

## Colony Founding by Pleometrosis in the Fire Ant, *Solenopsis invicta*\*

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**Summary.** Newly mated queens of the fire ant, *Solenopsis invicta*, found colonies either alone (haplo-metrosis) or by joining with other newly mated queens (pleometrosis). Surveys after mating flights showed that nests and queens were usually aggregated in space, that queens were aggregated among occupied nest chambers, and that the occurrence and degree of pleometrosis was related to the mean queen density. Queens and nests were strongly associated with slightly higher ground, away from rainwash areas and puddles.

The effects of queen density and microtopography (small hills) on pleometrosis were tested in a two-factor factorial experiment. A 64-fold increase in applied queen density resulted in a 2.19-fold increase in mean queens/nest (pleometrosis). Variation in queen density accounted for 70% of the variation in the mean queens per nest, as well as 78% of the aggregation of queens among the available nest chambers. Queen density also accounted for 86% of the aggregation of queens in area. Thus, at all densities, queens are moving into areas and nests of higher density, increasing both the local mean densities and the level of aggregation. Microtopography had no significant effect. Lab experiments suggest that the interactions leading to association take place on the surface.

A mechanism is proposed in which the central causal factor regulating pleometrosis is local queen density, local being one to a few square meters, and a variety of factors affect pleometrosis by their action upon the local queen density.

In the laboratory, groups of 5 foundresses produce more workers than do groups of 10 or 15,

or single queens. Nests founded by groups begin the growth period with about 3 times as many workers as do those founded by single queens, and the former remain about three times as large for at least the first 100 days of growth and probably more. Higher worker production rate probably confers an advantage in survival and competition throughout colony growth. These differences between haplo- and pleometrotically founded nests may be among the factors favoring foundress associations.

### Introduction

Social insects start new colonies in one of two basic ways (Wilson 1971). In swarming, as in honeybees and army ants, some fraction of the worker force accompanies the queen to found the new colony. This mode is uncommon among ants. In most ant species, queens found new colonies independently without the aid of workers. Usually, founding is claustral, meaning that the queen seals herself in a chamber and rears the first brood on reserves stored in her body. In some independently founding, claustral species queens have the option of joining other founding queens (pleometrosis), rather than founding alone (haplo-metrosis). While a number of ant species have been reported to indulge in pleometrosis facultatively (see Bartz and Hölldobler (1982), for species list and references), very little is known about the factors which effect the occurrence and degree of pleometrosis. Foundress associations show higher survival of the claustral period and produce a larger number of workers initially, possibly conferring selective advantage to pleometrosis (Mintzer 1979; Stumper 1962; Waloff 1957; Wilson 1966; Bartz and Höll-

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dobler 1982; Thorne 1982). Bartz and Hölldobler have modeled the natural selection of unrelated queens founding in associations.

The fire ant, *Solenopsis invicta* Buren, introduced to the United States from Brazil, shows considerable complexity with respect to queen number during its life cycle. Mature colonies may be monogynous, polygynous or functionally monogynous (Glancey et al. 1972; Tschinkel and Howard 1978; Fletcher et al. 1980). Colonies can be founded in haplometrosis, but pleometrosis is also common. Markin et al. (1972) reported that somewhat fewer than half the newly founded colonies were pleometrotic and contained from 2 to 5 queens. At the end of the claustral period, all colonies contained only a single queen. Wilson (1966, 1971) also indicated that when several queens were introduced into queenless colony fragments the workers eventually killed all but one. It is thus presumed that pleometrotically founded fire ant colonies are reduced to monogyny before colony growth begins in earnest.

It is the purpose of this paper to determine some of the factors which control the number of queens during colony foundation, and to gain some insight into the possible selective advantages of the observed patterns.

## Materials and Methods

All study sites were recently cleared, mostly flat, unvegetated construction sites within 5 miles of Tallahassee, Florida and were in the initial stages of colonization by fire ants. These sites contained no or very few active fire ant colonies. Our data are thus uncomplicated by the effects of workers killing newly mated queens which land in their colony territory (Wilson et al. 1971). Temperatures at mid-day were seldom less than 455 °C.

*Location of Nest Chambers.* Mating flights in *S. invicta* usually take place on warm mornings the day after a heavy rain (Morrill 1974). Most of the mated females are back on the ground and de-alated by mid-afternoon. Nest chamber excavation begins from a few minutes to hours after de-alation, and is usually well underway by nightfall. Once a substantial portion of the nest tunnel and chamber had been dug, the nest entrance is closed.

Founding nest chambers were easily recognized by the small crater of dirt pellets which surround the nest entrance. Because further rain could wash away these pellets, a small circle of colored paper was pinned near each nest entrance. The locations of all nests in each study site were mapped for analysis.

*Nest Excavation.* Nests were excavated by following the tunnel downward until the nest chamber at the bottom was reached. Queens rarely leave the nest once they are shut within the founding chamber. The dispersion of queens from a mating flight could thus be determined at some leisure by digging up nests over a period of up to about 25 days, the approximate

time when the first workers begin execution of supernumerary queens.

Nests in which no queens were found were excluded from most analyses. Queens regularly dig 'trial nests' up to 4 or 5 cm deep which they subsequently abandon.

*Surveys, 1979, 1980.* Rectangular plots from 52 to 168 m<sup>2</sup> were laid out after large mating flights on May 27, June 22 and July 13 and 15, 1979 and June 10, 21, and July 7, 1980. Founding nests were marked, mapped and dug as described above. Soils were all sandy with varying amounts of clay.

*Experiment on the Effects of Queen Density and Soil Topography 1981.* A completely flat, vegetationless building site with fairly homogeneous soil (sand with some clay) was divided into 5-by-5 meter plots. These 26 plots were used to test the effects of the density of newly mated queens and small rises in topography on pleometrosis. For topography, four small oval hills were symmetrically located in each of 13 randomly chosen plots by transporting in dirt from outside the plots.

