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Colony Founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the Evolution of Foundress Associations*

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Summary. 1. Field studies of the honey ant *Myrmecocystus mimicus* have revealed that colonies are often founded by groups of foundresses ranging in size from 2–9 females, with groups of 2–4 females being most common. Founding nests are also aggregated together in patches which are distant from existing *M. mimicus* colonies.

2. Laboratory experiments have shown that colony founding involves inter-colony raiding: the brood from neighboring incipient colonies is transported by workers from one nest to another. Ultimately all of the brood ends up in a single nest chamber which the workers adopt as their own. Workers frequently abandon their mothers in favor of these nests. We conclude that competition among founding nests favors foundress associations and that inter-colony raiding is a natural consequence of aggregated pleometrotic founding nests.

3. A general theory of the evolution of foundress associations is developed which describes the conditions under which foundress associations will be favored. It is shown that the evolution of foundress groups of particular sizes depends on the shape of the colony productivity function. Increasing relatedness among foundresses will generally result in a larger optimum foundress group size. Production data on foundress groups of different sizes gathered in the laboratory on *M. mimicus* are analyzed using the theory developed. It is shown that the size of foundress associations expected on the basis of the theory is very near the value observed in nature.

Introduction

Although the manner of colony founding varies enormously among the social insects (for a review see Wilson 1971), there are 2 major colony founding processes. One is swarming, also known as budding, in which reproductives depart and start new colonies with the aid of supporting workers. This pattern of colony founding is common among meliponine bees and many polygynous ant species (Hölldobler and Wilson 1977), and it is the only mode of foundation in the honey bees (*Apis*) (Michener 1974) and army ants (*Ecition*) (Schneirla 1971). The other major mode is independent colony founding, in which case the queens make the colony founding attempt without the aid of any workers. Independent founding may also be claustral, meaning that the queens seal themselves in nest chambers and rear the first brood in isolation. This is the predominant mode of independent founding among ants, although the queens of such primitive forms as *Myrmecia* and *Amblyopone* (Haskins and Haskins 1951, 1955), as well as those of more advanced species in the genera *Myrmica*, *Manica* (K. Hölldobler 1938; Le Masne and Bonavita 1969) and *Acromyrmex* (Weber 1972) forage outside the nest chamber during colony foundation.

In a few species which found colonies independently, founding females are occasionally joined by other queens in the same nest burrow (v. Buttel-Reepen 1905; Mrazek 1906; Schmitz 1911; Wheeler 1917, 1933; Eidmann 1926, 1928; Waloff 1957; Stumper 1962; Baroni Urbani and Soulié 1962; Hölldobler 1962; Baroni Urbani 1968; Buschinger 1968, 1974; Markin et al. 1972; Taki 1976; Mintzer 1979). However, in most of the cases the queens begin to fight when the first workers are ready to pupate or eclose, and they continue to fight until only one of them is left in the nest chamber (Schmitz 1911; Waloff 1957; Hölldobler 1962). In other instances, monogyny following pleometrotic foundation is accomplished when the workers eliminate queens until only one remains (v. Buttel-Reepen 1905; Eidmann 1928; Schneirla 1956; Waloff 1957; Wilson 1966; Hölldobler and Wilson 1977). Hence only one individual of the colony founding association survives with a

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* Dedicated to Dr. H. Kutter on the occasion of his 85th birthday

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chance to become the queen of a reproductively mature colony.

Queens of the honey ant *Myrmecocystus mimicus* frequently found colonies in pleometrosis. In the incipient colonies queens are eliminated by workers until only one is left. The colonies then remain monogynous for the remainder of their existence. We have chosen this species to investigate several important evolutionary questions posed by pleometrosis: 1. Under what conditions will natural selection favor females joining with other females in colony founding efforts. 2. Workers in pleometrotically founded colonies often cooperate in the elimination of queens. How could selection favor such behavior when it often results in workers committing matricide?

Materials and Methods

Myrmecocystus mimicus is one of the honey ant species in which workers belonging to a special honeypot caste (repletes) function as living storage containers. When their crops are filled, their gasters can be expanded to the size of a pea, or even larger. For a review of the literature, summary of the biology, and revision of the taxonomy of the formicine genus *Myrmecocystus*, see Snelling (1976).

Myrmecocystus is restricted to the nearctic region. Our study area was located in a mesquite-acacia community near Portal, Arizona, and Rodeo, New Mexico. The field work was conducted in 1973–1975, and 1977 during the months of July and August, when we observed the nuptial flights and colony founding behavior of *Myrmecocystus* and collected freshly mated queens for the laboratory experiments.

To study the development of incipient colonies in the laboratory, founding queens were housed in test-tube nests, each tube measuring 15 cm × 2.2 cm. Water was supplied in the tubes, trapped at the bottom with cotton plugs. Several hardwood applicator sticks were fixed on the ceiling of each horizontally positioned tube to enable developing repletes to suspend themselves. The young colonies were kept at 23–26° C and were regularly censused for the number of queens, eggs, larvae, pupae, workers and repletes. As soon as the first worker had eclosed, the nests were placed in arenas where the workers had access to honey-water and insect parts. Additional experimental details are given with the description of the individual experiments.

