

## **Queen Replacement in Orphaned Colonies of the Fire Ant, *Solenopsis invicta*\***

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**Summary.** 1. When field colonies of *Solenopsis invicta* Buren were orphaned by removing the functioning queen, re-collection 8–10 weeks later showed that 61% had replacement queens that were physogastric and attractive to workers. The weight of the original colony queens increases with the colony mound volume. The weight of replacement queens is inversely related to the number of such queens in the colony (1 to 99, but over half had only 1).

2. Laboratory rearing and later spermathecal dissections of these replacement queens established that 21% of the colonies had an inseminated queen and produced worker pupae. Of the remaining uninseminated replacement queens, about 20% nevertheless produced 1–25 worker pupae, probably by thelytokous parthenogenesis. Checking the brood present in orphaned field colonies showed that about 35% produced worker pupae, indicating an inseminated replacement queen was present. The remainder of the orphaned colonies produced all-male sexual broods only, a conditions not found in unorphaned colonies.

3. Combining the lab and field evidence, 27% of the orphaned colonies produced fertile replacements, and these were concentrated among the smaller, younger colonies. The hypothesis is developed that the inseminated replacements are surviving foundresses from pleometrotic colony founding, and that *S. invicta* is often polygynous but functionally monogynous.

### **Introduction**

Since there is only one reproductive female in monogynous colonies of social insects, her loss spells imminent colony death unless she can be replaced. The replacement of killed or damaged reproductives in monogynous colonies is smoothly accomplished in many of the lower termites (Lüscher, 1961) and in honeybees (Butler, 1967; Wilson, 1971). In both of these groups, the mechanism of replacement has been extensively investigated, and both rear replacement reproductives from existing immature stages.

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1000 of her colony's workers. The colonies were fed cut-up beetle larvae and sugar water, and were kept moist by watering a plaster of Paris floor in each nest. If a field colony yielded more than 5 queens, 5 were selected for monogynous lab colonies and all the rest were housed in a single colony with 1000 workers. A total of 80 such lab colonies were set up and then scored weekly (up to 4 months) for the type and estimated quantity of brood present.

Of the 104 colonies experimentally orphaned, we re-collected from 56. The remainder of the colonies ( $n=36$ ) were lost to mowers or other human interference, or were used for other observations and not re-collected ( $n=12$ ). Of the 56 orphaned, re-collected colonies, at least one replacement queen was captured in 34 and none in the other 22. Replacement queens were usually recognized by their physogastry and almost always by their strong attractiveness to the workers clustering closely around them.

In addition to re-collecting the orphaned colonies, we also sampled 19 colonies (controls) that were not successfully orphaned at the time of the original collection. Re-collection yielded the queenmother in 10 of these attempts. Two of these control queens were set up in lab nests with 1000 of their own workers and, like the replacement queen, maintained and scored for brood.

After re-collection was complete (April 6), we returned to the mounds twice (April 8 and June 1) for field checks of brood. Colonies were opened with a shovel and the presence of worker pupae and sexual brood was noted. The presence of worker pupae implied that a fertilized queen was present, while a brood of male pupae only (no worker pupae) implied the queen(s) was not inseminated. Another such brood sampling was performed on all colonies that could still be found on July 20, 1977, and its results were combined with the previous checks. Of the colonies checked in the field, those twice orphaned were represented by lab colonies as well.

Table 1 summarizes, in flow-chart form, the procedure followed (exclusive of the brood checks in the field) and lists the number of colonies in each treatment or category.