On the afternoon of a very large mating flight on June 10, 1981, over 2,000 newly mated queens were collected at a site distant from the experimental plot. These queens were then randomly divided into four groups each of 5, 20, 80 and 320 queens, a total of almost 1,800 queens. A thin line of a mixture of equal parts of Louisiana Light, Bunker C and Kuwait Crude oil was poured along all the plot boundaries and the queens of each group were then sprinkled randomly into a plot chosen at random such that each number of queens was replicated twice with flat plots and twice with hill plots. Queens rarely if ever crossed the oil lines.

The 10 plots to which we did not add newly mated queens were used to determine the background queen density resulting from the natural mating flight. This varied from zero to 8 and averaged about 2 queens per 25 m<sup>2</sup> plot.

The newly founded nests were marked and all plots were mapped as noted above. Digging the 770 marked nests began on June 13 and was completed June 25, well before the first minim workers were produced. The treatment groups were dug in random order.

## Results

### Surveys

The survey maps of 1979 and 1980 suggested that the likelihood and degree of pleometrosis is related to the local density of newly mated queens and to 'microtopography' such as small rises, dirt clods, low wet areas and so on. Figure 1 shows these associations especially clearly. In this and all subsequent analyses, three variables are derived from the maps for analyses: (1) queen density in queens/m<sup>2</sup>; (2) nest density in occupied nest/m<sup>2</sup> (unoccupied nests or nests in which queens were not found were excluded in most analyses); (3) queen density in the nest chambers, expressed as queens/occupied nest. This is the meaningful measure of pleometrosis and is referred to hereafter simply as queens/nest.

In Fig. 1, there is a very strong association between the higher areas and the location of newly

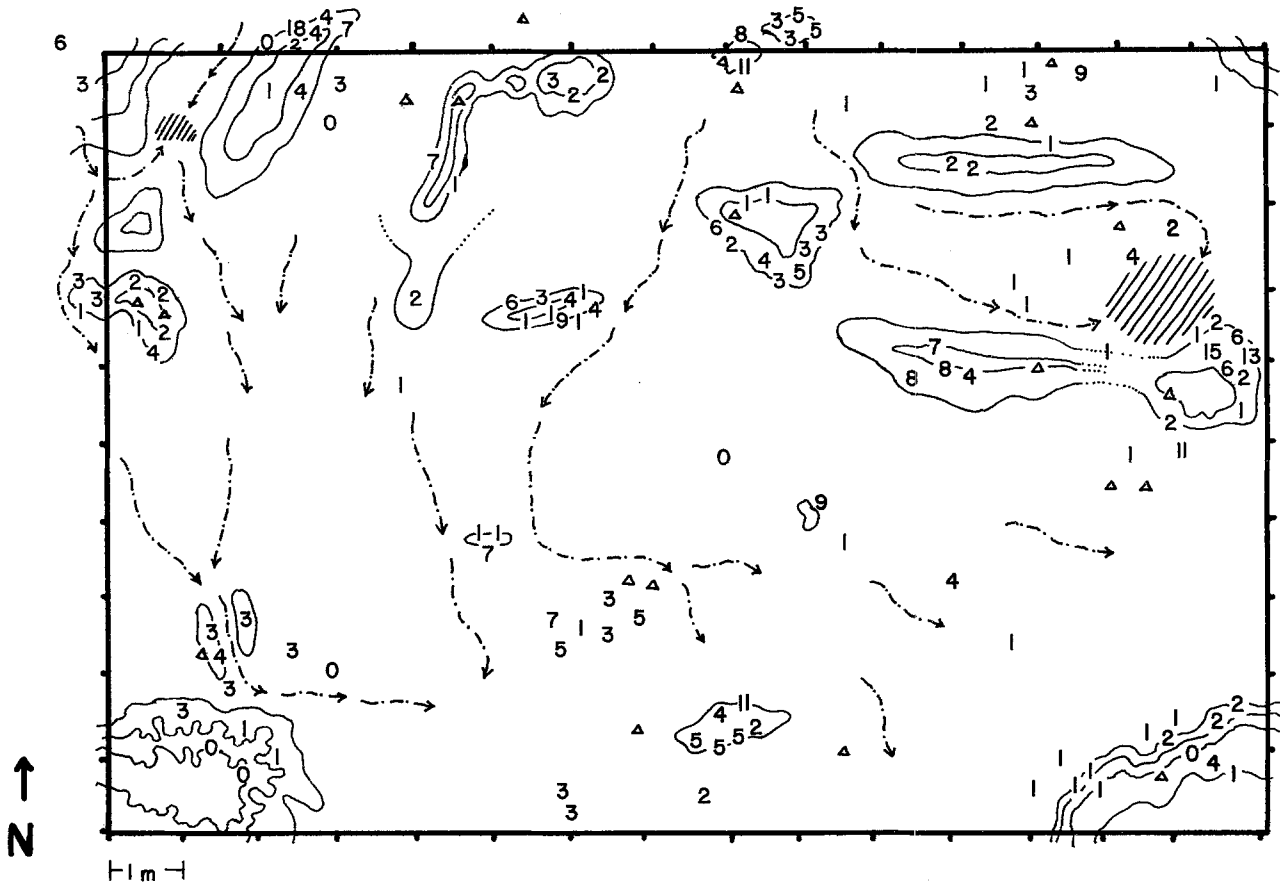


Fig. 1. Nest locations and queen number after the mating flight of June 10, 1980. This map of a recently cleared construction site was chosen to show the apparent effects of microtopography. Contours indicate small rises, dashed lines and arrows the path of runoff during rains, hatched areas puddles. The general slope is approximately 5% and mostly toward the southeast. Ticks represent 1 m. Open triangles indicate nests which were marked but a queen was not found. Nests and queens are significantly associated with higher features ( $P < 10^{-6}$ ), and queens are significantly clumped among the available nest chambers

founded nests ( $P < 0.000001$ ). These features are no more than a few inches higher than the surrounding surface, but they are high enough so that storm runoff does not inundate them. They also consist of more compacted soil, while the lower surfaces and watercourses (dashed arrows) are often soft sand and alluvium. Nest site preference could thus be for either soil characteristics or microtopography or both.

