior and intensity of competition (Buschinger et al. 1980) and may exaggerate the apparent importance of competition in comparison to other selective forces. Most tests of the hypothesized advantages of pleometrosis have been conducted in the laboratory (but see Bartz and Hölldobler 1982; Tschinkel 1993).

Among ants displaying pleometrosis, incipient colonies of several well studied species compete by brood raiding (*Myrmecocystus mimicus*: Bartz and Hölldobler 1982; *Solenopsis invicta*: Stamps and Vinson 1991; Tschinkel 1992a, b; Adams and Tschinkel 1995a, b; *Messor* (= *Veromessor*) *pergandei*: Pollock and Rissing 1989). In brood raids, workers move eggs, larvae, and pupae between nests until they are concentrated within the nest of the victorious colony. Workers from the raided colony then join the winning colony, leaving behind their mother (Bartz and Hölldobler 1982; Rissing and Pollock 1987; Tschinkel 1992b). Queens whose colonies have been raided may subsequently attempt to enter surviving nests, where they sometimes displace the original queens (Bartz and Hölldobler 1982; Rissing and Pollock 1987; Stamps and Vinson 1991; Tschinkel 1992a; Adams and Tschinkel 1995a). Thus, workers that move to new nests after brood raids may be rejoined by their mothers (Rissing and Pollock 1987; Pollock and Rissing 1989). To determine if pleometrosis is favored, the effects of queen number on competitive success must be followed beyond brood raids to include this period of queen relocation and usurpation (e.g., Rissing and Pollock 1987).

This study reports field experiments on the effects of variation in queen number on brood raid competition in the monogyne form (Ross and Fletcher 1985a) of the fire ant *S. invicta*. Several related questions were addressed by experimentally planting assemblages of incipient colonies in the field and by recording the occurrence and outcomes of brood raids. First, to examine factors controlling the frequency of raids, we manipulated the mean and variance of foundress number across replicate assemblages of colonies planted at different densities. The results show how the tendency of queens to found nests cooperatively or in proximity to one another affect the intensity of brood raid competition. Second, we compared the fates of single-queen and multiple-queen colonies within competing populations. By painting queens with distinctive marks and excavating surviving nests, it was possible to follow individual queens throughout the period of brood raiding and queen usurpation. Third, we examined a possible consequence of the abandonment of queens by their daughters after losing a brood raid. Specifically, we tested whether queens are better able to enter a foreign colony and displace the resident queen if the

colony contains their own daughters than a colony of similar size in which all the workers are unrelated to the invading queen.

Methods

Collection and rearing of queens

Mated queens were collected following nuptial flights in Tallahassee, Florida, in the spring of 1992 and 1993. The queens were sorted randomly into various numbers of foundresses (1, 2, 3, or 4) and maintained in the laboratory in test tubes supplied with moist cotton. In these conditions, queens lay eggs and rear developing workers using stored energy reserves (Tschinkel 1993). If queens within multiple-queen associations died within the first 7 days, they were replaced with queens of the same age; thereafter, associations with dead queens were discarded. Colonies which produced unusually small broods or diploid males (Ross and Fletcher 1985b) were also discarded. When workers began to eclose, the number of workers and pupae within each colony was counted to within 10%. For further details, see Adams and Tschinkel (1995a).

Preparation of field sites

Incipient colonies were planted in an unshaded spray-irrigated field. Prior to planting, mature colonies were removed and the fields were tilled, raked and flattened to homogenize conditions (see Adams and Tschinkel 1995a for details of methods). Adjacent assemblages of colonies were separated by at least 4 m. The position of each planted colony was marked with a small metal tag and an upright wooden label.

Planting assemblages of colonies

Colonies were transferred to small artificial nests, each consisting of a block of plaster, measuring approximately $5 \times 2 \times 2$ cm, with a 2 mm diameter hole drilled through the block and a chamber 12 mm in diameter and 15 mm deep drilled at one end to mimic the brood chamber naturally excavated by the queen. The artificial nests were wrapped temporarily in paper to prevent escape by the ants during transport to the field. To plant a colony, the paper was removed and the artificial nest was inserted into a hole 7 cm deep with the brood chamber at the bottom. The nest was then covered with soil. All plots were watered lightly after planting was completed to prevent desiccation.

Monitoring planted colonies

Plots were surveyed at least once per hour from 8:00 to 12:00 a.m. and from 6:30 to 8:30 p.m., when most raids occur (Tschinkel 1992a; Adams and Tschinkel 1995a). Each colony was examined for worker activity or raids. When raids were seen, additional surveys were added to allow more complete descriptions. To prevent biases in comparisons of raid frequencies, these additional surveys were carried out on all plots. Because worker activity appears to be sensitive to soil moisture, all plots were watered in the evening of any day that it did not rain. To help distinguish active from inactive colonies, nest entrances were sealed with moist soil at the end of each day. Colonies with active workers quickly excavated a new entrance, while nests of dead colonies remained sealed.