Results

Field Observations of Colony Founding

Nuptial flights of *Myrmecocystus mimicus* were observed after heavy rains in July. According to Snelling (1976) flights occur most frequently in the late afternoon. In our study area we observed flights both in the evening, between 17:30 and 19:00, and in the morning between 6:00 and 7:00. Usually the males flew first, followed by the heavier females which often climbed tufts of grass or similar objects before flying. Because we never observed mating on the ground, we presume that mating takes place in the air. Approximately 30 min after the nuptial flight many dealated females were wandering on the ground. Somewhat later we observed an increasing number of females digging into the wet soil. Many females that flew in the evening spent the night perched on blades of grass, and only the next morning began digging nest burrows.

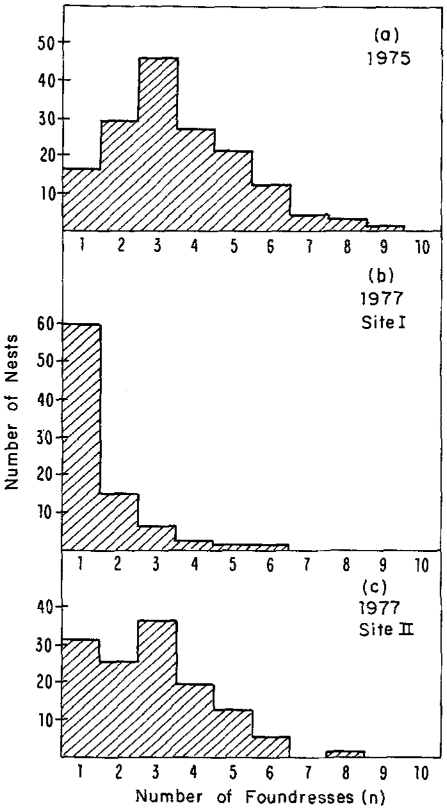

Fig. 1a–c. The number of founding nest chambers with different numbers of queens. **a** Representative sample of colonies collected the day after the nuptial flight. Most of the colonies were closed by this time. **b** Frequency distribution of nest burrows with different numbers of queens immediately after the nuptial flight. Most of these nests still had open entrances. **c** This sample was taken on the same day as the sample in **b** only later in the day. Most of the entrances to the nests in this sample were closed

Wheeler (1917) discovered that frequently two or more *M. mimicus* queens collaborate in the construction of the nest chamber. He estimated that about half of the incipient colonies were pleometrotic in origin. During our survey of founding chambers we found between 20% and 89% of the burrows occupied by more than 1 female (see Fig. 1). When we conducted the survey in the early phases of nest building, shortly after the nuptial flight, we found that the majority of the nest chambers contained only 1 female (Fig. 1b). Later, when many burrows were closed, the majority of the nests contained 2–4 females. This change in the proportion of nests occupied by more than 1 female during the early stages of colony founding may account for Snelling's report (1976) that none of the nest chambers he investigated were occupied by more than 1 female. The number of females found in one burrow might also depend on ecological factors such as the condition of the soil and the density of founding chambers at a certain site, but we have not yet been able to gather sufficient data which would indicate a clear correlation.

When a female was released in front of a burrow already being excavated by another female, in 16 cases of 20 the female readily joined the resident female and later participated in nest construction. In the four remaining cases, the released female merely wandered away. No aggressive interactions with the resident female were observed.

There seems to be a tendency for founding nests to be aggregated in particular areas which are relatively free of vegetation and away from established *M. mimicus* colonies. We have observed *M. mimicus* queens attempting to build nest chambers in the vicinity of mature *M. mimicus* colonies. Many of these attempts failed, because the foundresses were discovered and killed or driven away by workers of the resident *M. mimicus* colony. During 4 summers of observation, we recorded a total of 49 cases of *M. mimicus* queens being prevented from founding colonies by conspecific workers. In all of these cases, the queens attempted to dig their nests within the range of 0.5 to 5.5 m from a major *M. mimicus* colony (Hölldobler 1981).

Laboratory Experiments

Development of Incipient Colonies

Dealated queens were collected immediately after the nuptial flight, grouped together in different numbers and housed in nest tubes. The tubes were usually kept dark, and only when the colonies were censused did we remove the covers. Later, some of the tubes were covered with red cellophane paper so that the ants could be observed; in addition, several other nests were kept uncovered. After the ants became adapted to the light, we could observe no obvious effect of the light on the behavior of the ants or on the development of the incipient colonies.

Until the first worker eclosed, the founding queens remained sequestered in their nest tubes. As with all claustrally founding ant species, the first brood was reared entirely on the reserves in the queens' fat bodies and on nutrients derived from the resorption of the wing muscles.

Waloff (1957) found, for the ant *Lasius flavus*, that within a period of one year after flight the mortality rate of solitary queens was much greater than the mortality rates for queens kept in groups. We obtained very similar results for *M. mimicus* (Table 1), although the mortality rates in our species were generally higher.

Table 1. Mortality of queens during the period before the first workers emerged in each nest tube. The pooled data are given from series of colony founding experiments conducted with *M. mimicus* in 1973 and 1974

Number of ♀♀ per nest	Number of nests	Total number of ♀♀	Mortality of queens before the workers emerged
1	45	45	32 (71%)
2	12	24	10 (42%)
3	15	45	7 (16%)
4	10	40	6 (15%)
5	8	40	8 (20%)
6 or 8	6	42	14 (33%)

We censused the colonies at intervals of 5–10 days and the largest number of eggs, larvae, and pupae in any one census for each nest is illustrated in Fig. 2. These data were collected from an experimental series which began on 13 July 1975. Figure 2d shows the number of workers which had emerged by 3 September 1975 in the different founding chambers.