A second trend seen in Fig. 1 is that the number of queens per nest is higher (up to 18) in areas containing higher concentrations of queens. It thus appears that queens may be associating in some positive relation to local queen density.

This relationship of queen density, nest density, and queens per nest is depicted on Fig. 2 where the number of queens in a square meter is plotted against the number of nests in the same square meter. Increasing queen density seldom results in more than about 5 occupied nests per square

meter, even at very high queen densities. Clearly, increasing queen density must be accommodated by an increase in the mean number of queens per nest. Figure 3 shows the frequency distribution of queens in chambers for all surveys. Mean queens/m<sup>2</sup> and queens/chambers are correlated.

#### Experiment, 1981

We tested experimentally the relationship between the density of queens and the degree of pleometrosis. We also added a test of microtopography (small hills) to create a two by four factorial experiment in which two levels of topography (hills, no hills) were crossed with four levels of queen density (5, 20, 80, 320 queens per 25 m<sup>2</sup> plot).

Analysis of variance (ANOVA) showed that the number of queens per nest was strongly related ( $P < 0.005$ ) to the applied density of queens (Fig. 4). Variation in the queen density accounted

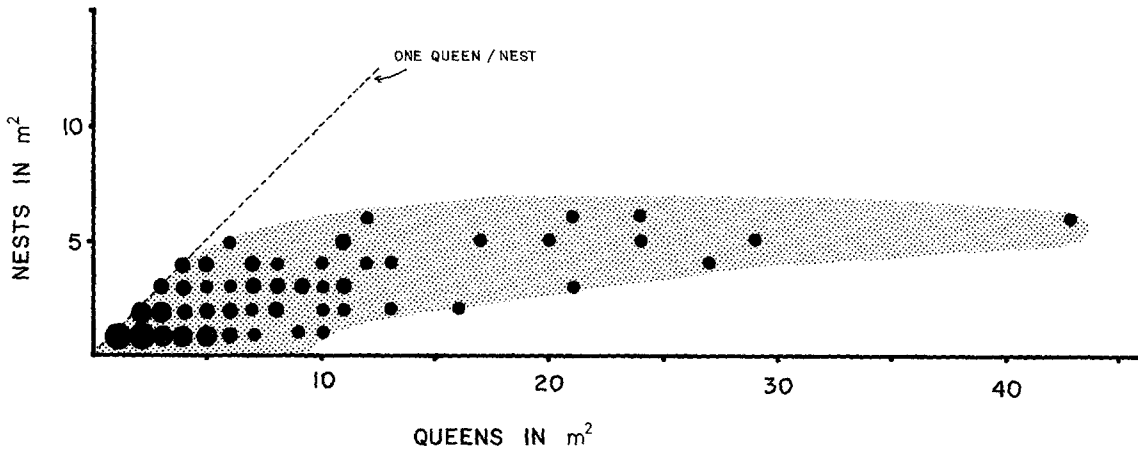


Fig. 2. The number of nests found in each  $m^2$  of the surveys in relation to the number of queens in that  $m^2$ . Dotted line indicates relationship if each queen had founded haplometrotically. Size of circle indicates the number of grid-units with that pair of values, the largest representing more than 50 grids, the smallest, a single grid. Shaded area simply encompasses the data points. As queen density increases, the number of queens founding pleometrotically increases, causing the number of nests to level off

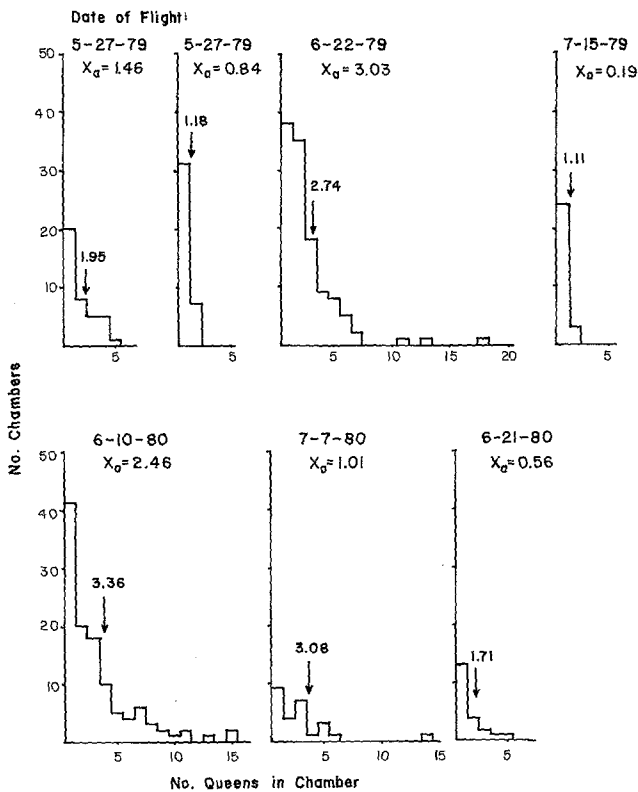


Fig. 3. Frequency distribution of queens in chambers following natural mating flights.  $X_q$  = mean queens/ $m^2$ ; vertical arrows indicate mean queens/chamber