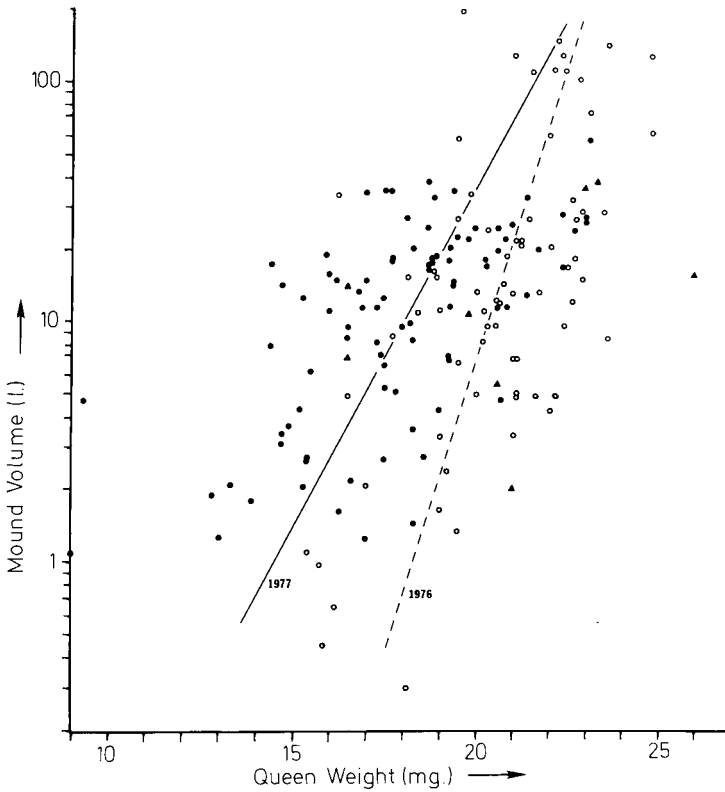
## Results

### *Queen Mothers*

Queen mothers were collected from 114 of 210 colonies, 104 on the first collection and an additional 10 upon re-collection. Due to ovarian hypertrophy, these queens were almost always recognizably to grossly physogastric and always highly attractive to their workers. The workers often clustered over the queens by the hundreds and many clung to the queen when she was picked up. The dealated females that were sometimes present in the queen-right colonies were neither distinctly physogastric nor attractive to the workers and could thus easily be distinguished from functioning queens.

One of the most striking conclusions from these original collections is that *S. invicta* is an almost totally monogynous species (see Discussion) as far as attractive, physogastric queens are concerned. While we were able to confirm the moderately common presence of nonattractive, nonphysogastric dealates (Glancey et al., 1973), only two of 114 colonies contained more than one physogastric queen (2 in one case and 3 in the other). The three queens were later shown by dissection to be uninseminated, but the two were discarded without dissection and are of unknown fertility.

Queen weight (physogastry) is semilogarithmically related to colony size as measured by above-ground mound volume (Fig. 1). During the cool months, at least, the mounds are built up for improved warming. Whether queen weight reaches an upper limit beyond which increasing colony size no longer has an effect is not known. However, the weights represented in Figure 1 are from the cool season and are probably lower than during the warmer months.



**Fig. 1.** The volume of the above-ground mound of *S. invicta* in relation to the weight of the colony's queen. Open circles, winter of 1976; closed circles, winter 1977 queens captured on first collection; closed triangles, winter 1977 queens captured on re-collection only. Semilog regression analysis indicated that both relationships are highly significant (correlation ( $r$ ), 0.60 in 1976; 0.50 in 1977; both significant at  $P < 0.00001$ ). In addition, the regressions for the two years significantly differ from one another

The relation of queen weight to colony size differs from year to year. Figure 1 shows this relationship for the cool months of 1976 (January–April). Colonies of a given size had heavier queens in 1976 than in 1977 and this effect is accentuated at lower colony sizes. At the largest colony sizes, the two seem to converge. The winter of 1977 was unusually cool and overcast, and we interpret the effect as being due primarily to the lower temperatures.

#### *Replacement of Queens in Orphaned Colonies*

Since dealated females were often present before orphaning, it is necessary to define 'replacement queen.' In the majority of cases, we denoted only those dealates with distinguishable physogastry and/or attraction for workers as appar-