From these results we can conclude that in *M. mimicus* pleometrotic associations of foundresses are considerably more successful in raising worker offspring in a certain period of time than solitary foundresses. Similar results were obtained with *Lasius flavus* and *L. niger* (Waloff 1957), *Camponotus vagus* (Stumper 1962) and *C. vicinus* (Mintzer 1979).

We did not observe fighting among grouped queens of *M. mimicus*. Even when queens taken from locations more than 1 km apart were placed together, they coexisted amicably. Prior to the emergence of the first workers, the queens usually aggregated near the moist cotton plug and cooperated in caring for the brood. Observations indicated that all of the queens contributed to the brood. Sometimes eggs were initially observed in separate clutches, each clutch presumably the product of 1 female, but later the eggs were usually found grouped together.

After the first workers had emerged the situation inside the nest chambers changed dramatically. Queens began to space themselves out along the length of the nest tube, and in nests with more than 4 or 5 queens some of the females were expelled from the nest by the workers. In nests with fewer than 4 queens, individuals were seldom expelled early in the development of the colony. It became clear that the queens in the nest tubes stood in some kind of hierarchy with respect to one another. The brood,

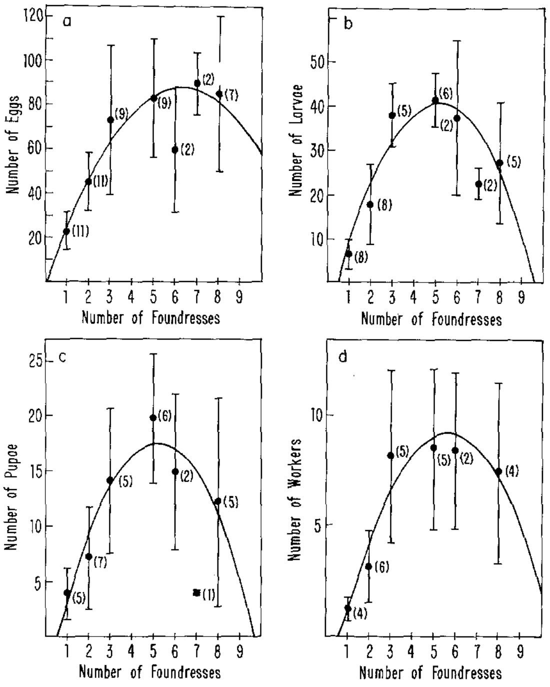

Fig. 2a–d. Colony production as function of the number of founding females ($\bar{x} \pm \mathrm{SD}$). The sample sizes are given in parentheses. The curves were fitted using the method of least mean squares. **a** Maximum number of eggs observed in incipient nests. The best fit regression is $y = -0.819 + 28.4x - 2.62x^2$; $r^2 = 0.469$; $P < 0.001$; 48*df*. **b** Maximum number of larvae observed; $y = -12.9 + 21.2x - 2.06x^2$; $r^2 = 0.633$; $P < 0.001$; 32*df*. **c** Maximum number of pupae observed. $y = 5.23 + 8.82x - 0.849x^2$; $r^2 = 0.364$; $P < 0.001$; 28*df*. **d** Number of workers in each colony on 3 September 1975, approximately 7 weeks after the beginning of the experiment. $y = -2.88 + 4.28x - 0.377x^2$; $r^2 = 0.431$; $P < 0.001$; 23*df*

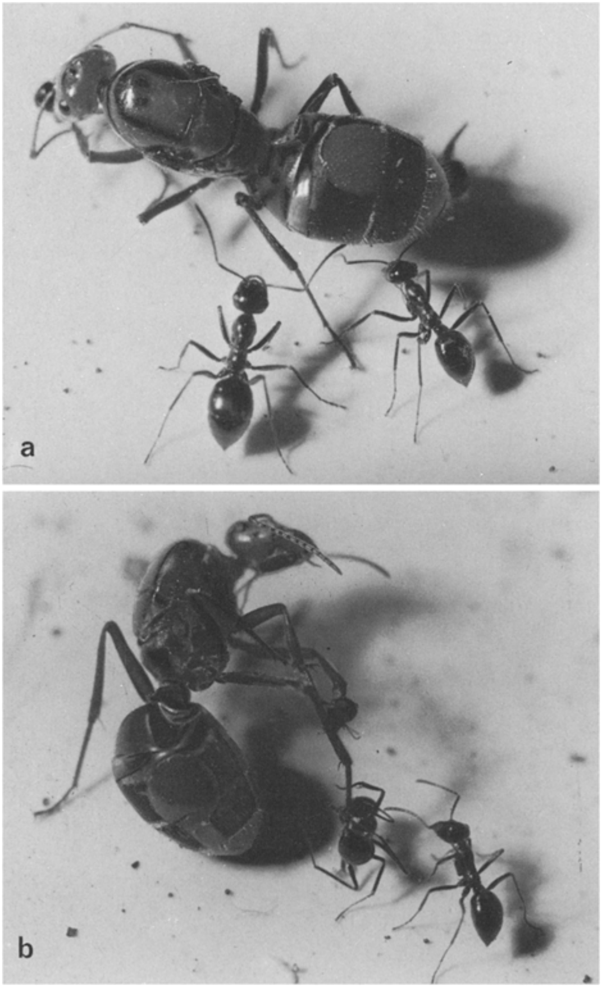

Fig. 3. a Two workers in guarding posture next to a *M. mimicus* queen. **b** Queen is attacked by workers. Note a worker's head attached to one of the queen's legs