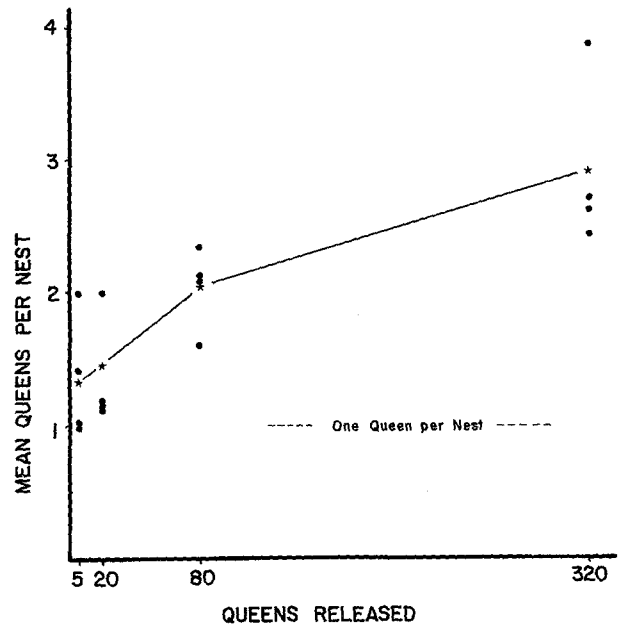
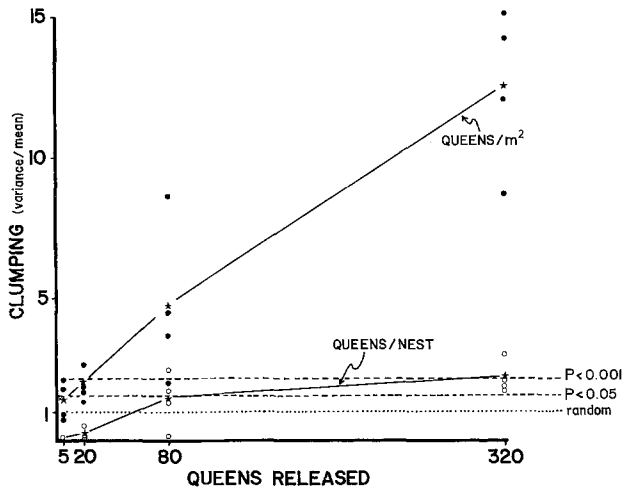


Fig. 4. Relation of the density of queens applied to the treatment plots and the mean number of queens per founding nest chamber. Circles indicate the four replicates of each density. Stars and line indicate mean values. The relationship of mean queens per nest to queen density is highly significant (ANOVA;  $P < 0.005$ ). Microtopography has no significant effect. Dotted line indicates relationship if all queens had founded haplometrotically

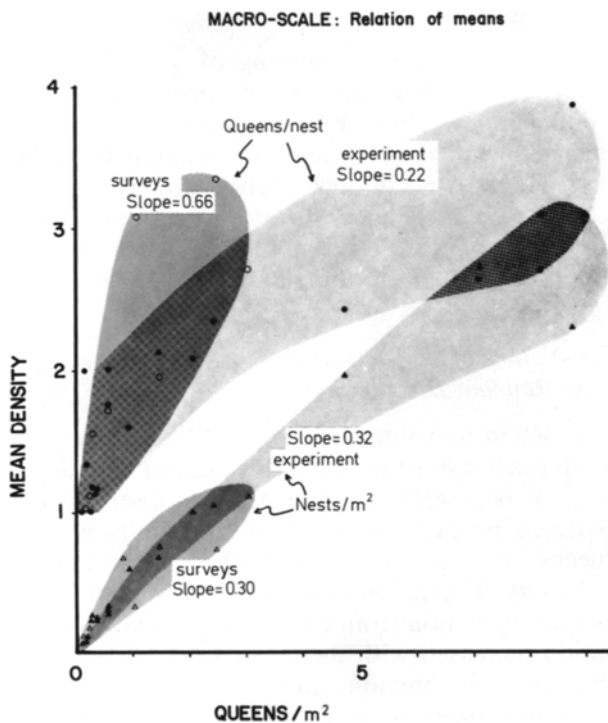
for 70% of the variation in the queens/nest. A 64-fold increase in the number of released queens resulted in a 2.19-fold increase in the mean number of queens/nest. The average degree of pleometrosis is thus causally related to the density of queens.

The nest density rises more slowly than the queen density, so queens must be joining with one another for colony foundation.

The second important question is, how are the queens assorting themselves among the available



**Fig. 5.** The aggregation (variance/mean) of queens within available area and among available nest chambers, in relation to the queen density applied to experimental plots. Circles represent replicates; open circles queens per nest; closed circles queens per square meter; stars and lines mean values. Clumping of queens in area and among nest chambers is significantly related to applied queen density (ANOVA;  $P < 0.001$ ). Dotted lines indicate significance levels for the variance-to-mean ratio for individual replicates



**Fig. 6.** Comparison of the means for nest density and queens per nest between surveys and experiment, both in relation to recovered queen density (queens/m<sup>2</sup>). Shaded areas include all points in each group. The relationship of nest density to queen density is the same for surveys and experiments, but queens per nest responds more strongly to queen density in the surveys

nests? When the variance-to-mean ratios for the variables queens/m<sup>2</sup> and queens/nest are plotted against the applied queen density (Fig. 5), it becomes apparent that increased queen density causes an increase in the clumping of queens, both within the available space in each plot, and among the available nest chambers. In other words, queens are aggregating in certain parts of the experimental plots, and within certain nest chambers, and this aggregation is driven by increasing queen density. Analysis of variance of these two variance-to-mean ratios shows that both are significantly related to applied queen density ( $P < 0.001$ ), and that queen density accounts for 86 and 78% of the variation in clumping, respectively.