Because most raids are initially bi-directional and because many raids involve more than two colonies (Tschinkel 1992a, b; Adams

and Tschinkel 1995a, b), it is usually not possible to identify which colony is winning during field surveys. We therefore report the percentage of colonies that engage in raids as a measure of the intensity of competition. This percentage provides a minimum estimate since some raids were undoubtedly not seen. However, in some replicates, more than 85% of colonies were seen to engage in raids and most raids were observed during more than one census, suggesting that only a small fraction of raids were not recorded.

Experiment 1: effects of queen number and colony density on brood raids

In a two factor experiment, assemblages of colonies were planted and monitored for brood raids and colony survivorship. Each assemblage consisted of 16 colonies planted in a 4 by 4 square grid. Treatments varied in the distance between rows and columns (high density: 30 cm; low density: 60 cm) and in the number of foundress queens per planted colony (1, 2 or 4). These values correspond to natural densities and queen numbers. In a large naturally founded cohort, the mean nearest neighbor distance for incipient colonies was approximately 60 cm, with a mode near 30–40 cm (Adams and Tschinkel 1995b). In several natural mating flights, the mean number of queens per founded colony ranged from 1.11 to 3.36 (Tschinkel and Howard 1983). Within each experimentally planted assemblage, the number of queens per planted colony was constant. Five replicate assemblages were planted for each treatment; thus, the experiment included a total of 6 treatments, 30 assemblages, 480 colonies, and 1,120 queens.

The mated queens were collected following nuptial flights on 17 and 26 May 1992. Assemblages were planted when sufficient numbers of workers had eclosed (1 to 11 July) so that equal numbers of replicates of each treatment were planted on any given day. All but one colony survived planting, as judged by whether the workers excavated a colony entrance and began to forage. Each plot was monitored for 10 or 11 days, by which time raids had ceased.

Experiment 2: effects of variation in queen number on brood raids

To examine the effects of variation in queen number on brood raids, assemblages of 16 colonies were planted in two replicated treatments. Each replicate contained 32 queens in 16 colonies. In the first treatment (constant queen number), each colony had two foundresses, while in the second treatment (variable queen number), eight one-queen colonies and eight three-queen colonies were planted in randomized positions. For each replicate, colonies were planted in a 4 by 4 square grid with 30 cm between rows and columns. Five replicate assemblages of each treatment were planted on 12 July 1992 and monitored for 10 days, by which time raids had ceased. In total, there were 2 treatments, 10 assemblages, 160 colonies, and 320 queens.

Experiment 3: relative success of single- and two-queen colonies

This experiment was designed to compare the success of single-queen and two-queen colonies within interacting groups. To vary the intensity of competition, colonies were planted at two different densities. Each replicate plot contained ten single-queen and ten two-queen colonies in a 4 by 5 grid. The positions of one- and two-queen colonies were determined by stratified random placement (Greig-Smith 1983). A single randomly generated pattern was used for all replicates. Six replicate assemblages were planted at each of two densities: high density (20 cm between rows and columns) and low density (60 cm between rows and columns). In all, there were 2 treatments, 12 assemblages, 240 colonies, and 360 queens. Brood raids and colony activity were monitored for three to four days, after which surviving colonies were excavated.

Experiment 4: effect of foundress number on queen survival and usurpation success

Mated queens were collected following the nuptial flight of 29 May 1993 and assigned randomly to one-, two- or four-queen colonies. Prior to planting, each colony was censused and each queen was painted with a color that identified her original colony. Shortly after the first workers emerged, the numbers of workers and pupae in each colony were counted.

One goal of this study was to measure rates of queen relocation. In order to mimic natural nests more closely, a modified planting method was used. First, the soil was watered to prevent desiccation. For each colony, a narrow hole was prepared by inserting a 2 mm wide nail 7 cm into the soil, matching the depth of the chambers naturally excavated by the queens. To prevent escape by the ants, a ring of plastic pipe, measuring 10.5 cm in diameter, was coated in fluon (Northern Products Inc., Woonsocket, R.I.) and inserted into the soil around the artificial chamber to form a barrier 3–4 cm high. The test tube containing the colony to be planted was then placed within this ring and the cotton plug was removed. Workers quickly discovered the artificial chamber and moved the colony below ground, usually within 30 min, then plugged the entrance with soil until it was just wide enough to allow passage by workers. Colonies were planted in pairs separated by only 5 cm to ensure a high likelihood of raiding. Fifty-nine pairs consisted of two single-queen colonies; 73 pairs consisted of a single-queen colony and a two-queen colony; 71 pairs consisted of a single-queen colony and a four-queen colony. Each colony was isolated within its own ring during planting. After 12 h, the rings were removed and a single ring, also coated with fluon, was placed around the pair of entrances to increase the probability of encounters. Adjacent pairs were separated by at least 2.5 m to prevent raids between replicates. Two to three days after planting, each nest was carefully excavated to record the locations of workers and brood and to recover marked queens. Cases in which brood raids did not occur, in which the chamber containing the winning colony and queen could not be located, or in which the queens' paint marks were not visible during microscopic examination were excluded. Colonies were planted between 17 and 23 July and were excavated between 19 and 25 July to recover queens, workers, and brood.