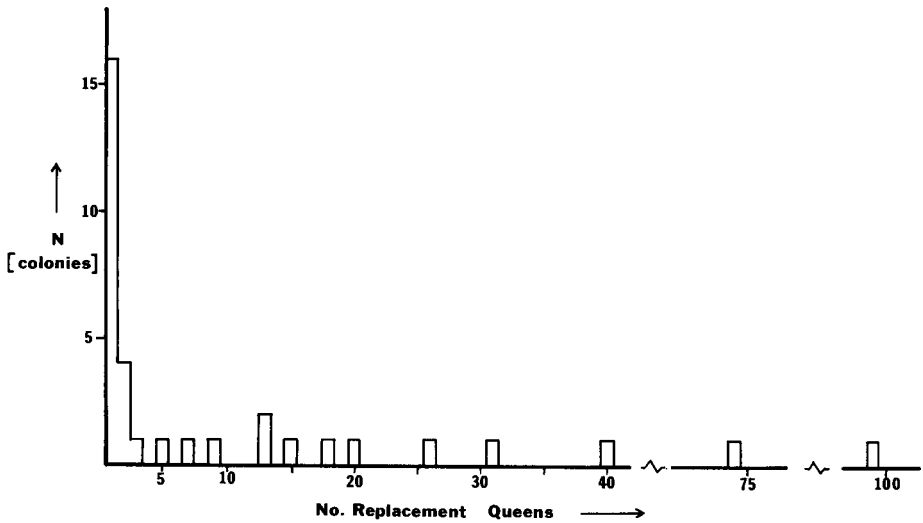


Fig. 2. The number of replacement queens captured from orphaned colonies upon re-collection ( $n=34$ ). Just over half the colonies yielded more than one replacement queen

ent 'replacement queens.' Other dealates were considered simply dealates. However, when a large number of dealates was present, there existed a continuum of physogastry and attractiveness that blurred the distinction between dealates and replacement queens. In these few cases, all dealates were collected and considered replacement queens. This was later found to be justifiable (see below and Fig. 4). Of the 56 orphaned colonies that were re-collected, at least one apparent 'replacement queen' was found in 34. The response of colonies to orphaning was often the appearance of multiple (1-99) dealated females as replacements (Fig. 2), but the most common number collected was one.

The great majority of apparent replacement queens from orphaned colonies were much heavier than dealates from queen-right colonies (Fig. 3). Dealates rarely exceeded 11 or 12 mg, while replacement queens from orphaned colonies seldom weigh less than this. Replacements sometimes weighed up to almost 17 mg and were indistinguishable in appearance and attractiveness from the original queen. Increased weight and (presumably) egg production among replacements is thus one of the most obvious effects of orphaning.

The degree of this weight increase is inversely related to the number of replacement queens found in the colony (Fig. 4). When the number of replacements is very large, the replacements are essentially indistinguishable from ordinary dealates in weight and attractiveness (which is probably linked to weight). Many colonies with multiple replacements had one to several individuals that were distinctly heavier than the rest, but replacement queen weights generally tend to cluster fairly compactly about the mean (SD's mostly about 1 mg or less), with consistent differences among colonies (Fig. 4).

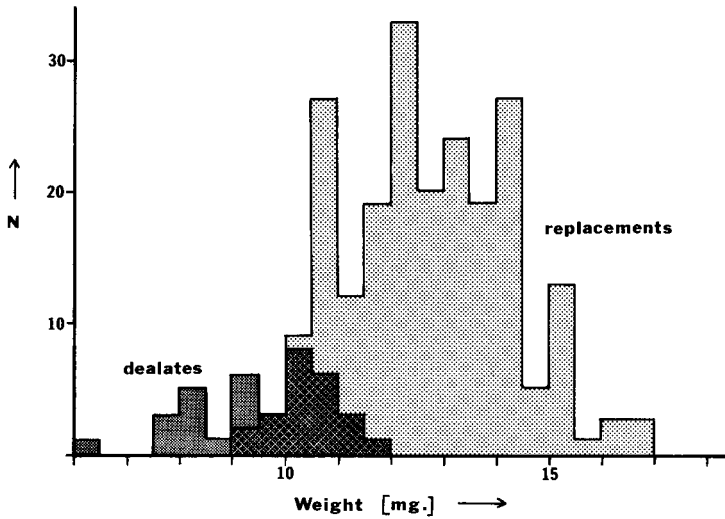


Fig. 3. Frequency/weight-class histograms for all dealated females captured from orphaned colonies (replacement queens) and unorphaned colonies (dealates). The replacement queens from orphaned colonies are significantly heavier (more physogastric), but are not distinguishable from dealates at the lower limits of their weight distribution