Variance-to-mean ratios for individual treatment plots indicate that clumping in area (queens/m<sup>2</sup>) is present even in two of the plots receiving only 5 queens and in all other plots. With respect to dispersion among nests, queens in plots receiving 5 and 20 queens showed uniform dispersion, perhaps as a result of the low probability of finding one another. In plots receiving 80 queens, two showed significant clumping, one was random and one uniform. This appears to be a transitional density, for in all plots receiving 320 queens, queens were significantly clumped with respect to available nest chambers.

Figure 5 also shows that the clumping of queens in area rises much more rapidly with queen density than does clumping among nests. It seems likely that clumping in area drives the aggregation among available nests. This is discussed below.

Microtopography had no significant effect on any of the primary variables (ANOVA) and was therefore dropped as a factor in further analysis.

#### Comparison of Surveys and Experiment

In order to make the data for surveys and experiments comparable, we used the density of queens recovered rather than applied. Applied density is unknown for the surveys. In the experiment, the proportion recovered ranged from 38 to 68% but was not significantly related to the applied queen density (ANOVA). It seems likely that the recovery rate and relation to density were similar in the surveys.

When the mean nest density for the experimental and survey plots are seen in relation to their recovered queen density, it is apparent that they fall on the same regression line (Fig. 6). The slopes of nest density vs queen density (0.30 and 0.32) are not significantly different ( $t$ -test for equality of slopes). Maximum queen density and therefore

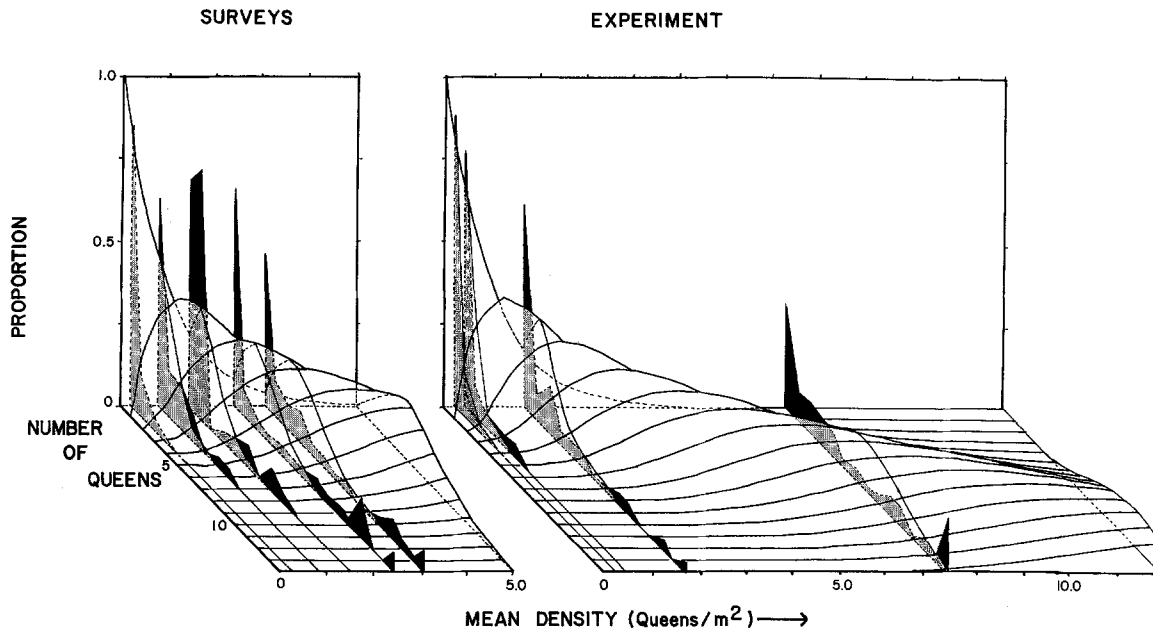


Fig. 7. Observed queens per square meter in relation to Poisson Distributions of increasing mean queen density. Surface indicates the expected values for the Poisson distribution, the planar sections allow comparison of an observed distribution with the Poisson of the same mean value. The intersection of each  $z-y$  plane with the surface describes the expected values. As the mean density increases, the observed distribution deviates increasingly from the random Poisson, and this trend is stronger for the surveys. Deviations are characterized by higher than expected proportions of grid units with very low and very high numbers of queens, and lower than expected proportions with intermediate numbers

nest density in the surveys were much lower than those applied in the experiment, but the relationship between the two variables was similar.

On the other hand, the slope of the relationship of queens/nest (pleometrosis) to recovered queen density is significantly different for the surveys and experiment ( $P < 0.01$ ;  $t$ -test for equality of slope) (Fig. 6). In other words, pleometrosis increased more rapidly in response to queen density following natural mating flights and settling than it did in our experiment (slopes = 0.66, 0.22, respectively). Perhaps this is because queens from natural mating flights have already undergone one level of aggregation as a result of site selection before alighting.

Comparison of clumping (variance-to-mean ratios) for surveys and experiment yields parallel results. The degree of clumping of queens in area (queens/m<sup>2</sup>) is significantly more sensitive to queen density (slope 3.60 vs 1.42;  $P < 0.001$ ;  $t$ -test) in the surveys than it is in the experiment, and the same is true for clumping of nests in area although the difference is smaller in this case (slope 1.32 vs 0.79;  $P < 0.02$ ;  $t$ -test). Thus, the aggregation of queens and nests within the available area increases more rapidly with queen density in surveys.