and most of the workers were found at the end of the nest tube near the cotton plug in the vicinity of one of the queens. The other queens in the same nest were found nearer the nest entrance in a linear sequence. In 3 colonies, each containing 3 queens which were individually marked, we never observed the queens to exchange positions within the nest. The α queen (the queen nearest the brood) was often approached by the β queen (the queen second nearest to the brood) who sometimes opened her mandibles and touched the α queen with her antennae. Alpha was never observed to respond to the approaches of β in any manner. Workers spent a great deal of time pulling β away from α. Similar interactions were observed between γ and β. The effect of the workers pulling γ away from β was often to expel γ from the nest and into the foraging arena. When this happened, γ always attempted to reenter the nest. This process, of expulsion and reentry continued for several days until γ was discovered dead, outside the nest.

Although open aggression among the queens in a nest tube was very rare, we did observe a subordinate queen physically attack the dominant queen on one occasion. In this instance α was severely injured and died one day later. The β queen was then accepted by the workers in the α position. In 3 cases we removed α from nests containing 3 females. In each case one of the other queens was accepted by the workers in her stead.

It appeared that interactions among the queens in a nest tube were somehow mediated by the workers. The least dominant queen, positioned near the nest entrance, was usually accompanied by only a few workers which did not groom or feed her, as they did the dominant queen, but stood almost motionless with antennae outstretched. This behavior of the workers seemed to have the effect of restricting the movement of the queen. Such attentive behavior could last for several days before some of the workers started to grasp the queen's appendages and pull her

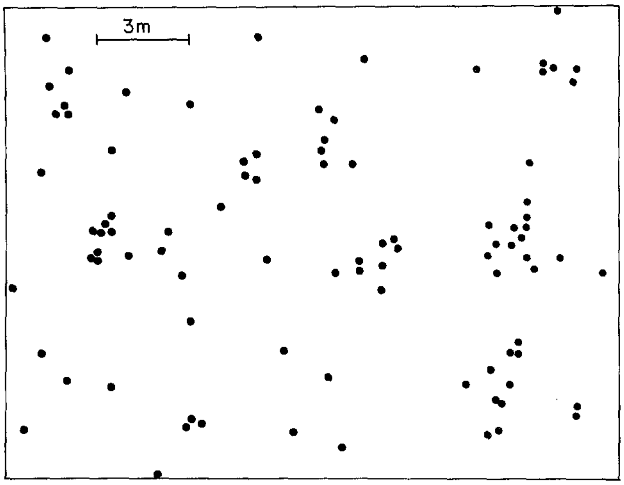

Fig. 4. Map of nest entrances over an area 15 by 20 m at a site where *M. mimicus* queens were attempting to start colonies. The mean distance from one nest entrance to its nearest neighbor is 0.51 m. This is significantly different ($P<0.00001$; *t*-test) from the mean nearest neighbor distance expected ($\bar{x}=0.98$ m) if the colonies were distributed randomly throughout this area. The colonies are therefore clumped. Mean to variance ratios indicate that maximum clumpedness is found at a quadrat size of about 3 square m

out of the nest (Fig. 3a). Sometimes the queen would resist the workers' efforts, attacking and injuring or killing some of the workers (Fig. 3b). These expelled queens were not fed by the workers, and judging by the atrophied condition of their fat bodies, died eventually from starvation. The mean weight of 12 queens which were eliminated by workers was 27.8 ± 1.3 mg. The mean weight of 7 dominant queens was 40.5 ± 1.9 mg. All of the expelled queens were inseminated. In a few cases the queens were actually killed by the actions of the workers as they were pulled from their nests. Dead queens were often dismembered, transported back into the nest and fed to the developing larvae.

The Elimination of Incipient Colonies by Incipient Colonies

The nest chambers built by founding females after the nuptial flight are often very close to one another. Not only are the incipient colonies distributed patchily in the environment, but within each patch of founding colonies, the nest burrows often tend to be clumped (Fig. 4). Mature colonies, however, are widely and evenly spaced (Hölldobler 1981). Many new colonies must therefore be eliminated during the development of mature colonies. To observe the growth and development of incipient colonies we set up several experimental arenas (diameter 30 cm) in which we placed nest tubes with 1, 2, 3 and 5 queens. In most of the colonies the first workers had already eclosed and had access to the common foraging arena. Three times per week the young colonies were censused for number of queens, workers, eggs, larvae, pupae, and honeypots.

During the course of our observations a remarkable sequence of events began to unfold. Within 4 weeks only one of the founding chambers in each arena contained any brood. In fact, this one chamber contained all of the brood plus the majority of the workers that had eclosed in the other nest chambers.

Extensive observation revealed that the workers of the incipient colonies not only foraged in the arena to feed the queens and developing larvae, but also engaged in raids on the other nest chambers. During these raids, brood was taken from nest chambers and transported back to the workers' natal nests. All of the workers from all of the nests in the arenas engaged in such behavior, so that the brood was moved from nest to nest. Ultimately, all of the brood and all of the workers were assembled in one of the nest chambers. The process of mutual raiding proceeded peacefully. We never observed any aggressive interactions among the workers, and workers from 'defeated' colonies readily joined forces with the victor. Queens in the other nest chambers were left alone to starve. In some instances these abandoned queens would leave their own nests and attempt to enter other nests. Invariably they were repulsed by workers.