Experiment 5: effect of daughters on the ability of invading queens to displace resident queens

This experiment was designed to test whether, after losing a brood raid, a queen is better able to enter a surviving colony and displace the resident queen if she is the mother of some of the workers within the invaded colony. This circumstance arises when abandoned queens are able to find the colony to which their daughters have moved. Mated queens were reared singly in test tubes until their workers began to eclose. Each colony was housed separately and fed dilute honey daily until there were at least ten workers per colony. The number of workers within each colony was counted and the queen was painted with distinctive colors on the sides of her thorax.

Half of the 160 colonies were randomly selected as "resident" colonies. Each resident was provided with a plastic cup (535 ml) containing moist, sifted soil to a depth of 8 cm and with the upper rim coated with fluon to prevent escape. A hole 2 mm wide and 7 cm deep was prepared. The test tube containing the resident colony was unplugged and placed on the surface of the soil. The ants quickly moved below ground using the hole provided as a nest chamber. The test tubes were removed and the resident colonies were left overnight to allow the ants to modify the nests and to become accustomed to their new environment.

The remaining 80 colonies were presented to the resident colonies in simulated raids. For each raid, the marked queen from a single "intruder" colony was removed and held aside by herself. The test tube containing her brood and workers was then placed on the sur-

face of the soil containing the resident colony. The brood from the introduced colonies was carried into the resident nest and the workers entered the resident colonies as well. All 80 colonies were "raided" in this fashion within approximately 3.5 h. At the end of this period, the marked queens from the "intruder" colonies were introduced to cups containing the resident colonies. There were two treatments:

1. In 40 cases, the queen was introduced to the colony containing her own brood and workers. In this case, she was the mother of approximately one half the active workers within the colony.

2. In the remaining 40 cases, the queen was introduced to a container in which she was related neither to the resident queen nor to the brood and workers that had been raided. Thus, these treatments differ only in the relationship of the introduced queen to the raided brood and workers.

The introduced queens were observed for 2.5 h to monitor their ability to enter the resident colonies and to record instances of attack by workers visible on the surface of the soil. Each container was checked each day for 4 days to record the identity of any dead queens discarded from the nest. On the 5th day, the soil was carefully excavated to establish the identity of surviving queens.

Results

Experiment 1: effects of queen number and colony density on brood raids

Augmenting the number of foundress queens increased the total numbers of workers (Kruskal-Wallis $H = 117.0$; $df = 2$; $P < 0.001$) and pupae ($H = 315.8$; $P < 0.001$) produced in the first cohort; however, the production per queen declined with increasing queen number (Fig. 1; workers: $H = 651.8$, $df = 2$; $P < 0.001$; pupae: $H = 211.5$, $P < 0.001$).

Queen number and distance between colonies were treated as fixed factors in a two-way analysis of variance. Since there was no significant evidence for unequal variances of the proportions of colonies raiding among the six treatments ($F_{\max} = 10$, NS; Sokal and Rohlf 1981) and no significant deviations from normality for any of the treatments (Lilliefors test, $P > 0.2$ in all cases), the untransformed data were used. Both the distance between colonies ($F_{1,24} = 65.3$, $P < 0.001$) and the number of foundresses per colony ($F_{2,24} = 10.6$; $P < 0.001$) significantly affected the proportion of colonies that engaged in brood raids (Fig. 2). There was no significant interaction between these factors; together, they accounted for 78% of the variation in the proportion of colonies raiding. The greatest rate of raiding was seen on the 2nd day following planting (15.0% of colonies) and only one raid was seen after the 8th day.

Experiment 2: effects of variation in queen number on brood raids

All colonies survived planting and began to forage. There were no significant differences in raiding or

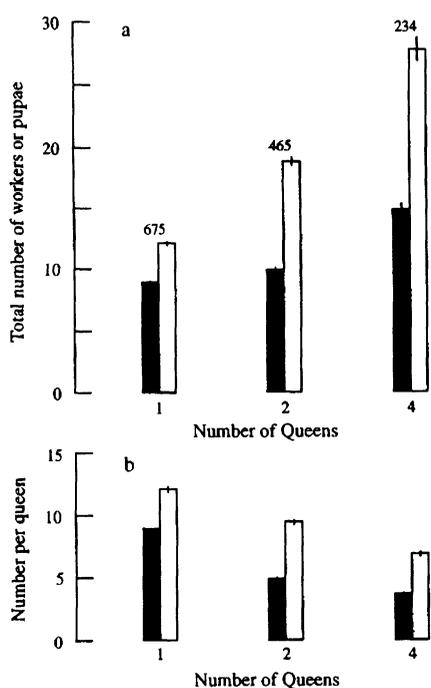


Fig. 1 **a** The effect of foundress number on the mean (\pm SE) production per colony of workers (*solid bars*) and pupae (*open bars*) prior to the onset of brood raids. The number of colonies censused is shown above the bars. **b** The same data expressed as production per queen

