

DIFFERENTIAL VIABILITY OF EGGS LAID BY QUEENS IN POLYGYNE COLONIES OF THE FIRE ANT, *SOLENOPSIS INVICTA*

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Abstract—The viability of eggs laid by individual functional queens from polygyne colonies of the fire ant, *Solenopsis invicta* Buren, was examined by staining for chromatin. In isolation units held in the laboratory inseminated queens laid nearly 100% viable eggs, compared to <10% for uninseminated queens. Experiments in which the quantity of brood was manipulated demonstrated that the number of brood and workers present has little, if any, effect on the ability of a queen's eggs to form embryos, in contrast to the stimulatory effect of larvae on oviposition rate. In field colonies, although there was considerable variability among queens, inseminated queens laid a significantly greater proportion of viable eggs than did uninseminated queens. Inseminated queens taken directly from polygyne colonies in the field laid a smaller proportion of viable eggs than those maintained individually for several weeks in the laboratory, suggesting that there is mutual inhibition among cohabiting inseminated queens which affects viable egg production. Among queens taken from the field, there was no significant correlation between the proportion of viable eggs laid and queen weight, a reliable indicator of oviposition rate. Thus caution should be exercised in equating relative rates of egg production with reproductive success in studies of reproductive roles in social insect colonies.

Key Word Index: Fire ants, *Solenopsis invicta*, polygyny, oviposition, embryonation, egg viability, reproductive success

INTRODUCTION

Among the ants, nonviable eggs are routinely produced in a variety of species and in a number of contexts. Such eggs fail to form embryos and generally appear to have a trophic function, serving as an important source of food for the queens and/or larvae (Wilson, 1971). Trophic eggs are most commonly produced by workers, as in *Myrmica rubra* (Brian, 1953; Brian and Rigby, 1978) and *Plagiolepis pygmaea* (Passera, 1966). Newly-mated queens in the process of colony founding may also produce trophic eggs which are eaten by larvae in the incipient colonies, e.g. in *Atta sexdens* (Bazire-Benazet, 1957). In addition, production of nonviable eggs by winged virgin queens may occur, as in *Pheidole pallidula* (Passera, 1978).

Given the widespread occurrence in ants of nonviable egg production by some colony members, it is of interest to know whether some functional (i.e. egg-laying) queens in multiple-queen (polygyne) colonies produce nonviable eggs, and if so, whether individual queens vary in the proportion of such eggs produced. Such variability among nestmate queens would be particularly significant since it can be expected to contribute to differential repro-

ductive success. Despite the common occurrence of polygyny among ants, the relative viability of eggs produced by individual polygyne queens has not been investigated.

The fire ant, *Solenopsis invicta*, forms polygyne colonies throughout its range in the southeastern and south-central U.S.A., although the monogyne (single-queen) form of this introduced species is more widespread (Ross and Fletcher, 1985a; Vargo and Fletcher, 1989). Queens of the monogyne form produce nonviable eggs in certain social and physiological contexts, raising the possibility that some functional queens in polygyne colonies of this ant also produce nonviable eggs. Newly-mated monogyne queens engaged in colony founding lay some eggs which are unable to form embryos and presumably serve as an important source of food for the larvae of young colonies (Glancey *et al.*, 1973; Cherix and Fletcher, 1982; Voss and Blum, 1988). In addition, when virgin queens from monogyne colonies are isolated, removing them from the inhibitory pheromone of the mother queen which ordinarily prevents oviposition (Fletcher and Blum, 1981), they lay almost exclusively nonviable eggs (Voss, 1981; Fletcher and Blum, 1983a). However, if such disinhibited virgin queens are maintained in the presence of large numbers of workers and brood or treated topically with juvenile hormone, they produce some eggs which form embryos (Voss, 1981; Fletcher and Blum, 1983a; Voss and Blum, unpublished). The

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abnormal mitotic events resulting in developmental arrest of nonviable eggs have been documented by Voss *et al.* (1987).

As part of a series of studies on the reproductive structure of polygyne colonies of *S. invicta*, the present study was conducted to determine whether, and to what extent, individual polygyne queens produce nonviable eggs, with particular attention paid to variability among individuals and between inseminated and uninseminated queens.