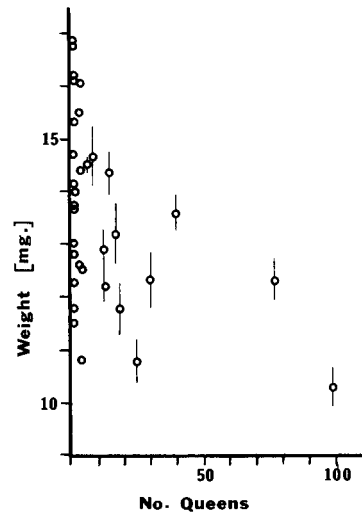


Fig. 4. Weight of replacement queens from orphaned colonies in relation to the number of replacement queens in the colony. Vertical bars are standard deviations calculated for colonies with more than 5 queens

*Determination of Replacement Queen Fertility in the Lab*

From the functional viewpoint, an apparent 'replacement queen' deserves the title in the full sense only after it has been established that she is inseminated and capable of producing worker brood. Inseminated, nonphysogastric, dealated females have been found in fire ant colonies by Glancey et al. (1973), but the reproductive activity of these dealates was not reported. We therefore

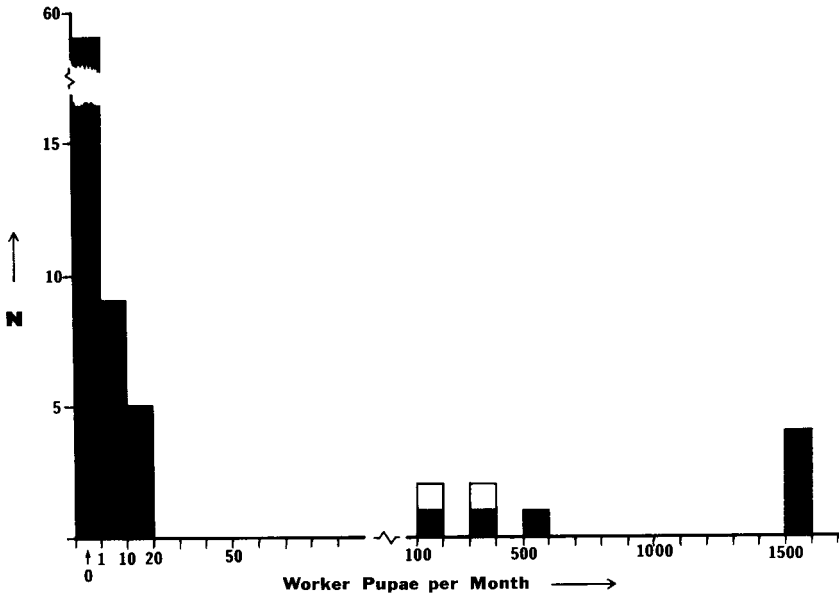


Fig. 5. Worker pupae production in the lab by replacement queens from orphaned colonies over a period of about 4 months. Numbers were estimated when production was more than 100 per month. All queens were in colonies with 1000 of their own colony's workers. Open bars are control queens from nests not previously orphaned. All queens producing fewer than 20 workers per month were uninseminated, while those producing 100 or more were inseminated

chose the production of worker pupae in laboratory nests as the more important criterion of whether an individual could be considered a functional replacement queen. The presence of sperm in the spermatheca was included as a secondary criterion, since a number of ant species are able to produce workers parthenogenetically (see Discussion).

In laboratory colonies consisting of candidate replacement queens and workers, brood production fell into three distinct classes (Fig. 5): (1) those that yielded no worker pupae, whose larvae either did not develop or developed into male pupae ( $n=59$ ), (2) those that produced 1–15 worker pupae per month, along with varying numbers of male pupae ( $n=14$ ), and (3) those that yielded worker pupae at the rate of 100–1500 per month, usually without producing any male pupae ( $n=7$ ). Controls ( $n=2$ ) fell into the last category.

At the end of 3–4 months of laboratory rearing, representatives of the queens belonging to each of these classes were dissected and a sperm count was made on the contents of the spermatheca. No sperm were detected in the spermathecae of any nonworker-producing or low worker-producing queens. These apparent 'replacement queens' were therefore uninseminated and any worker pupae they produced probably arose from parthenogenesis.

Replacement queens producing more than about 100 workers per month (and few male pupae) (7 colonies: 7 lab nests) were found to contain 3.6–5.0 million sperm in their spermathecae, the same number as newly mated queens.