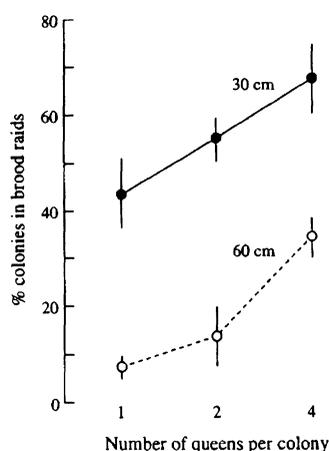


Fig. 2 The effect of foundress number per colony and distance between colonies on the proportion of colonies participating in brood raids (mean \pm SE). Each *point* is based on five replicate assemblages of 16 colonies each

survival between plots composed entirely of two-queen colonies (“constant queen number”) and plots composed of a mixture of single- and three-queen colonies (“variable queen number”; Table 1). Within plots with variable queen number, no significant differences were found between the fates of single-queen and three-queen colonies (Table 1). Raids among single- and three-queen colonies were common, and some raids involved more than two colonies (e.g., Fig. 3).

Experiment 3: relative success of single- and multiple-queen colonies

Colonies were more likely to engage in raids when planted 20 cm apart than when planted 60 cm apart (Table 2). There was no evidence of an effect of distance on either the number of colonies surviving planting (19.3 ± 0.2 versus 19.7 ± 0.2 ; $df = 10$; $t = -1.118$, NS) or on the proportion of colonies surviving at least three days (Table 2). Since colony excavations were begun after three days, survivorship was not followed any further. Within plots, no effect of queen number on colony performance was detected (Table 2).

After 3 days, active colonies were excavated; however, few brood chambers with surviving queens were found. Among excavated colonies containing live queens and workers, the queens were more often from two-queen colonies. With 20 cm spacing, 12 of 17 (70.6%) surviving colonies contained one or both queens from a two-queen colony; the remainder were from single-queen colonies. With 60 cm spacing, 8 of 14 (57.1%) nests contained one or both queens from a two-queen colony. Neither of these ratios was significantly different from 50% (one tailed binomial test, NS for both proportions). The difference in percentages did not differ significantly with spacing ($\chi^2 = 0.61$; $df = 1$; NS). When the data were combined, the fraction of surviving colonies that were founded by two queens was not significantly more than 50% (20 out of 31 cases, one-tailed binomial test, $P = 0.075$).

Experiment 4: effect of foundress number on queen survival and usurpation success

When colonies founded by solitary queens were paired with colonies founded by one, two or four queens, raids were seen within 66.5% of planted pairs – a conservative estimate of raiding, since observations were not continuous. Careful excavations of nests revealed other cases in which raids had occurred and allowed determination of the outcome. A colony was judged to have won a raid when the brood and workers from both colonies were consolidated within its nest chambers near the queen (or queens) and when queens from the opposing colony were not present. Because some queens migrate to surviving nests following brood raids, the success of single- and multiple-queen colonies is best compared after migrations and usurpations have taken place by recovering individually marked queens. Examination of paint marks on queens in the winning colonies indicated queen relocation in 40.6% of contests ($n = 101$); that is, one or more queens planted moved from their original nest site to an opponent’s nest site where they replaced the original queens (Table 3).

In contests between single-queen colonies and two-queen colonies, the two-queen colony was significantly more likely to win (Table 3). However, the two-queen

Table 1 Effects of variation in foundress number on the intensity of competition among colonies. Each replicate consisted of 16 colonies planted in a 4 × 4 grid with 30 cm between nearest neighbors. In replicates with constant queen number, each colony was

founded by two queens. In replicates with variable queen number, half the colonies were founded by a single queen and the other half by three queens. Within these assemblages, the fates of single-queen colonies and three-queen colonies were compared

Treatment	<i>n</i>	Colonies per replicate	% Colonies in raids (mean ± SE)	Median date of colony death (days) (mean ± SE)
Comparisons between treatments				
Constant queen number	5	16	42.5 ± 9.6	8.6 ± 0.2
Variable queen number	5	16	47.5 ± 3.2	9.2 ± 0.2
<i>t</i> -values ^a			-0.50 NS	-1.90 NS
Comparisons within assemblages with variable queen number				
Single-queen colonies	5	8	45.0 ± 0.03	9.2 ± 0.2
Three-queen colonies	5	8	50.0 ± 5.6	8.6 ± 0.7
<i>t</i> -values ^b			-0.78 NS	0.89 NS