METHODS AND RESULTS

Queens isolated in the laboratory

Polygyne colonies were collected in the spring of 1986 from Walton Co. Georgia, U.S.A. ($n = 2$) and the spring of 1987 at Brackenridge Field Laboratory of the University of Texas at Austin, Austin, Texas, U.S.A. ($n = 6$). The ants were removed from the soil by flooding (Jouvenaz *et al.*, 1977) and maintained in the laboratory at $29 \pm 1^\circ\text{C}$, where they were fed *ad libitum* on an artificial diet after Banks *et al.* (1981), as well as on frozen crickets, live mealworm larvae, and pureed vegetables. After several weeks in the laboratory, the colonies were sieved (1.4 mm mesh) to remove all sexual forms, including functional (dealate) queens, winged adults, sexual pupae, and large sexual larvae (>4 mm long).

To sample the eggs laid by selected individual queens, isolation units consisting of a single queen and 3–10 g of nestmate workers and worker brood (larvae and pupae) were set up. The units were housed in plastic trays ($48 \times 58 \times 7$ cm) equipped with a single nest (14 cm dia Petri dish half-filled with damp plaster). These rearing units were maintained for at least 6 weeks, at which time all pupae and larvae are known to be the offspring of the resident queen (Ross and Fletcher, 1985a, b; Porter, 1988).

Polygyne colonies of *S. invicta* contain three distinct categories of functional queens based on the types of eggs laid. Queens of these different categories can be readily distinguished after 5–6 weeks of isolation in small rearing units. Uninseminated queens comprise about 30% of all functional queens in a colony (Fletcher *et al.*, 1980; Vargo and Fletcher, 1987, 1989) and are easily distinguished from inseminated queens because they produce no brood or only a few haploid males. Among inseminated queens, some 15–20% are diploid-male producers which have 'match' mated to a single male bearing an allele in common with the queen at the major sex-determining locus (Ross and Fletcher, 1985b). Diploid-male-producing queens are readily distinguishable from non-diploid-male-producing inseminated queens by the characteristic pattern of brood production, in which approximately half of the brood of diploid-male-producing queens is comprised of large diploid males (Ross and Fletcher, 1985a). In this study, the insemination status of all presumed uninseminated queens and about 75% of the presumed inseminated queens (some being retained for other experiments) was confirmed by dissection and examination of the spermatheca for sperm. This

method of separating queens into reproductive categories allowed us to compare the proportion of viable eggs produced by individual queens belonging to different reproductive categories as well as queens within each category.

A sample of eggs of each selected queen was taken from the egg pile in the nest of its respective isolation unit and incubated for 24 h at $29 \pm 1^\circ\text{C}$ with 5–10 nestmate workers in a small cup containing a layer of damp plaster. The eggs were then mounted on a slide and stained for chromatin using the Feulgen reaction as adapted by Voss (1985). The eggs of each queen were examined with a dissecting scope to see whether they were embryonated, i.e. whether they had retained the stain.

All together, the eggs of 115 queens were examined, of which 54 queens were inseminated, including 14 diploid-male producers, and 61 queens were uninseminated. A mean (\pm SD) of 99.6 ± 30.7 (Range = 8–175) eggs per queen was examined. At the time that the eggs were sampled, the weights of 43 inseminated queens and 41 uninseminated queens were taken.

There was a striking difference between the inseminated and uninseminated queens in the proportion of their eggs forming embryos. With the exception of 2 of the 115 queens studied, there was no overlap in the frequency of embryonation between inseminated and uninseminated queens (Fig. 1). The exceptional individuals consisted of one inseminated queen weighing only 7.7 mg (52% of the mean weight of the inseminated queens studied) and having only 17.9% of her eggs embryonated and one uninseminated queen with 90.3% of her eggs forming embryos. Excluding these 2 queens, the lowest proportion of embryonated eggs for an inseminated queen was 0.856, with 42 (79.2%) such queens over 0.950, whereas the highest proportional embryonation for an uninseminated queen was 0.535, with 23 (38.3%) uninseminated queens having no embryonated eggs at all. Among inseminated