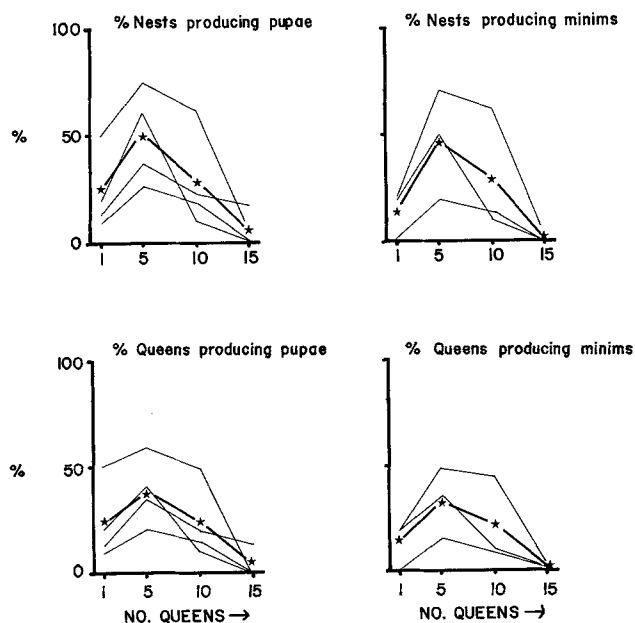
On the other hand, the effect of density

(queens/nest) on the clumping of queens among nest chambers is similar for surveys and the experiments (slopes 1.26 vs 1.17; N.S.;  $t$ -test). Thus, the final assortment of queens into chambers reacts similarly to its mean queen density in both.

All these differences in rates of clumping were confirmed by a nearest neighbor distance analysis (Southwood 1978) of the mapped data.

#### *The Nature of the Deviation from Random Distribution*

For each mean value of queen density, nest density, or queens/nest from the experimental or survey plots, it is possible to compare the observed and expected proportion [ $P(x)$ ] of grid units with  $x$  queens or nests, or nests with  $x$  queens ( $x = 1, 2 \dots n$ ). The  $X^2$  goodness-of-fit test confirmed that the deviation from the random Poisson distribution increased with the mean value of the variable, as in the previous analyses. For example, as the mean queen density increases, there appears an increasingly larger-than-expected number of grid units with low numbers of queens (0, 1, 2) and with very high numbers of queens (3 to 5 times the mean) (Fig. 7). On the other hand, there is an increasing deficit of grids with intermediate



**Fig. 8.** Production of pupae and minim workers in relation to the number of queens in foundress associations. Stars and heavy lines indicate the means for the four sets of replicates. Success was maximal at 5 queens both for proportion of nests and proportion of queens. Thinner lines are individual sets of replicates following four separate mating flights. Kruskal-Wallis test indicated a significant ( $P < 0.05$ ) effect of queen number on both colony and queen success

numbers. It thus appears that non-random interactions are causing the queens to stock the grids which have larger numbers by draining all grids with lower numbers. This, aggregation takes place at lower densities in the surveys than in the experiment. The variable nest/m<sup>2</sup> showed a similar relation to its mean values although mean values were necessarily much lower.

Queens/nest was compared to a Poisson distribution truncated for zero, because only occupied nests were analysed. Again, as mean queens/nest increased, the occurrence of nests with single queens and very large numbers of queens was increasingly larger than expected, while those with intermediate numbers fell below. It appears that queens moved preferentially into nests with more queens no matter how many queens were already in their previous nest. These patterns are similar for surveys and the experiment.

#### *Possible Benefits of Pleometrosis*

A commonly suggested advantage of pleometrosis is the increased probability that a nest will survive the claustral period and produce minim workers. Experimental nests consisted of 1.8 cm thick plexi-

glass plates (10 × 10 cm) with 25 one-cm holes drilled almost through the plastic. When covered with a glass plate, these holes provided 25 experimental founding chambers. A smaller hole was drilled through the bottom of each cell so that water could be attained from damp paper towelling by the queens within the chambers.

Newly mated queens were randomly sorted into the chambers so that each plate contained one row (5 chambers) with one queen per chamber, one row with 5, one with 10, and one with 15, but not necessarily in this order. Eggs, larvae, pupae, minim workers, and queen mortality were scored for each chamber every few days as development proceeded. A total of 23 plates were set up over four mating flights, resulting in over 400 experimental founding chambers.

Colony success in pupal production and worker production was greatest for associations of 5 queens (Fig. 8) (Kruskal-Wallis test;  $P < 0.05$ ). Larger and smaller associations succeeded less frequently. Associations of 15 queens very rarely produced pupae and never produced workers.

A similar pattern emerges for the proportion of queens which find themselves in a nest producing pupae and workers. This measure of individual queen success is also greatest for associations of 5 queens (Kruskal-Wallis test;  $P < 0.05$ ). Thus, both the association and the individual queen improve their chances by pleometrotic founding. These differences in success seem not to be the result of differential mortality. While there was a much higher mortality rate among queens in the unsuccessful nests (Mann-Whitney test,  $P < 0.001$ ), there was no significant relationship of the mortality rates of queens or colonies to association size (ANOVA).