These were therefore mated queens and were truly functional replacements of the queens that were originally removed. Our laboratory evidence indicated that at least 12.5% of the collected replacement queens were inseminated. Field evidence described below indicated that the total fraction of colonies with inseminated replacements was considerably higher than this.

#### *Worker Pupae Production as Evidence of Replacement Fertility in the Field*

The brood of most re-collected colonies was checked at least once after the original collection, and in many cases two to three times. Judging from the laboratory-rearing results, production of a large number of worker pupae indicates that an inseminated queen is present in the nest, while an all-male pupae brood indicates that the queen(s) is not inseminated. We judged that a small number of worker pupae produced parthenogenetically would not be readily detected among an all-male brood, and we accepted worker pupae as evidence of fertility only if they made up a substantial fraction of the brood. Before about early May, the brood was mostly in the larval stage and could not be readily identified for our purposes, especially if it consisted of a variety of sizes. Only in a few cases in which the brood consisted exclusively of mature-sex larvae did we use data from nests not containing pupae. A survey of previously undisturbed colonies beginning in May showed that an all-sex larvae brood is practically never found normally. We therefore reasoned that the entirely sexual broods we observed had resulted from our treatments. The analysis of the brood checks was carried out as follows: Brood of a colony at the time of original queen capture or before was considered 'preorphan' brood as was the brood found at all checks of colonies that were never orphaned. 'Postorphan' brood was that found by checking colonies at least 4 weeks, and usually 6 or 8 weeks, after the colony had been orphaned. Many colonies were checked two or even three times over a period of up to 4 months after orphaning or attempted orphaning at re-collection. It should also be kept in mind that 34 of the colonies were apparently orphaned twice, and in at least two cases colonies that contained fertile replacements at time of re-collection changed to producing all-male broods at the next check. Fertility of the captured replacements was established by lab-rearing.

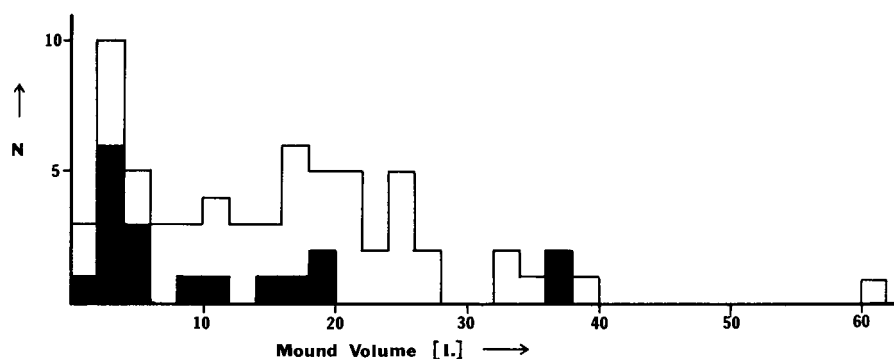
The results of the brood analysis (Table 2) indicate that 'preorphan' colonies (unsuccessful attempts at capture made) almost always produce largely worker brood and almost never produce all-male or all-sex larval broods. The one exception was a colony that contained over 100 dealated females and that was probably already queenless at the time of collection. On the other hand, when we succeeded in orphaning the colony, the majority of the nests began to produce all-male or all-sex larval broods, indicating that the egg-laying queens now functioning in these colonies were not inseminated. Nevertheless, in 13 of the colonies, the brood contained at least a substantial fraction of worker pupae, indicating the presence of an inseminated queen. Brood check evidence overlaps with the lab-rearing evidence to some degree. In two colonies shown fertile by brood check, lab rearing and dissection established that these colonies contained inseminated replacement queens.