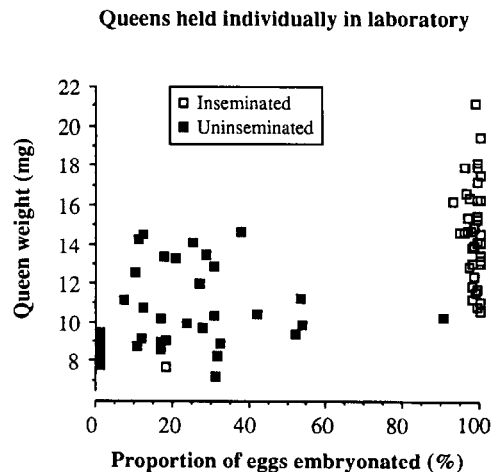


Fig. 1. The proportion of viable eggs laid by queens of the polygyne form of *S. invicta* in relation to insemination status and weight. Queens were held individually in small rearing units in the laboratory. $n = 43$ for inseminated queens and 41 for uninseminated queens.

queens, those producing diploid males had a slightly higher proportion of their eggs embryonated than did those not producing diploid males (0.922 ± 0.006 and 0.965 ± 0.037 , respectively), but this difference was not significant ($t_{32} = 1.89$, $P > 0.06$; angular transformation).

Effect of brood on the ability of a queen's eggs to form embryos

Among the uninseminated queens in the previous experiment, 28 individuals (46%) lacked brood entirely in their rearing units, while the remainder had only very small amounts of brood, in contrast to the substantial quantities of brood in units with inseminated queens. In addition, rearing units containing inseminated queens had more workers present at the time of sampling than did those containing uninseminated queens, for although inseminated and uninseminated queens originating from the same colony were given equivalent numbers of workers to start with, inseminated queens continued to produce workers. Thus it is of interest to know whether differing quantities of brood and/or workers might have been a factor influencing the ability of a queen's eggs to form embryos, especially since recent evidence shows that larvae can affect queen reproductive physiology in *S. invicta*. Tschinkel (1988) has found that the number of fourth- (last) instar larvae is correlated positively with oviposition rate in *S. invicta* queens, while the number of workers and pupae is not related to oviposition rate (see also Vargo and Fletcher, 1989). Should the quantity of larvae or workers exert such an effect on egg viability, all or part of the difference in the proportional embryonation of eggs laid by inseminated and uninseminated queens in small rearing units could be due to differences in this regard.

To investigate this possibility, the following experiment was performed. Twelve isolation units containing inseminated queens and 12 units containing uninseminated queens from the above study were used. Just after the eggs were sampled, 9 inseminated and 9 uninseminated queens originating from three different field colonies were exchanged. Thus, inseminated queens coming from units containing relatively large quantities of brood and workers (mean weight

in 6 representative units was 8.3 ± 3.2 g, Range = 5.1–13.7) were placed in units formerly containing resident uninseminated queens and therefore having very little or no brood and fewer workers, and vice-versa. The queens involved in each exchange were paired so as to be former nestmates originating from the same field colony. Three resident inseminated queens and 3 resident uninseminated queens were left in their original isolation units (i.e. not exchanged) to serve as controls.

Eggs from the standing crop in the nest of each unit were sampled just before the exchange of queens and again 10 and 15 days later. To determine relative oviposition rates, the weights of queens, which are a reliable indicator of oviposition rates in both inseminated and uninseminated queens (Ross, 1988; Tschinkel, 1988; Vargo and Fletcher, 1989; see also Willer and Fletcher, 1986), were also taken at these times. The first sample following the exchange of queens was well after the 6-day period needed for eggs of *S. invicta* to hatch under these laboratory conditions (Porter, 1988), ensuring that all eggs sampled after queen exchange were laid by the queen which was currently occupying each unit. Any change in egg viability would be expected to occur within a few days since queens of *S. invicta* show a marked decrease in oviposition rate when deprived of fourth-instar larvae after only 2 days, and the addition of such larvae to broodless nests results in peak laying in about 4 days (Tschinkel, 1988).