#### *Effects of Pleometrosis Beyond the Claustral Period*

We set up newly mated queens in plaster-floored plastic petri dishes (50 mm diam.) at densities of 1, 5, 10, and 15 queens per dish. Fifteen dishes at each density were maintained at 28 °C and checked once a week for brood, workers and queen mortality. Because growth in these young colonies is exponential, the values of the growth exponent and log *Y*-intercept were calculated from the regression of the log number of workers against time (Fig. 9). The growth rate showed no significant relationship to the queen number (ANOVA). However, the *y*-intercepts of all pleometrotic nests differed significantly from those of the haplometrotic ones ( $P < 0.005$ ), but not from one another. Pleo-

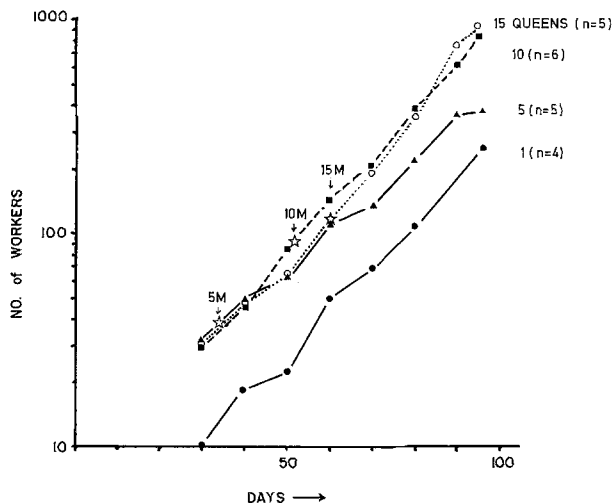


Fig. 9. Mean early growth in worker number in colonies founded by four different sized queen associations in the laboratory. The mean time at which colonies in a treatment achieved monogyny is indicated by a star and *M*. Standard deviations were between 4 and 8 days. Higher queen number during founding period results in later monogyny and higher initial worker numbers. Only successful colonies are shown. Standard error bars for worker number are omitted for clarity. Most were less than 5% of the value

metrotic nests end the claustral period with about three times as many workers as do haplotretic nests. Because of the nature of exponential growth, the pleometrotic colonies remained about 3 times as large for the 100 day experimental period (Kruskal-Wallis test,  $P < 0.05$ ). This should remain true as long as growth is approximately exponential (1.5 yr. Markin et al. 1973). The benefits of this early boost should be felt throughout later life, far beyond the claustral period and far beyond the time the colony achieves monogyny (Fig. 9).

#### *Self-Assortment of Queens into Chambers in the Laboratory*

As a preliminary attack on how the newly mated queens assort themselves among the available nest chambers, we studied their self-assortment among a fixed number of equivalent chambers in the lab. The apparatus used (Tschinkel and Van Belle 1976) was constructed from a circular piece of plexiglass near whose perimeter were 26 evenly spaced large holes drilled from the bottom about halfway through and continued all the way through as small entrance holes. When this disc was set upon a solid bottom and fitted with a collar to serve as a fence, the set-up provided an arena with 26 equivalent chambers among which fire ant queens could assort themselves. The queens prefer

the chambers over the open arena, especially under bright light.

Newly mated queens were collected during afternoon mating flights. Test groups were selected randomly from the total collection and were placed into the arena. The number of queens in the test group was equal to or a multiple (1, 2, 3, 4, 8 ×) of the number of chambers. Visual orientation cues were blocked by surrounding each dispersarium with a 30 cm high collar of white poster board and suspending a single incandescent light directly over the center of each dispersarium. After assorting freely overnight, the number of queens in each chamber was counted. Queens were used only once.

The dispersion of the queens among the chambers was estimated by the ratio of the variance to the mean number of queens per chamber. The ratio was significantly greater than 1.0 even for a mean of one queen per chamber, indicating aggregation, and this aggregation increased with increasing mean queens per chamber (Fig. 10). Thus, in spite of the many profound differences between the field and the apparatus, the assortment of queens responded to queen density in a parallel fashion in both.

A number of variations of this experiment give some insight into how this assortment might be taking place. First of all, if one queen was placed directly into each of the 26 chambers, and these ants allowed to re-assort themselves at will for 24 h, there was very little movement of queens. The variance-to-mean ratio, which was zero at the start of the experiment, increased to only 0.55, still overdispersed.

In the second experiment, 26 queens were once again used, but they were added to the arena in one of three ways. (1) One at a time, after the previous queen had entered a chamber; (2) in groups of five (the last group was 6), after all queens in the previous group had entered chambers; (3) in a single group of 26. The number of queens in each chamber was counted after 24 h in each treatment.

When queens were added singly, they assorted themselves randomly, resulting in a variance-to-mean ratio of 1.05. When they were added in groups of 5, the ratio increased in the direction of clumping to about 1.3, but was not yet significantly clumped. Finally, when all 26 were added simultaneously, the ratio indicated strong and significant clumping (2.7;  $P < 0.001$ ).

While these experiments are somewhat preliminary, they indicate that whatever queen-queen interaction brings about the density-related associa-



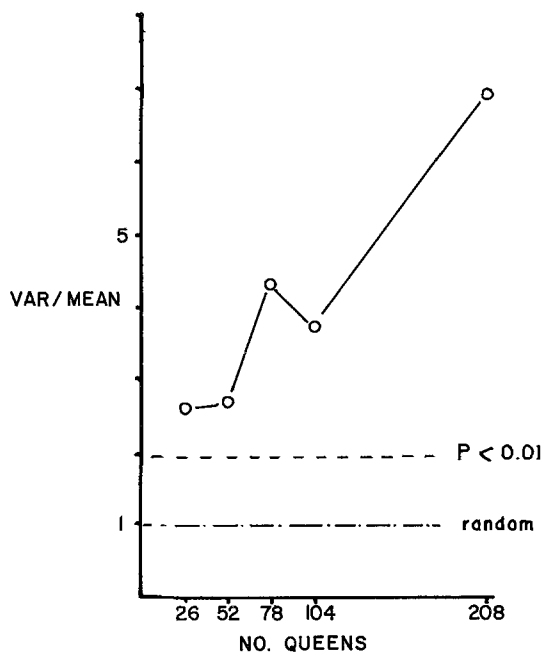


Fig. 10. Aggregation of queens in the dispersarium chambers in relation to queen density. The variance-to-mean ratio indicates that queens are clumped with respect to available chambers, and that the intensity of clumping increases with queen density. The dotted lines indicate random dispersion, and significant clumping at the 0.01 level

tion, it takes place on the surface before queens enter the chambers. Once the queen enters a chamber, there is only a small chance she will leave it again. Experiments to check these results in the field are underway.