In 16 of 23 experimental arenas, the colony which started with 5 queens was the one which eventually contained all of the brood. In 7 cases it was the colony that had 3 queens that was victorious. In no case did the colonies started with 1 or 2 queens end up with all of the brood. Furthermore, in 19 cases the colony with the largest worker force at beginning of the experiment was the nest which contained all of the workers and brood. In 3 instances the initial worker forces of two tubes (with 3 and 5 queens) were equal and each time the tube with 3 queens finally succeeded. In only one case was the initial number of 10 workers of the winning colony (3 queens) slightly smaller than that of the colony with 5 queens which contained 12 workers.

From these results we can conclude that generally the colony with the largest worker force in the initial stages of colony growth was able to succeed in taking over the rest of the neighboring incipient colonies.

During this phase of colony founding the gradual elimination of queens from the victorious nest, and from other colonies in the arena, proceeded. Because queens resisted workers' efforts to remove them from the nests, this process of queen elimination resulted in the death of many of the workers. The development of 3 representative groups is illustrated in Fig. 5. The loss of workers is not obvious in Fig. 5a, because

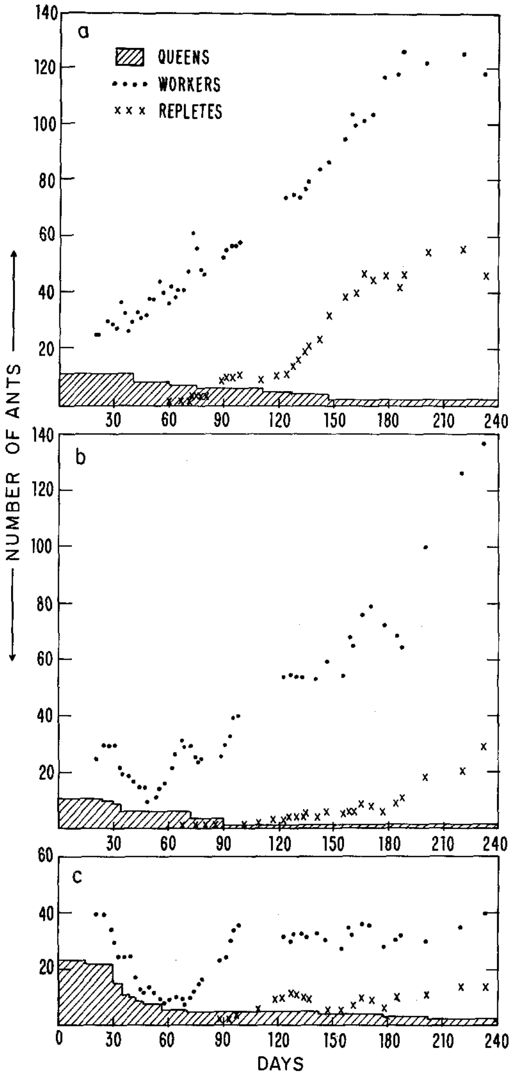

Fig. 5. Three representative examples illustrating the development of founding colonies. For further explanation see text

additional workers eclosed during the rather extended period of queen elimination. However, in the case illustrated in Fig. 5b, where the elimination of queens took place in a shorter period of time, or in the case illustrated in Fig. 5c, where the number of queens is initially considerably larger, the decline in the worker population following the elimination of queens is remarkable.

The development of the honeypots (Fig. 6) seems to be contingent upon the existence of a worker force that is large enough so that food in excess of what is required to feed the queens and the developing larvae is collected. In most of our experimental colonies, the repletes began to appear and increase in number only when most of the queens had been eliminated and the worker force had recovered from its decline (Fig. 5). From this time onwards most of the colonies grew rapidly, and only the limitations of space in the laboratory seemed to curtail their exponential growth.

Fig. 6. *Myrmecocystus* honeypots suspended from a hardwood applicator stick at the ceiling of a nest tube

We cultured the colonies in the laboratory for several years, and each of them produced hundreds of repletes. After the first year, most of the colonies were occupied by only one queen, but in one of 23 experimental nests a pair of queens persisted through two years of colony growth. Ultimately one of them was ejected by the workers. In 2 cases of another series of 18 colony founding experiments, 2 queens coexisted for 14 months, and one nest contained 3 queens for a period of 16 months. In all cases the colonies were monogynous after 2 years.

We have conducted preliminary studies of colony founding in four other species of *Myrmecocystus* (*M. depilis, M. mendax, M. mexicanus, M. navajo*) which are sympatric with *M. mimicus*. Only in *M. mendax* have we found that colonies are frequently founded in pleometrosis and that the incipient colonies engage in inter-colony raiding during colony founding (Hölldobler, unpublished observations; Alpert personal communication).

Discussion

Natural selection may favor females joining with other females in colony founding efforts for a variety of reasons. If females fail to mate during the nuptial flight, and thus have no potential for starting a colony of their own, selection would favor their joining if they were able to insert some sons into the reproductive brood, or if they were able to aid relatives' efforts to start a new colony.

Ecological reasons may favor reproductively competent females associating with other females. Recent studies of foundress associations in wasps have shown, for *Polistes* species (Gibo 1974, 1978; West-Eberhard 1978) and *Mischocyttarus* species (Litte 1977), that the rate of nest destruction by predators is substantially reduced when females associate to found nests. Gamboa (1978) has shown that the chance that a female is replaced by another female from outside as an egg-layer on *Polistes metricus* colonies is reduced when females found nests in association. Work on bees (Michener 1958; Lin 1964) has suggested that attacks by parasites may be more easily prevented by groups of foundresses because the incipient nest is never left unguarded. Similarly, Litte (1977) has suggested that the mortality rate of females in larger foundress groups may be lower because they each spend less time off the nest foraging than they would if they were alone.