Inseminated queens showed very little change in the proportion of their eggs forming embryos following placement in units lacking brood and containing fewer workers (Table 1). On the other hand, the weights of these queens decreased over time, with the change from the original weight being significant at both 10 and 15 days (both $t_8 \geq 2.25$, $P < 0.03$; 1-tailed paired-sample test). In the most dramatic case, one queen lost over 30% of her weight, yet the proportion of her eggs forming embryos (0.988) did not change over the 15-day period. In contrast, the weights of the 3 inseminated controls increased on average 1 mg (9.4%) by day 15.

For uninseminated queens, the proportion of eggs forming embryos unexpectedly decreased after placing them in units containing brood and having

Table 1. Effect of brood (larvae and pupae) and worker number on the viability of eggs laid and the weights of inseminated (I) and uninseminated (U) queens in isolation units before, 10 days, and 15 days after the resident queens of these two reproductive classes were exchanged. Queens in the control units (I_c and U_c) were not exchanged

	Type of queen	Days after exchange		
		0	10 days	15 days
Prop. eggs embryonated*	I	0.977 ± 0.006	0.972 ± 0.011	0.983 ± 0.004
	U	0.323 ± 0.079	0.197 ± 0.063	0.186 ± 0.037†
	I_c	0.991 ± 0.009	0.984 ± 0.002	0.989 ± 0.002
	U_c	0.251 ± 0.002	0.172 ± 0.076	0.283 ± 0.005
Queen weight (mg)	I	15.9 ± 2.8	14.4 ± 2.0†	14.3 ± 1.8†
	U	12.5 ± 2.1	13.5 ± 2.8	14.0 ± 3.4†
	I_c	16.5 ± 1.3	17.0 ± 0.5	17.5 ± 0.8
	U_c	12.9 ± 0.8	11.7 ± 2.0	11.4 ± 2.2

*Retransformed from the angular transformation.

†Differed significantly from day 0 ($P < 0.05$, one-tailed t -test).

Isolation units housing inseminated queens contained relatively large quantities of brood and workers, whereas those housing uninseminated queens had very little or no brood and fewer workers. Values given are means ± SD; $n = 9$ for experimentals and 3 for controls.

more workers; this decrease being significant only at 15 days ($t_8 = 13.76$, $P < 0.003$; angular transformation). The weights of the uninseminated queens tended to increase during the course of the experiment, but only the difference between the original weight and that at day 15 was significant ($t_8 = 1.91$, $P < 0.05$). The weights of the uninseminated controls decreased slightly but insignificantly during the experiment, whereas the proportion of their eggs forming embryos did not change.

Thus isolated uninseminated queens, in the presence of substantial quantities of brood and workers, increase their weight (and therefore their oviposition rate), but the relative inability of their eggs to develop does not increase. Conversely, when inseminated queens are deprived of brood and large numbers of workers their oviposition rate decreases but the viability of their eggs remains at the same high level. Under these laboratory conditions, then, the quantity of brood or workers does not appear to be a major factor in determining the proportion of a queen's eggs forming embryos. In contrast, queen fecundity is affected by the quantity of brood (Tschinkel, 1988), suggesting that oviposition rate and egg viability are likely to be independent phenomena.

Relative embryonation of eggs laid by queens under field conditions

It is of interest to know whether and to what degree egg viability under field conditions differs between inseminated and uninseminated queens, as well as among individuals of the same insemination status. This was investigated in the following experiment.

Polygyny colonies ($n = 14$) were collected from 14 May to 8 September, 1987 at the Brackenridge Field Laboratory of the University of Texas at Austin. The ants and nesting material were taken immediately to the laboratory where the soil was spread out in a thin layer, under which conditions dealate queens are easily seen. Each queen so obtained was weighed and then placed immediately in a small cup for 24 h with 5–10 small nestmate workers. Upon removal from the cups, all queens were dissected to determine their insemination status and the eggs were incubated for 72 h at $30 \pm 1^\circ\text{C}$ with workers before staining as above.

Sequential sampling of eggs following isolation of queens from the colony milieu showed no significant change in viability of eggs laid during the course of the 24-h sampling period used above, indicating that the eggs of queens sampled by this latter method are more than likely representative of the eggs they are laying in the nest at the time of collection.