NS = not significant at $P > 0.05$

^aUnpaired *t*-test, two-tailed

^bPaired sample *t*-test, two-tailed

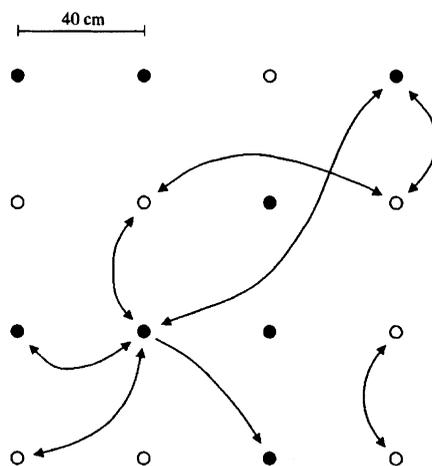


Fig. 3 Cumulative map of brood raids in an assemblage of eight single-queen (solid circles) and eight three-queen colonies (open circles). Lines connect colonies between which raiding workers moved; arrows indicate the direction of brood transport. Raids occurred 1, 2, 4, and 7 days after planting

Table 2 Comparison of the fates of single-queen and two-queen colonies in replicated assemblages. Each replicate consisted of 10 single-queen and 10 two-queen colonies placed randomly in a 4 × 5 grid of nest positions. Within replicates with a given colony spacing, there were no differences between single-queen and two-queen colonies in the percentage of colonies in raids or the percentages surviving at least three days (paired sample *t*-test, two tailed, all $P > 0.05$)

Colony spacing	<i>n</i>	Colonies	% Colonies in raids (mean ± SE)	% Surviving ≥ 3 days (mean ± SE)
60 cm	6	Single-queen	26.9 ± 10.2	88.3 ± 7.5
		Two-queen	24.8 ± 10.1	80.0 ± 6.8
		All	29.7 ± 9.9 ^a	84.0 ± 6.3 ^b
20 cm	6	Single-queen	73.9 ± 5.4	87.4 ± 6.7
		Two-queen	78.0 ± 5.3	80.6 ± 7.1
		All	75.8 ± 4.0 ^a	86.0 ± 4.5 ^b

^aUnpaired *t*-test, two-tailed, $t = 4.32$, $P < 0.05$

^bUnpaired *t*-test, two-tailed, $t = 0.27$, NS at $P > 0.05$

colony was not more than twice as likely to win (one-tailed binomial test with $p = 2/3$, $q = 1/3$, NS). Since only one of the two queens will live, this implies that the per queen survival did not differ between single- and two-queen colonies. On average, the two-queen colonies had larger populations of workers (14.6 ± 0.5 ; mean ± SE) than the single-queen colonies (9.9 ± 0.3) when planted. The difference in worker number between the two-queen colony and the one-queen colony was no greater in the 23 cases where the two-queen colony won than in the 12 cases where the single-queen colony won (Mann-Whitney $U = 104.5$, NS).

In contests between single-queen colonies and four-queen colonies, the four-queen colony was significantly more likely to win (Table 3); moreover, the four-queen colony was significantly more than four times as likely

to win (one-tailed binomial test with $p = 0.8$, $q = 0.2$, $P < 0.01$). Thus, even though three of the four queens were eliminated within each multiple-queen colony, the average survival of these queens exceeded that of solitary queens through the period of brood raiding and subsequent queen execution. In the replicate in which the single-queen colony won, the difference in worker number between the four-queen colony and the single-queen colony (15.0) was no lower than in the other 30 replicates (mean difference ± SE: 13.7 ± 0.6 , Mann-Whitney $U = 10.0$, NS).

During regular monitoring of the planted pairs of colonies, queens were sometimes seen wandering on the surface of the soil near their original nests, trying to enter the opposing nest, or under attack by workers. Live queens were seen outside of the nests in 34 of the 203 pairs of colonies (16.7%).

Table 3 Survival of colonies and queens during brood raids and subsequent queen executions. Each replicate consisted of a pair of brood raiding colonies. The probability of queen survival was calculated as the probability of colony survival divided by the number of queens

culated as the probability of colony survival divided by the number of queens

Treatment	Number of pairs	Probability of colony survival (<i>n</i>)		<i>P</i> ^a	Number of queens relocating	Probability of queen survival		<i>P</i> ^b
		Single queen	Multiple queen			Single-queen colonies	Multiple-queen colonies	
Single-queen colony versus single-queen colony	35	50% (35)	–	–	11	50%	–	–
Two-queen colony versus single-queen colony	35	34.3% (12)	65.7% (23)	< 0.05	8	34.3%	32.9%	NS
Four-queen colony versus single-queen colony	31	3.2% (1)	96.7% (30)	< 0.0001	12	3.2%	24.2%	< 0.01

NS = not significant at $P > 0.05$

^aOne-tailed binomial test for colony survival ($p = q = 0.5$)

^bOne-tailed binomial test for queen survival. The null hypothesis is that the relative probability of colony survival is equal to the relative number of queens (see text)

Experiment 5: effect of daughters' presence on the ability of invading queens to displace resident queens

survived (2.0 ± 1.3 versus 2.3 ± 0.5 ; Mann-Whitney $U = 174$, NS).