These authors and others (Batra 1966; Metcalf and Whitt 1977; Klahn 1979) have also indicated that foundresses may very often be close relatives and that association may be favored by kin selection. Pickering (1980) has shown, for *Polistes canadensis* in Panama, that the combination of greater nest productivity and relatedness among foundresses indicates that females increase their inclusive fitness by joining larger foundress groups.

Few attempts have been made to analyze the conditions for the evolution of foundress associations. Although West-Eberhard (1969) has produced a model which gives the conditions of colony productivity and relatedness which may favor associating, her model does not admit the possibility of unrelated females joining in founding efforts. If we take the natural history of *Myrmecocystus mimicus* as a prototype, a general theory of the evolution of foundress associations may be developed. Recall that in this species groups of females found new nests, but individual foundresses are gradually eliminated by the workers until only one remains as the progenetrix of future generations. If we assume that the chance that a particular female will become the sole reproductive is the reciprocal of the number of foundresses, and if we assume that ultimate colony reproductivity is a function of the number of founding females, we may write

$$E(RS)=\frac{1}{n}[f(n)] \qquad (1)$$

for the expected reproductive success (RS) of each female in a foundress group of size n. Clearly, this is the quantity that selection will act to maximize when the foundresses are unrelated.

If colony productivity is a linear function of the number of foundresses and passes through the origin,

$$f(n)=an \qquad (2)$$

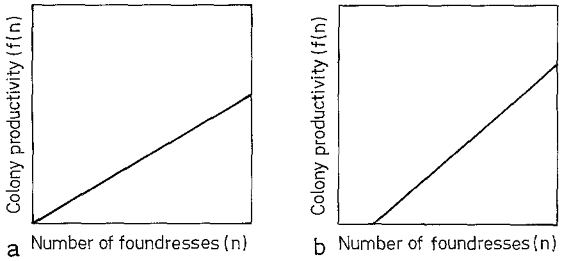

Fig. 7a, b. Linear colony production functions. **a** A colony production function f(n) = *an*. In this case, there is no selection for any particular foundress group size. **b** A colony production function f(n) = *an*–*c*. In this case, there is selection for increasing foundress group sizes

where *a* is a constant (Fig. 7a), then there is no selection for foundress group size at all. One group size is as good as any other because, at all group sizes, the expected reproductive success of each female is equal to *a*.

There may, however, be some benefit that accrues to associating females that is not itself a function of the foundress group size. In this case, the colony production function becomes:

$$f(n)=an-c \qquad (3)$$

(Fig. 7b). In this instance there is selection for joining ever larger foundress groups. The selection pressure (as measured by the marginal increase in expected reproductive success) to join a larger group diminishes with increasing group size because in the limit, as n increases, *an*-*c* approaches *an*.

Perhaps more realistic colony production functions are non-linear, such that there is some benefit to associating with other females that changes when foundress group sizes vary. Such non-linear functions are depicted in Fig. 8a and b. When colony production functions are of this form, there is selection for a particular foundress group size. The group size that maximizes each female's expected reproductive success is given by the point at which a straight line, through the origin, is tangent to the production function (Fig. 9). Because n^* is the foundress group size which maximizes colony production per female, selection will act to favor females joining groups of size n^*-1. We might also expect that females in groups of size n^* would exclude other females from joining the group.

If a founding female expects to be related to her co-foundresses by some degree of relatedness b, then selection will act to maximize her expected inclusive fitness (IF):

$$E(IF)=\frac{1}{n}[f(n)]+\frac{n-1}{n}[f(n)]b. \qquad (4)$$

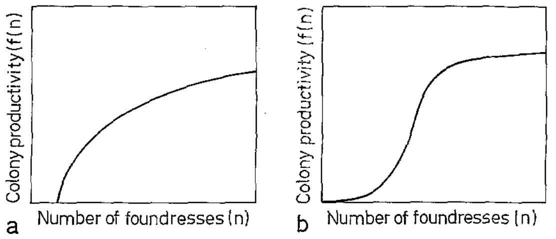

Fig. 8a, b. Non-linear colony production functions. **a** This shape of a colony production function indicates that there is some advantage to joining larger foundress group sizes up to a point, after which the addition of more queens to the foundress association has no effect on the ultimate reproductivity of the colony. **b** In this case, the addition of 1 or 2 queens has little effect on the colony productivity. There is a kind of threshold that must be crossed (in number of foundresses) before colony productivity assumes any appreciable value

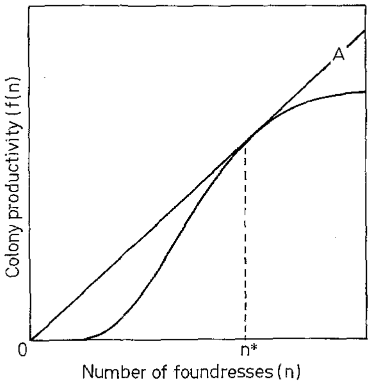

Fig. 9. Graphical solution to the problem of optimal group size. The straight line AO has slope equal to f(n)/n. f(n)/n is the quantity which selection will maximize. Given the colony production function f(n) the maximum value of f(n)/n is given by the point at which line AO is tangent to f(n). n* is therefore the optimal foundress group size

This is the expected direct reproductive success of a female plus the inclusive fitness gain she expects if one of the other foundresses becomes the sole surviving reproductive. Note that when $b=0$, when the foundresses are unrelated, Eq. (4) reduces to Eq. (1). In the case of related foundresses the colony size which maximizes the expected inclusive fitness of each foundress is given by:

$$\frac{f'(n)}{f(n)}=\frac{1-b}{n[1+b(n-1)]}. \tag{5}$$

The effect of increasing relatedness among the foundresses is to make an individual's interests more and more similar to the colony's interests. This results in the optimal foundress group size increasing to the group size which maximizes colony productivity as b goes from zero to one.