In all, the eggs of 119 queens (8.5 ± 6.5 queens/colony, Range = 1–19) were investigated, of which 84 queens (70.6%) were inseminated and 35 were uninseminated. A mean of 118.9 ± 55.5 (Range = 20–272) eggs per queen was examined.

Both categories of field-collected queens produced a high proportion of nonviable eggs, but this proportion was considerably higher in inseminated queens (Fig. 2; $t_{117} = 16.26$, $P < 0.0001$; angular transformation). Of the 84 inseminated queens examined, 80 (95%) had over 50% embryonated eggs, whereas only 7 (20%) of the 35 uninseminated queens were in

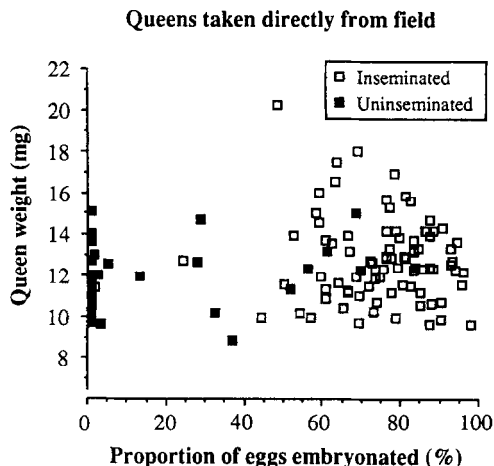


Fig. 2. The proportion of viable eggs laid by polygyny queens of *S. invicta* in relation to insemination status and weight. Queens were taken directly from field colonies. $n = 84$ for inseminated queens and 35 for uninseminated queens.

the same category. Moreover, 20 (57%) of the uninseminated queens had no embryonated eggs at all.

To determine whether possible intercolonial differences exist among queens in the proportion of their eggs forming embryos, an analysis of variance test was performed on all colonies for which 5 or more queens were sampled. There was a significant difference among colonies in the proportion of embryonated eggs laid by inseminated queens ($F_{9,85} = 5.47$, $P < 0.0001$; angular transformation). It is not clear to what this intercolonial difference might be due, but it does not appear to be related to the season in which the colonies were collected; of the 11 colonies compared, 3 were collected in late summer (4–8 September) and the mean proportion of embryonated eggs laid by inseminated queens of these colonies did not differ significantly (Newman–Keuls test, $P > 0.05$) from those of 6 of the 8 colonies collected in spring (14 May–6 June). There was no significant difference in the mean proportion of embryonated eggs laid by uninseminated queens of different colonies ($F_{3,26} = 0.43$, $P > 0.7$, angular transformation).

There was no significant correlation between queen weight and the proportion of embryonated eggs for either inseminated or uninseminated queens ($r_{83} = -0.111$ for inseminated and $r_{34} = 0.165$ for uninseminated queens, both $P > 0.5$; angular transformation of proportions; see Fig. 2), giving further support to the hypothesis that oviposition rate and egg viability are independent phenomena.

Comparison of the proportion of embryonated eggs obtained from queens in the field and those maintained in the laboratory in isolation units gave interesting results (see Figs 1 and 2). Among inseminated queens, those coming directly from the field had a significantly smaller proportion of eggs forming embryos than those held individually in the laboratory (mean = 0.765 ± 0.026 and 0.974 ± 0.031 , respectively; $t_{136} = 11.83$, $P < 0.0001$; angular transformation). Among the uninseminated queens, there was no significant difference in the mean proportion

of embryonated eggs between those coming directly from the field and those held individually in the laboratory ($t_{94} = 0.59$, $P > 0.55$; angular transformation).

DISCUSSION

Under field conditions, functional queens in polygyne colonies of *S. invicta* produce a remarkably variable yet generally high proportion of nonviable eggs. Much of this variability is related to insemination status, with uninseminated queens laying a far greater proportion of nonviable eggs than their inseminated counterparts. Nevertheless, there is significant variation among nestmate queens of the same insemination status in their ability to produce viable eggs. These results, together with those showing variability in fecundity (oviposition rate) among nestmate queens of this species (Vargo and Fletcher, 1989), suggest that individual queens belonging to the same reproductive category may differ markedly in realized reproductive success.