Ants in the resident colonies moved soil to narrow the entrance to the nest until it was scarcely wider than the workers. Introduced queens therefore needed to dig actively in order to enter the resident colony. No difference was seen in the fraction of queens that entered the nest chamber during the initial 150 min observation period or in the average time to entry (Table 4). During initial observations and daily monitoring, thirteen introduced queens and four resident queens were attacked by workers. During the first three days following introduction of the second queen, one of the two queens was evicted or killed and discarded in most colonies. Considering those cases with a single survivor, the introduced queen was significantly more likely to survive if her daughters were present than if no related workers were present (Table 4).

The difference between the number of workers produced by the resident queen and the number of workers produced by the intruder queen was calculated for those replicates in which the intruder's daughters were present. This value did not differ significantly between the 13 cases in which the intruder queen survived and the 24 cases in which the resident queen

Discussion

These results show that brood raids among incipient colonies can favor cooperative nest founding, but only under particular circumstances. As hypothesized, multiple-queen colonies produced more workers than single-queen colonies (Fig. 1), and colonies with larger numbers of workers were more likely to win brood raids (see also Bartz and Hölldobler 1982; Rissing and Pollock 1987, 1991; Tschinkel 1992b). However, since only one queen from each multiple-queen group survives the first few months of colony life, the competitive superiority of larger colonies will favor cooperative founding only if this advantage more than counterbalances the increased mortality of queens within groups. In competition with single-queen colonies, this condition was met for four-queen colonies but not for two-queen colonies.

When two-queen colonies were planted near single-queen colonies, the two-queen colonies were approximately twice as likely to survive brood raids. This

Table 4 Success of attempted usurpations as a function of the presence of the invading queen's daughters within the resident nest. The

mean time required for queens to enter the resident nest is given for all queens that entered within the first 150 min of observation

Treatment	<i>n</i>	Number entering within 150 min	Mean time to entry (min) \pm SE	Surviving queen(s)			
				Resident	Intruder	Both	Neither
Intruder's daughters present	40	34	40.9 \pm 8.8	24	13	1	2
Intruder's daughters not present	40	34	35.8 \pm 8.1	35	2	2	1
Significance			NS ^a	$P < 0.001$ ^b			

^aMann-Whitney U -test, $U = 810.5$, NS = not significant at $P > 0.05$

^bLog-likelihood ratio test, $G = 11.1$, $df = 1$

was true when the colonies were planted in pairs (experiment 4; 65.7% of 35 survivors were two-queen colonies) or in larger sets (experiment 3; 64.5% of 31 survivors were two-queen colonies). Combining these data, 64.2% of surviving colonies were founded by pairs of queens, while only 35.8% were founded by solitary queens. Since one of the two queens within the multiple-queen colonies was killed (or destined to be killed), the average survivorship of queens was nearly identical if they started colonies alone or in groups of two (Table 3). By contrast, colonies founded by four queens were far more likely to win brood raids than single-queen colonies. Even though three of the four queens were subsequently killed, the average survivorship of queens in four-queen colonies was higher than that of solitary queens when raids occurred (Table 3).

The relative performance of single-queen and multiple-queen colonies also depends upon the frequency of brood raids. Field experiments showed that raid frequency increased with colony density and with the average number of queens per colony (Fig. 2), consistent with the hypothesis that raids are initiated whenever workers discover other incipient colonies (Adams and Tschinkel 1995a, b). Average foundress number and colony density in turn depend upon the density of mated queens arriving within a given area (Tschinkel and Howard 1983). This suggests that there is a threshold density of mated queens above which queen cooperation is favored and below which solitary nest founding is favored. When mated queens colonize available habitat in high densities, many colonies are founded by groups of four or more queens (Tschinkel and Howard 1983) and brood raids are common (Adams and Tschinkel 1995a). In these conditions, queens founding colonies alone presumably fare poorly. But when initial queen density is low, brood raid competition may be too infrequent and queen number per colony too low to favor cooperative nest founding. *S. invicta* is native to South America and was introduced to the United States around 1918 (Lofgren 1986). In comparison to the southeastern United States, colonies of *S. invicta* are smaller and less abundant along roadsides in Brazil (Porter et al. 1992). While the ecology of colony founding has not been studied in detail in South America, the lower population density in Brazil suggests that brood raiding is no more likely to favor pleometrosis in the countries of origin than at out study sites in Florida.