In nature many queens of *Myrmecocystus mimicus* attempt to found colonies in association with other females. In 1975 and 1977 nearly ninety percent of all females in our survey (Fig. 1a and c) made their colony founding attempt in pleometrosis. Of the colonies founded in the laboratory experiments, only those that began with multiple queens persisted beyond the first few weeks following colony foundation. The reason that the colonies founded by fewer queens failed to survive was that their brood was stolen and their workers deserted in favor of nests founded by a larger number of females. In this situation the advantage of associating with other females in colony founding is clear. If females attempt to make the founding effort alone, they cannot produce enough workers quickly enough to successfully engage in inter-colony raiding. With a deficient worker force, it is only a matter of time before the colony succumbs to the marauding efforts of surrounding colonies.

Our data indicate that females tend to group themselves in foundress associations of 2–4 females (Fig. 1). If a few foundresses are better than one, then why are more not even better? The answer to this question can, in part, be found in the colony production functions generated during our laboratory experiments. In Fig. 2a, b, c, and d we have illustrated the number of eggs, larvae, pupae, and workers produced in colonies started by foundress groups of different sizes. In all cases, the production of brood or workers has a significant tendency to decrease at the larger foundress group sizes. This would indicate that some intermediate foundress group size would be preferred by founding females. If we view these figures as reflecting ultimate colony reproductivity, then we can address the question of just how big the foundress group ought to be.

The number of eggs or larvae present in a colony may not be particularly good indicators of ultimate colony productivity. This is because eggs and larvae require continued investment of care and food before they become productive members of the colony. In addition, egg eating was observed during the course of our experiments, and thus many eggs never have a chance to contribute constructively to colony founding efforts.

The number of pupae and the number of workers may be much better predictors of colony success. When larvae pupate, they receive no more food from foraging workers, and it is only a matter of time before they become productive members of the colony. We have shown that it is the colony with the largest worker force that is able to accumulate the brood and workers from nearby colonies and thus persist throught the initial phases of colony foundation. Consequently, the number of workers produced during the first few weeks following the nuptial flight may be the best predictor of ultimate colony success.

In Fig. 2d a curve has been fitted to the data on production of workers. The best fit is accomplished by the second order equation:

$$f(n) = -2.88 + 4.28n - 0.377n^2. \qquad (6)$$

If we take this equation to be the colony production function, we find that the foundress group size which maximizes the production of workers is 5.7 queens. If we use the equation generated by the number of pupae, the group size which maximizes colony production is 5.2 queens. Thus, if natural selection were acting on foundress group size to maximize the production of workers by the colony, and if our laboratory production functions are similar to the production functions of colonies in the field, we would except to find that most colonies were founded by 5 or 6 queens. Our data on the incidence of foundress groups of different sizes in nature (Fig. 1) suggests that most females are joining in groups of about 2–4; smaller groups than we would anticipate if selection were acting to maximize the production of workers. If we solve the production functions for the foundress group size which maximizes the number of pupae or workers per female, we find that foundress group sizes should be 2.5 or 2.8 queens respectively. These values are much nearer those observed in nature.

However, the chance of mortality expected by a female is also a function of the foundress group size. The data in Table 1 indicate that mortality is lowest in foundress groups of 3 or 4 females. Thus, we have detected two reasons why colonies of *M. mimicus* should be founded by only 3 or 4 females. At these foundress group sizes, mortality is lowest and production per female is highest.

The situation may be more complex, however. For example, relatedness among foundresses, which was assumed to be zero, is unknown. Also, the variance in success of equal sized worker groups may diminish selection for a specific group size.

It is not hard to imagine how foundresses might regulate their numbers in nature. When females first begin to dig their nest burrows, they leave them open. It is only later, after associations have had time to form, that the nest entrances are sealed (see Fig. 4).

In Fig. 4 we presented our observations on the tendency of nest burrows to be clumped. We have already suggested that one of the reasons that founding chambers may be patchily distributed is that nests founded in close proximity of existing *M. mimicus* colonies are quickly destroyed by the resident workers. It is possible that founding chambers are preferably built in those few patchily distributed areas where there are no extant *M. mimicus* colonies.

On the smaller scale, however, different reasons may be responsible for the clumped pattern of nest entrances. Our laboratory experiments suggest that the inter-colonial raiding behavior is a very important aspect of colony foundation. If this is true, there would be selection favoring females who built their nests near other nests. Based on our experiments, though, this is true only in so far as females are in large foundress groups. Given the poor performance of haplometrotically founded nests in inter-colony raiding, we would not be surprised to find nests founded by single females to be more isolated than the pleometrotically founded nests. Unfortunately, we cannot test this prediction with the available data.