In studies of reproductive roles in social insect colonies, relative egg production is often equated with relative contribution to the adult members of the colony, including sexuals (e.g. Franks and Scovell, 1983; Rissing and Pollock, 1986; Keller, 1988). However, such a relationship may not be entirely valid. The finding that oviposition rate and the proportion of viable eggs laid are independent in field-collected queens demonstrates that fecundity alone is not an accurate measure of reproductive success in polygyne *S. invicta*. Rather, realized reproductive success of individual queens appears to involve an unsuspected degree of complexity. It is reasonable to suspect that similar complexity in reproductive activity may exist in other species of social insects.

Recent genetic evidence corroborates that significant variability in short- as well as long-term reproductive success may occur among nestmate queens of *S. invicta*, and that it is not related in simple fashion to varying levels of fecundity. Using enzyme genetic markers to identify the female progeny of individual inseminated queens in polygyne colonies in the laboratory, Ross (1988) found significant disparity in apportionment of maternity of workers and especially female sexuals. This variance among representation of female offspring did not appear to be associated strongly with fecundity. Although the relative viability of eggs produced by individual queens was not studied, it seems likely that the observed disparity in realized reproductive success of these inseminated queens was due, at least in part, to differences in this regard. Differences in post-embryonic developmental ability, including the ability to develop into sexuals, and/or selective treatment of larvae or pupae by workers could also contribute to differential reproduction, serving to enhance or reduce differences arising from varying levels of fecundity and egg viability.

Uninseminated queens comprise a substantial proportion of the functional queens in polygyne colonies of *S. invicta* but lay surprisingly few viable eggs. This, together with the fact that they to be 5–25% less found than their inseminated nestmates (Vargo and Fletcher, 1989), suggests that most, if not all,

uninseminated polygyne queens do not produce significant numbers of males, their only possible contribution to the pool of reproductives. On the other hand, they lay many nonviable eggs which are probably eaten by the larvae (see below) of their inseminated nestmate queens, to which they are largely unrelated (Ross and Fletcher, 1985b). These findings raise important questions concerning the factors promoting and maintaining such an abundance of functional uninseminated queens in these colonies.

The production of mostly nonviable eggs by uninseminated queens might be explained if unfertilized eggs inherently have a very low rate of viability. However, the fact that some uninseminated queens from the field lay a relatively high proportion of viable eggs (up to 80%) as well as the fact that some uninseminated queens in isolation units do produce males, indicate that the generally low viability of eggs laid by these queens cannot be attributed solely to inferior developmental ability of unfertilized eggs. Rather, these results suggest that uninseminated polygyne queens are generally less capable of providing their eggs with the necessary ingredients for normal development.

There are several hypotheses consistent with the production of impoverished eggs by uninseminated polygyne queens. It is possible that there is some physiological change following insemination which improves the quality of eggs produced, for instance, due to some nutritional or neuro-endocrine factor produced by the male accessory glands (see Chen, 1984). Another possibility is that viable egg production is somehow associated with mating success such that queens producing a higher proportion of viable eggs are more successful at acquiring mates. And finally, there exists the possibility that the ability to produce viable eggs is age-related and uninseminated dealate queens merely represent an early phase in the life history of functional polygyne *S. invicta* queens. These hypotheses are neither mutually exclusive nor exhaustive. Long-term studies of the viability of eggs produced by individual queens may help identify the factors contributing to varying levels of viable egg production.

The fate of the nonviable eggs in these colonies is not known, but it seems likely that they are eaten by the larvae. Petralia and Vinson (1978) found that fourth- (last) instar larvae consume eggs, presumably indiscriminately. Nonviable eggs remain intact for 6 weeks or longer if cared for by workers (Voss and Blum, 1988), whereas viable eggs hatch in 6–8 days (Porter, 1988). Nonviable eggs therefore stand a good chance of being eaten. Given the presumed abundance of such eggs in these colonies, they apparently serve as an important component in the colony nutrient flow. Nonviable eggs have been found to contribute significantly to the nutrient budget of colonies in *Myrmica rubra* (Brian, 1953; Brian and Rigby, 1978) and *Dolichoderus quadripunctatus* (Torossian, 1979).