High queen density is also associated with an increased variance in the number of queens per colony (Tschinkel and Howard 1983). However, when average queen number was held constant, an increase in the variance had no detectable effect on raiding or colony survivorship. This shows that the intensity of competition among colonies is not strongly affected by small changes in the group sizes chosen by newly mated queens.

It is conceivable that queens monitor the density of other foundresses when deciding whether to initiate colonies singly or in groups. After dropping their wings, queens move about on the surface of the soil examining other queens and potential nest sites (W. Tschinkel and E. Adams, personal observations). The encounter rate among queens provides information which may allow each queen to predict the eventual density of incipient colonies. If so, queens could adjust their preferred group size based on the likelihood of brood raid competition. In a related theoretical paper, Nonacs (1989) has shown that the optimal decision rule by ant foundresses depends upon the magnitude of pleometrotic advantage, which could vary with colony density. Thus, the preferred group size should be greater when queen density is higher. Consistent with this hypothesis, the average number of *S. invicta* foundresses per nest increases with the density of recently mated queens (Tschinkel and Howard 1983) and the statistical significance of queen aggregation rises with queen density in *Lasius pallitarsis* (Nonacs 1992). However, these patterns could also be the unselected consequence of increased encounter rates among queens if queens show fixed preferences for joining other queens during colony initiation.

In addition to superior brood raiding success, there are several other possible explanations for the evolution of pleometrosis. Pleometrosis may reduce exposure to predators during colony founding and the initial boost in colony size in multiple-queen colonies may increase colony fitness in other contexts, even after reduction to a single queen (Bartz and Hölldobler 1982; Tschinkel and Howard 1983). For example, larger colonies may be better able to survive the first winter and may be able to produce alate reproductives at an earlier age (Tschinkel and Howard 1983). Furthermore, most queens probably land at sites occupied by mature colonies of *S. invicta* or other ants. In this case, attacks by workers from mature colonies are likely to be a more important source of mortality than brood raids with other incipient colonies. There are currently few field data that would allow comparison of the fates of single- and multiple-queen colonies faced by these other challenges (but see Bartz and Hölldobler 1982; Tschinkel and Howard 1983). It is likely that several selective forces act in concert to govern queen number with brood raids contributing an occasional advantage to multiple-queen colonies.

When colonies lose brood raids, the workers join the winning colony leaving behind, at least temporarily, their mother and any other familiar queens (Bartz and Hölldobler 1982; Rissing and Pollock 1987; Tschinkel 1992a). Little aggression is seen among the workers from different colonies during or after raids (Bartz and Hölldobler 1982; Rissing and Pollock 1987; Stamps and Vinson 1991; Tschinkel 1992b). Newly acquired workers labor within the surviving colony and may even act as "traitor raiders," helping to transport brood from

their natal colony into the nest of the victorious colony (Tschinkel 1992a). It is possible that the lack of aggression among the first cohort of workers and the abandonment of mothers could be maladaptive consequences of the inability of workers from incipient colonies to recognize nestmates; however, recent experimental work has shown that the first cohort of workers in young colonies of *S. invicta* readily distinguish unfamiliar queens from familiar queens and that unfamiliar queens attempting to enter a colony are often vigorously attacked by resident workers (M. Balas and E. Adams, unpublished work). Alternatively, defection by workers may represent "hopeful co-emigration" of workers and their queens (Pollock and Rissing 1989); that is, workers that lose raids may move to surviving nests because their mother may subsequently be able to join them. In support of this hypothesis, experiment 5 shows that when a raided queen attempts to enter a foreign colony of a given size, her probability of success is greater if some of the workers are her own daughters. This may be because there are fewer unrelated workers resisting her entry or because her daughters are able to assist her displacement of the resident queen.

Worker relocation may be adaptive if colonies that lose brood during raids have little ability to replace the captured brood. The initial cohort of brood is fed by the foundresses, which deplete their internal energy reserves (Tschinkel 1993). Although workers forage and retrieve food soon after eclosion, the delay in the production of new workers coupled with the loss of weight by the queen (Tschinkel 1993) may doom raided colonies to failure. If so, a worker may enhance its inclusive fitness by joining surviving colonies and by assisting in the replacement of the resident queens by their own mother (Rissing and Pollock 1987). If the ability of queens to displace queens in other colonies is enhanced by having a larger worker force, this may provide an additional advantage of cooperative nest associations.

Acknowledgements We thank the Mission Road Biological Station of Florida State University and its manager Karen Graffius-Ashcraft for the opportunity to conduct field studies. Michael Balas, Deby Cassill, Christopher Jerome, Tom Macom, Vinod Srihari, and April Williford assisted with field work and data analysis. M. Balas, D. Cassill, and Don McInnes made helpful comments on the manuscript. This research was funded by a Fellowship in Science and Engineering from the David and Lucile Packard Foundation to E.S.A. and by NSF grant BSR-8920710.