## Discussion

We propose the following general mechanism regulating pleometrosis. All factors affecting pleometrosis do so by acting upon the local queen density, local being one to several square meters. Local queen density increases with overall queen density, of course, but it also increases above this in spots through aggregation. Aggregation is itself increased by increasing queen density, probably because it is affected by the likelihood of contact between queens. Higher local queen density increases nest density and frequency of contacts. Increased queen-queen contact leads ultimately to increased frequency and size of pleometrotic association. Any factor which increases the overall or local queen density thus increases pleometrosis.

This scheme is supported by the decreasing relative sensitivity of clumping of queens, nests and queens/nest, respectively, to their mean densities. This is consistent with a mechanism in which ag-

gregation of queens in area drives aggregation of nests, and these both drive aggregation among chambers. This is also physically reasonable in light of the sequence of events during mating flights and post-flight behavior of queens.

Many other factors undoubtedly influence the occurrence and mean size of foundress groups as well as the dispersion of queens among groups, but we propose that these act primarily through their effect upon local queen density. Examples of such factors are: (1) the size of the mating flight (number of sexuals released from the mounds); (2) site selection before alighting. Queens seem to prefer partly vegetated areas, higher ground and absence of large shade areas; (3) After de-alation, queens contact other queens, probably react to soil moisture, soil texture, microtopography, presence of vegetation and shade. All these factors probably cause each queen to elect either to spend more time in that area or to move on. Favorable conditions thus must tend to increase the local queen density and the occurrence and size of foundress associations. The link between the input, queen density, and the output, the occurrence and size of foundress associations, remains to be clarified.

Associations normally seem not to be formed upon first contact between queens. Queens joining an association all seem to share in the excavation, hence, they are all likely to return regularly to the surface and possibly to leave the association. Probably, the association is stabilized only once the nest is closed.

Considering the strength of association between queens and higher ground in the surveys, the failure of microtopography to show a significant effect in the experiment requires some comment. Our hills differed from natural high spots in that they were composed of less compacted soil transported by us to the site. In this, they more closely resembled the soft-alluvium areas in the washes which the queens seemed to avoid. If the queens are responding to soil texture, rather than elevation, our 'hills' would be ineffective.

*S. invicta* colony founding is similar to that of *Myrmecocystus* in many respects (Bartz and Hölldobler 1982). In both, the frequency of pleometrosis varied widely among sites and mating flights. Queens and nests tended to be clumped in distribution, queens showed no aggression but a strong tendency to join one another for chamber excavation. Very large associations were usually not successful at rearing minors. In addition, queens of either species attempting to found within the territory of a mature conspecific colony are killed by the workers of that colony.

While pleometrosis provides a clear advantage both to foundress associations and to individual queens during the claustral phase, the selective advantage of pleometrosis probably acts throughout the entire period between colony foundation and maturity. We have shown that pleometrosis results in higher growth rates in addition to increased survival. High growth rates may be important for at least four reasons. (1) Earlier maturation and reproduction lead to shorter generation time and higher population growth rate. (2) Fire ants are territorial and war with conspecific colonies along their mutual territorial boundaries (Wilson et al. 1971). Such border wars probably result in attrition of the worker force, so that a higher worker production rate might give a competitive edge. (3) In the early post-claustral phase of *Myrmecocystus mimicus* and *S. invicta* colonies, workers move into whatever colony has the largest number of workers, bringing the brood with them. Their mothers are abandoned to die of starvation (Bartz and Hölldobler 1982; Markin et al. 1973; Tschinkel, unpublished). The winner is almost always the colony with the largest initial number of workers. This stresses the benefit of pleometrosis. (4) A colony's ability to survive adverse physical conditions is linked to colony size. Markin et al. (1973) showed that *S. invicta* colonies not attaining a certain minimum size by the onset of cold weather did not survive the winter. High worker numbers can be achieved in part by high worker production rates. While the native homeland of *S. invicta* in southern Brazil seems to lack a distinct winter, it is subject to a long dry season. Perhaps survival of drought is similar to winter from the point of view of the worker population required. Bartz and Hölldobler (1982) suggest that high growth rate aids *M. mimicus* colonies to survive drought.

The chance that an individual queen will cash in on the advantages of pleometrosis is inversely proportional to the number of queens in the association ( $1/n$ ). Clearly there must come a point when the chances of being the chosen queen in a surviving colony are smaller than the chances of success by haplometrosis. At this point, it would be to a queen's advantage not to join such a group, but to search on or found alone. Bartz and Hölldobler (1982) found that in *Myrmecocystus*, the group size showing optimal survival and production per queen was also nearest the mean natural group size, implying that *Myrmecocystus* queens may 'count' the number of foundresses before joining a group. Fire ants seem to have no ability to count, however, for there seems to be no upper limit on

the number of foundresses in an association. We and Markin et al. (1972) found up to 30 queens in a single chamber and several hundred under litter in the field.

Why has inhibition against joining large groups not evolved in fire ants? *S. invicta* is reported not to be very abundant in the areas in which it is native (S. Brazil), and appears to be mostly restricted to disturbed or seasonally flooded habitat (Buren, personal communication). Thus, mating flights and post-flight queen density would rarely be high, pleometrosis would be rare and of low average queen number, resulting in little opportunity to select against joining excessively large groups. However, selection for joining any available group would be strong. Only after introduction to the United States and the subsequent development of large populations would the opportunity for selection against joining large groups have arisen.

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