Little is known about the physiological mechanisms regulating egg viability in *S. invicta* queens, but there is evidence to suggest that juvenile hormone plays a role. Voss (1981) and Voss and Blum (unpublished) have hypothesized that starvation-induced low titres of juvenile hormone are responsible for the

production of nonviable eggs by virgin queens of monogyne *S. invicta*. This is evidenced by the finding that such queens produce only nonembryonated eggs unless treated with juvenile hormone or maintained individually in large queenless colonies with access to high protein food and larvae (Voss, 1981; Voss *et al.*, 1988; Voss and Blum, unpublished). Juvenile hormone has also been found to be involved in regulating oögenesis in *S. invicta* (Barker, 1978) as well as many other insects (Engelmann, 1983). Thus the finding in the present study that oviposition rate and the proportion of viable eggs laid by queens in the field are apparently unrelated is somewhat puzzling. One possible explanation is provided by the results of Voss *et al.* (1988), who found that treatment of virgin queens with 20-hydroxyecdysone before administration of juvenile hormone blocks the stimulatory effect of the latter on egg viability. It is possible that while juvenile hormone plays a role in determining both fecundity and egg viability, its effect on the latter may be modified by independently controlled mechanisms.

A particularly interesting result obtained in this study is that inseminated polygyne queens held in isolation units in the laboratory laid nearly 100% embryonated eggs, the same high proportion laid by inseminated queens in established monogyne colonies (Fletcher and Blum, 1983a; Voss and Blum, 1988), whereas field-collected inseminated polygyne queens laid a significantly lower proportion. Since the quantity of brood and workers did not affect the proportion of viable eggs produced, this difference does not appear to be the result of variable levels of nutritional factors provided by larvae or a higher worker/queen ratio. The higher proportion of viable eggs laid by queens held individually in the laboratory could be explained in part if workers and/or larvae in the rearing units preferentially consumed nonviable eggs; the eggs of such queens were sampled from the egg piles which could be subject to inspection by workers and larvae, whereas the eggs sampled from field queens came directly from oviposition tests. However, the results of the experiment in which inseminated and uninseminated queens were exchanged render this possibility unlikely. Based on samples from the egg piles, it was found that the proportion of viable eggs laid by uninseminated queens decreased after transfer to units containing substantially higher numbers of larvae and workers, in contrast to the expected increase in the case of preferential oophagy of nonviable eggs. Also, the fact that the proportion of viable eggs laid by inseminated queens did not change when placed in units containing fewer workers and little or no larvae is consistent with a lack of a significant change in the proportion of viable eggs due to oophagy. Rather, an intriguing possibility is that the higher proportion of viable eggs produced by inseminated queens under monogyne conditions is due to mutual inhibition of egg viability among inseminated queens in polygyne colonies.

There is growing evidence that in some ant species queens influence the viability of eggs produced by workers, providing an important precedent for mutual inhibition among queens in polygyne societies. In *Plagiolepis pygmaea*, only small, nonviable

eggs are laid in the presence of the queen, but both nonviable and viable eggs are laid when she is absent (Passera, 1965, 1966). Workers of *Leptothorax* (= *Temnothorax*) *recedens* lay only viable eggs in the spring when the queen's inhibitory capability is weak, but as the queen's inhibitory capability strengthens during the new season they lay an increasing proportion of nonviable eggs (Dejean and Passera, 1974). Brian and Rigby (1978) showed that functional queens of *Myrmica rubra* actually stimulate workers to lay nonviable eggs rather than viable eggs. The possibility of mutual inhibition of egg viability among inseminated queens of *S. invicta* is especially appealing considering the extensive control over reproduction which queens of this species exert pheromonally, including inhibition of oögenesis and dealation in alate queens (Fletcher and Blum, 1981), regulation of queen number (Fletcher and Blum, 1983b), and inhibition of the production of sexuals (Vargo and Fletcher, 1986).

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