The behavior of workers during our experiments on colony founding was quite remarkable in that they showed no apparent fidelity to their natal nests or to their mothers. As we mentioned earlier, during the inter-colony raiding phase of colony foundation, workers often returned to nests other than their own, and ultimately, all of the workers produced in an experimental arena adopted a single colony. This often resulted in workers abandoning their mothers. In addition, during the process of queen elimination, workers often cast their own mothers from the nest.

Forsyth (1980) has shown that selection may favor the evolution of such behavior if workers are able to assess only the relative productivity of the co-founding queens. If workers eliminate all but the most productive queen, they will be maximizing the chance that they preserve their mother. In such a situation selection may favor the evolution of queens which produce workers with the ability to recognize their own mother and help only her. In *M. mimicus* this would lead to the breakdown of the inter-colony raiding system, and colonies would tend to be founded by single females. Because the queens of *M. mimicus* found their colonies claustrally it is clear that the benefits of founding in association derive from the cooperative activities of the workers. If some workers were behaving selfishly, and aiding only their own mother, then the colony founding efforts may fail.

One effect of the cooperation of workers, apart from aiding in inter-colony raiding, is to hasten the production of repletes. In the desert environment of the Southwest, the advantage to incipient colonies in surviving periods of drought, provided by a few repletes may be sufficiently large to prevent the evolution of such 'selfish' workers.

Because of the territorial behavior of colonies of this species, at most only one of the aggregated incipient colonies will survive. This results in tremendous competition among incipient colonies. In such a situation, it is not hard to imagine that selection for the rapid production of a large worker force, perhaps to compete more effectively with other incipient colonies, and perhaps to hasten the production of repletes, would favor females cooperating in the colony founding effort.

But in this situation of claustrally founding females, cooperation among foundresses really means cooperation among the worker forces that they produce. To the extent that such cooperation is favored, the evolution of workers which are tolerant of one another and of queens other than their mother would be favored. So, the selection pressures on workers are contradictory. They must be tolerant of one another and cooperate in order for their mother to have any chance of surviving at all. At the same time, they are favored to insure that it is, in fact, their own mother that does survive. It is in just such a situation that we would imagine that workers with the ability to discern the most productive foundress would be favored.

In the early stages of colony founding, when all the incipient nests are aggregated together, workers would initially be selected to choose the most productive nest burrow. This process would lead, naturally, to the inter-colony raiding behavior we have observed. Workers, selected to treat the most productive nest as their own, would move any brood they encountered to this most productive nest. They would be, as it were, simply returning 'misplaced' brood to the proper location. Such behavior would, incidentally, increase the worker force of the most productive colony and help insure its survival.

Once established, however, this process would create strong selection for foundress associations. Workers are selected to choose the most productive nest, and we have shown that nests begun by 3 to 5 foundresses are most productive. Single foundresses, or even nests begun with two foundresses, were never observed to prevail in the inter-colony raiding process. In short, we imagine that competition among founding colonies initially favored foundress associations. Foundress associations then allowed the evolution of the inter-colony raiding behavior, which, in turn, enforced selection for foundress associations.

Gamboa (1978) reports a similar situation in the paper wasp *Polistes metricus*. In populations with high densities of colonies, nest usurpations in single-foundress colonies were frequently observed. This resulted in multiple foundress colonies which were usually more productive. In areas where the density of wasps was lower this phenomenon was not observed, and most colonies were founded by single females.

In a situation somewhat similar to *Polistes*, in *Myrmecocystus mimicus* a hierarchical order among the queens is established when the first workers appear. Although after the first year most of our laboratory colonies were monogynous, in some cases we observed two and three queens coexisting for periods of fourteen to twenty-four months. In these cases, however, one queen appeared to be the dominant individual and the major egg-layer. We assume that in natural nests, where queens can space out more easily, several queens could possibly coexist for even longer periods.

Tschinkel and Howard (1978) discovered, particularly in younger colonies of the fire ant *Solenopsis invicta*, that the dominant physogastric queen would be replaced by another fertilized female if she were removed from the colony. Apparently these colonies contain several inseminated queens, although usually only one of them is physogastric. It is possible that the functional monogyny in *S. invicta* is a transitional stage between a pleometrotic association of foundresses (Markin et al. 1972) and true monogyny. It is likely that we have discovered a similar situation in *Myrmecocystus mimicus* where in young colonies subordinate females may replace the dominant queen if something happens to her.

Finally, the discovery of inter-colony raiding during colony foundation helps explain aspects of the phenomenon of intraspecific slavery practiced occasionally by mature *M. mimicus* colonies (Hölldobler 1976, 1981). Mature colonies of *M. mimicus* conduct ritualized tournaments in order to defend foraging territories. Opposing colonies summon their worker forces to the tournament area, where often hundreds of ants perform highly stereotyped display fights. When one colony is considerably stronger than the other, that is, when it can summon a larger worker force, the tournaments end quickly and the weaker colony is raided. During these raids, the queen is killed or driven off and the larvae, pupae, callow and honeypot workers are transported to the raiders' nest. Field observations and laboratory experiments have revealed that the surviving workers of the raided colony ultimately join the raiders' colony. This behavior of conquered workers is very similar to the behavior of workers in the early stages of colony founding when workers are selected to join the most productive nest. It is not unreasonable that the workers of a colony conquered during a territorial battle are simply behaving as they would during colony founding, and that this behavior can best be explained as an artifact of selection for inter-colony raiding during the founding process.

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