References

- Adams ES, Tschinkel WR (1995a) Density-dependent competition in fire ants: effects on colony survivorship and size variation. *J Anim Ecol*, 64:315–324
- Adams ES, Tschinkel WR (1995b) Spatial dynamics of colony interactions in young populations of the fire ant *Solenopsis invicta*. *Oecologia*, in press
- Bartz SH, Hölldobler B (1982) Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behav Ecol Sociobiol* 10: 137–147
- Buschinger A, Ehrhardt W, Winter U (1980) The organization of slave raids in dulotic ants – a comparative study (Hymenoptera: Formicidae). *Z Tierpsychol* 53:245–264
- Greig-Smith P (1983) Quantitative plant ecology, 3rd edn. University of California Press, Berkeley
- Hagen RH, Smith DR, Rissing SW (1988) Genetic relatedness among co-foundresses of two desert ants, *Veromessor pergandei* and *Acromyrmex versicolor*. *Psyche* 95:191–201
- Heinze J (1993) Queen-queen interactions in polygynous ants. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 334–361
- Herbers JM (1993) Ecological determinants of queen number in ants. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 262–293
- Hölldobler B, Carlin NF (1985) Colony founding, queen dominance and oligogyny in the Australian meat ant *Iridomyrmex purpureus*. *Behav Ecol Sociobiol* 18:45–58
- Lofgren CS (1986) History of imported fire ants in the United States. In: Lofgren CS, Vander Meer RK (eds) Fire ants and leaf-cutting ants: biology and management. Westview, Boulder, pp 36–47
- Mesterton-Gibbons M, Dugatkin LA (1992) Cooperation among unrelated individuals: evolutionary factors. *Q Rev Biol* 67: 267–281
- Mintzer A (1987) Primary polygyny in the ant *Atta texana*: number and weight of females and colony foundation success in the laboratory. *Insectes Soc* 34:108–117
- Nonacs P (1989) Competition and kin discrimination in colony founding by social Hymenoptera. *Evol Ecol* 3:221–235
- Nonacs P (1992) Queen condition and alate density affect pleometrosis in the ant *Lasius pallitarsis*. *Insectes Soc* 39:3–13
- Nonacs P (1993) The economics of brood raiding and nest consolidation during ant colony founding. *Evol Ecol* 7:625–633
- Peeters C, Andersen AN (1989) Cooperation between dealate queens during colony foundation in the green tree ant, *Oecophylla smaragdina*. *Psyche* 96:39–44
- Pollock GB, Rissing SW (1989) Intraspecific brood raiding, territoriality and slavery in ants. *Am Nat* 133:61–70
- Porter SD, Fowler HG, MacKay WP (1992) Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *J Econ Entomol* 85:1154–1161
- Rissing SW, Pollock GB (1986) Social interaction among pleometrotic queens of *Veromessor pergandei* (Hymenoptera: Formicidae) during colony foundation. *Anim Behav* 34: 226–233
- Rissing SW, Pollock GB (1987) Queen aggression, pleometrotic advantage and brood raiding in the ant *Veromessor pergandei* (Hymenoptera: Formicidae). *Anim Behav* 35:975–981
- Rissing SW, Pollock GB (1988) Pleometrosis and polygyny in ants. In: Jeanne RL (ed) Interindividual behavioral variability in social insects. Westview, Boulder, pp 179–221
- Rissing SW, Pollock GB (1991) An experimental analysis of pleometrotic advantage in the desert seed-harvester ant *Messor pergandei* (Hymenoptera: Formicidae). *Insectes Soc* 38:205–211
- Roisin Y (1993) Selective pressures on pleometrosis and secondary polygyny: a comparison of termites and ants. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 402–421
- Ross KG, Fletcher DJC (1985a) Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 17: 349–356
- Ross KG, Fletcher DJC (1985b) Genetic origin of male diploidy in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae), and its evolutionary significance. *Evolution* 39:888–903
- Sokal RJ, Rohlf FJ (1981) Biometry. Freeman, New York

- Stamps WT, Vinson SB (1991) Raiding in newly founded colonies of *Solenopsis invicta* Buren (Hymenoptera: Formicidae). *Environ Entomol* 20:1037–1041
- Tschinkel WR (1992a) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. *Ecol Entomol* 17:179–188
- Tschinkel WR (1992b) Brood raiding in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae): Laboratory and field observations. *Ann Entomol Soc Am* 85:638–646
- Tschinkel WR (1993) Resource allocation, brood production and cannibalism during colony foundation in the fire ant, *Solenopsis invicta*. *Behav Ecol Sociobiol* 33:209–223
- Tschinkel WR, Howard DF (1983) Colony founding by pleometrosis in the fire ant, *Solenopsis invicta*. *Behav Ecol Sociobiol* 12:103–113
- Waloff N (1957) The effect of the number of queens of the ant *Lasius flavus* (Fab.) (Hymenoptera: Formicidae) on their survival and on the rate of development of the first brood. *Insectes Soc* 4:391–408

Communicated by P. Pamilo