**Table 2.** Brood found in field colonies. Data from 67 of 113 colonies summarized below, the remaining 46 colonies being abandoned or containing brood that could not be identified to caste. One colony first produced worker pupae and after re-collection changed to male pupae only. It was therefore counted twice

Results of queen capture	Brood found		Totals
	Worker pupae	Male pupae only <sup>a</sup>	
Unsuccessful (queen present)	31	1 <sup>b</sup>	32
Successful (colony orphaned)	13	22	35
Totals	44	23	

<sup>a</sup> Includes some colonies with sex larvae only and four without brood but with adult males only

<sup>b</sup> Colony had more than 100 dealate females upon first collection and was probably queenless



**Fig. 6.** Size frequency of orphaned colonies with apparently inseminated replacement queens (solid bars) in comparison with size frequency of collected colonies (open bars). The colonies having inseminated replacements are predominately smaller colonies ( $P=0.07$ )

In sum, field evidence (Table 2) indicated that 97% of the nonorphaned colonies contained fertile queens, as did 37% of orphaned colonies. The remaining 63% of the orphaned colonies had only sterile replacements.

Combining field and lab evidence of fertility, 18 (27%) of 67 colonies apparently contained an inseminated replacement queen. Of these, a single case is in some doubt, for the worker pupae were found only three weeks after the queen mother had been removed, and we are not certain that the pupae were not remnants from her tenure.

#### *Fertility of Replacements and Colony Size*

Colonies that produced inseminated replacement queens are predominantly smaller colonies (Fig. 6), especially colonies with mound volumes of less than



6 l. When the colony mound volumes are grouped in either 10- or 20-l classes, the occurrence of inseminated replacements is higher in the smallest size class ( $\chi^2$  test;  $P=0.07$ ).

## Discussion

It is evident from our results that over one-fourth of *S. invicta* colonies are able to replace lost queens with inseminated, apparently normally functioning queens. Most of the remaining colonies seem able to replace lost queens with unmated, male-producing queens.

It seems likely that queen replacement is somehow linked with polygyny. The fact that the fertile-replacement ability is concentrated in the smaller, younger colonies leads to the hypothesis that the source of the inseminated replacements is a reserve of mated but non-egg-laying queens derived from multiple queen colony foundation (pleometrosis). Let us develop this hypothesis as follows: It has been reported that for *S. invicta* colonies, although they almost never contained more than one physogastric queen, a minimum of 3 of 35 colonies contained one or more inseminated, nonphysogastric dealates in addition to the physogastric queen (Glancey et al., 1973). Multiple inseminated queens were also reported for *S. xyloni* (Summerlin, 1976). Since cooperation in nest founding is widespread among ants (Hölldobler and Wilson, 1977) and has been reported from *S. invicta* as well (Markin et al., 1972; Wilson, 1966), it is most parsimonious to view the survival of these foundresses as the source of the mated queen reserve. The literature on *S. invicta* does not really settle the question of survival of supernumerary queens beyond first worker production. Thus, Markin et al. (1972) report that young colonies in the field become monogynous soon after first worker production, but they do not indicate how many colonies were examined or whether dealates were present. Wilson (1966) introduced multiple queens to queenless workers and found that the workers executed all but one. This experiment, however, is not comparable to pleometrosis and cannot well illuminate the source of multiple fertile queens. We have found in several cases that lab colonies founded by 5 queens remain polygynous well beyond the production of the first workers (unpublished data).

Whatever the source of the multiple inseminated queens, *S. invicta* is clearly, in many cases, functionally monogynous, according to the terminology of Buschinger (1968). In functional monogyny, one of the inseminated queens becomes reproductively dominant over the others, inhibiting their ovarian development and function. Buschinger (1968) indicates that *Leptothorax gredleri* is such a species. *S. geminata* is probably another (Travis, 1941; Banks et al., 1973), but few other examples have been reported in ants. A somewhat related case may be that of *L. curvispinosus* in which the multiple queens differ in oviposition rate to some degree while appearing to practice differential oophagy. There is thus some indication that one queen contributes more to the brood than others (Wilson, 1974).

It seems common among social hymenoptera for queens to inhibit ovarian development and egg laying of workers. Even considering only those species

in which the queen-worker dichotomy is large and dominance is not primarily behaviorally achieved, removal of the laying queen often causes the ovaries of the workers to develop to the point of oviposition. Examples can be drawn from the bees (Butler, 1967), the wasps (e.g., the Oriental hornet, *Vespa orientalis*: Ishay et al., 1965), and the ants (e.g., *Leptothorax tuberum unifasciatus*: Bier, 1954). These eggs are, of course, usually not fertilized and generally result in males, but in some cases the workers may mate and lay female-determined eggs.

Thus, there is evidence of reproductive inhibition by queen ants over other inseminated queens and over workers. Our work implies an additional inhibition over unmated dealates (possibly derived from alates already in the nest), but how it operates is unknown. Once disinhibited by orphaning, the degree of physogastry achieved by uninseminated dealates is inversely related to the number of such dealates, possibly pointing to a 'profertile' substance as suggested by Bier (1954). A similar explanation could account for the relation of the original queen's physogastry to colony size, if one assumes that the profertile substance is generated in proportion to colony size. Whatever factor causes ovarian hypertrophy, it apparently has less individual effect when shared among increasing numbers. Among replacement queens, there is no clear relation of physogastry to colony size, but this could be due to the rather short time (8–10 weeks) allowed for the development of this relation.

This is the first report that uninseminated dealates of *S. invicta* are capable of producing workers parthenogenetically. Sperm content possibly was so low as to escape detection, but the ability to produce occasional parthenogenetic females (thelytoky) is widely scattered among the ants. Such thelytoky usually involves workers or, less frequently, virgin queens. Thelytoky has been reported from *Lasius niger* (Bier, 1952), *Atta cephalotes* (Tanner, 1892, cited in Wilson, 1971), and *Formica polyctena* (Otto, 1960). The thelytoky reported by Ledoux (1950) for *Oecophylla longinodis* has been contested by Way (1954). Recently, Suzzoni and Gagniant (1975) have advanced evidence that workers of *Cataglyphis cursor* Fonsc. can produce workers, queens, and males by thelytokous parthenogenesis. In four species of *Crematogaster*, Soulie (1960) found that all queens are produced by apomictic thelytoky by workers who can also produce males and workers. Queens can produce only workers and these from fertilized eggs. Thelytoky is thus a central phenomenon in the life cycle of these species. Most relevant to our findings with *S. invicta* is the work of Haskins and Enzmann (1945) with *Aphaenogaster rudis* and *A. lamellidens*. In both species, among the few virgin females that reared brood to the pupal stage, only 10–15% produced any females. The thelytokous performance of uninseminated *S. invicta* queens is considerably better than this, for about one-fifth of them produced at least one worker, and the individual production ranged up to 25. None produced enough workers to offset normal worker mortality, and the meaning of this phenomenon is obscure. Perhaps large numbers of unmated queens can produce enough thelytokous workers to extend the life of the colony and to increase its fitness via male production.

If our assessment is correct, pleometrosis that develops into functional monogyny preserves the advantage of monogyny (Baroni-Urbani, 1968; Hölldobler

and Wilson, 1977) while perhaps enhancing survival during early colony growth. Small, young colonies are certainly at greater risk, and having spare queens around may reduce that risk. On the other hand, it is difficult to invoke natural selection for the maintenance of (probably) unrelated replacement queens. Perhaps selection operates on the inhibited queens by favoring those who escape execution. Chances of eventual reproduction by such inhibited queens would still be much higher than after execution.

As the colony grows and ages, it loses its capacity to produce fertile replacement queens, perhaps because these reserves gradually die off or are killed. Maintenance of a reserve may be more important in small colonies since risk is greater.

Although the ultimate fate of orphaned colonies without a reserve mated queen is probably an early death, such colonies still have a chance to pass on their genome through male production. One to a large number of unmated, dealated females begin to lay unfertilized eggs that develop into males, often in large numbers. These unmated queens are superficially indistinguishable from normal queens, becoming both physogastric and attractive. Our impression is that brood production eventually ceases and that these same colonies gradually dwindle in size. This trend is probably due to the fact that workers lost to normal mortality are no longer replaced.

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## References

- Banks, W.A., Plumley, J.K., Hicks, D.M.: Polygyny in a colony of the fire ant *Solenopsis geminata*. *Ann. Entomol. Soc. Amer.* **66**, 234–235 (1973)
- Baroni-Urbani, C.: Monogyny in ant societies. *Zool. Anz.* **181**, 269–277 (1965)
- Bier, K.: Zur scheinbaren Thelytokie der Ameisengattung *Lasius*. *Naturwissenschaften* **39**, 433 (1952)
- Bier, K.: Über den Einfluß der Königin auf die Arbeiterinnenfertilität im Ameisenstaat. *Insectes Soc.* **1**, 7–19 (1954)
- Buschinger, A.: Mono- and Polygynie bei Arten der Gattung *Leptothorax* Mayr. *Insectes Soc.* **15**, 217–226 (1968)
- Butler, C.G.: Insect pheromones. *Biol. Rev.* **42**, 42–87 (1967)
- Free, J.B., Butler, C.G.: Bumblebees. New naturalist series. London: Collins 1959
- Glancey, B.M., Craig, C.H., Stringer, C.E., Bishop, P.M.: Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. *J. Ga. Entomol. Soc.* **8**, 327–328 (1973)
- Haskins, C.P., Enzmann, E.V.: On the occurrence of impaternate females in the Formicidae. *J. NY Entomol. Soc.* **53**, 263–277 (1945)
- Hölldobler, B., Wilson, E.O.: The number of queens: An important trait in ant evolution. *Naturwissenschaften* **64**, 8–15 (1977)
- Ishay, J., Ikan, R., Bergmann, E.D.: The presence of pheromones in the oriental hornet, *Vespa orientalis* F. *J. Insect Physiol.* **11**, 1307–1309 (1965)
- Janzen, D.H.: Evolution of polygynous obligate acacia-ants in western Mexico. *J. Anim. Ecol.* **42**, 727–750 (1973)
- Ledoux, A.: Recherche sur la biologie de la fourmi filense (*Oecophylla longinoda* Latr.). *Ann. Sci. Naturelles* **12**, 313–461 (1950)
- Lüscher, M.: Social control of polymorphism in termites. *Symp. Roy. Entomol. Soc. Lond.* **1**, 57–67 (1961)
- Markin, G.P., Collins, H.L., Dillier, J.H.: Colony founding by queens of the red imported fire ant, *Solenopsis invicta*. *Ann. Entomol. Soc. Amer.* **65**, 1053–1058 (1972)

- Otto, D.: Zur Erscheinung der Arbeiterinnenfertilität und Pathogenese bei der kahlrückigen Roten Waldameise (*Formica polyctena* Först.). Dtsch. Entomol. Z. 7, 1–9 (1960)
- Pardi, L.: Dominance order in *Polistes* wasps. Physiol. Zool. 21, 1–13 (1948)
- Schneirla, T.C.: A preliminary survey of colony division and related processes in two species of terrestrial army ants. Insectes Soc. 3, 49–69 (1956)
- Soulié, J.: Des considerations écologiques peuvent-elles apporter une contribution à la connaissance du cycle biologique des colonies de *Crematogaster*. Insectes Soc. 7, 283–295 (1960)
- Summerlin, J.W.: Polygyny in a colony of the southern fire ant. Ann. Entomol. Soc. Amer. 69, 54 (1976)
- Suzzoni, J.P., Cagniant, H.: Etude histologique des voies génitales chez l'ouvrière et la reine de *Cataglyphis cursor* Fonsc. (Hymenoptera Formicidae): Arguments en faveur d'une parthénogenèse thélytoque chez cette espèce. Insectes Soc. 22, 83–92 (1975)
- Tanner, J.E.: *Oecodorna cephalotes*. 2nd paper. Trinidad Field Naturalists' Club 1, 123–127 (1892)
- Travis, B.V.: Notes on the biology of the fire ant *Solenopsis geminata* (F.) in Florida and Georgia. Fl. Entomol. 24, 15–22 (1941)
- Vanderplank, F.L.: The bionomics and ecology of the red tree ant, *Oecophylla* sp. and its relationship to the coconut bug *Pseudothrips wayi*. J. Anim. Ecol. 29, 15–33 (1960)
- Way, M.J.: Studies of the life history and ecology of the ant *Oecophylla longinoda* Latr. Bull. Entomol. Res. 45, 93–112 (1954)
- Wilson, E.O.: Behavior of social insects. Symp. Roy. Entomol. Soc. Lond. 3, 81–96 (1966)
- Wilson, E.O.: The insect societies. Cambridge: Harvard 1971
- Wilson, E.O.: Aversive behavior and competition within colonies of the ant, *Leptothorax curvispinosus*. Ann. Entomol. Soc. Amer. 67, 777–780 (1974)