

Reproduction by virgin queen fire ants in queenless colonies: Comparative study of three taxa (*Solenopsis richteri*, hybrid *S. invicta/richteri*, *S. geminata*) (Hymenoptera: Formicidae)

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Summary

In the fire ant, *Solenopsis invicta*, some winged virgin queens are known to shed their wings (dealate) upon removal of the mated mother queen. These virgin queens then develop their ovaries and begin to lay eggs, thereby foregoing the option of leaving on mating flights and attempting to found their own colonies. Such a response of virgin queens to queenlessness has not been reported for other ants. In order to determine if virgin queens of some other fire ants (subgenus *Solenopsis*) would respond in the same way, experiments were conducted on *S. richteri*, hybrid *S. invicta/richteri* and *S. geminata*, a member of a species complex different from that of the other taxa. Just as in *S. invicta*, virgin queens of *S. richteri* and the hybrid dealated and began to lay eggs within days of the removal of the queen. In addition, workers executed many of the reproductively active virgin queens, a phenomenon also found in *S. invicta*. In contrast, virgin queens of *S. geminata* did not dealate or quickly begin to lay eggs upon separation from the queen. Reasons for the variability in the response of virgin queens of the different species may be: 1) higher probability of reproductive success for unmated dealated queens compared to normal claustral founding in *S. invicta* and *S. richteri* linked to relatively frequent loss of the mother queen; or 2) phylogenetic constraint.

Introduction

Although mated queens are the primary egg-layers in colonies of eusocial insects, other colony members may reproduce opportunistically (Fletcher and Ross, 1985). The nature and extent of reproduction by other colony members strongly influences many characteristic colony traits, including social cohesion, colony efficiency, and sex allocation ratios (Bourke, 1988).

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In ants, egg-laying by workers is widespread, generally occurring under queenless conditions (Fletcher and Ross, 1985; Bourke, 1988; Choe, 1988). Workers of the genus *Solenopsis* are sterile (Fletcher and Ross, 1985; Hölldobler and Wilson, 1990), but winged virgin queens of the fire ant *S. invicta* reproduce opportunistically in the nest in the absence of a functional (egg-laying) queen. The winged virgin queens of this species, like those of most ants, undertake mating flights under suitable conditions. While they remain in the nest, the winged virgin queens are normally inhibited from shedding their wings (dealating) and developing their ovaries by a pheromone produced by the mother queen (Fletcher and Blum, 1981). However, if the mother queen dies or is removed, thereby extinguishing the inhibitory pheromone, many of the virgin queens present will dealate, develop their ovaries and begin to lay eggs. Some of these eggs are viable and will produce males (Tschinkel and Howard, 1978; Voss, 1981; E. Vargo, unpublished data). Not all dealate virgin queens are permitted to produce significant numbers of sons; within a few days of dealation, workers will begin to execute these reproductively active virgin queens and will generally proceed until only one or two remain (Fletcher and Blum, 1981; Fletcher and Blum, 1983).

Although reproduction by virgin queens under queenless conditions has been well-studied in *S. invicta*, it is not known if such reproductive options exist for virgin queens of other ants, because few other species have been carefully studied in this regard. As a first step in extending these studies to other species, we examined the effect of queenlessness on virgin queens in three additional fire ant taxa, all within the *S. geminata* species group (*sensu* Trager, 1991). The taxa studied represent two different species complexes: *S. richteri* and hybrid *S. invicta/richteri*, like *S. invicta*, belong to the *S. saevissima* complex; *S. geminata* belongs to the *S. geminata* complex.

Materials and methods

Sites of origin of *S. richteri* and hybrid *S. invicta/richteri* were based on previous studies of the ranges of each of these (Vander Meer et al., 1985; Ross et al., 1987; Ross and Robertson, 1990). Eight colonies of *S. richteri* were collected in Tishomingo County just off the Natchez Trace Parkway near the Jamie L. Whitten Bridge, some 30 miles NE of Tupelo, Mississippi. Five colonies of the hybrid were collected just off Alt. Highway 45 in Crawford, Lowndes County, Mississippi. Colonies of *S. richteri* and the hybrid were monogyne (possessing a single functional queen) and contained numerous winged virgin queens. These field-reared virgin queens were those tested in the experiments.

Colonies of *S. geminata* originated from Austin, Texas and Gainesville, Florida. The five colonies used from Austin were from a single polygyne population and were collected on 3 April 1991. This population may be a hybrid between *S. geminata* and *S. xyloni* (Hung and Vinson 1977; Trager, 1991, personal communication), but is here called *S. geminata* for convenience. These colonies did not have winged virgin queens present at the time of collection and contained a mean of 15 (SD = 2.6, range = 11–18) dealated, egg-laying queens. As part of a separate experiment, on 2 May 1991 the

workers and brood of these colonies were divided into equal halves based on weight. One queen was placed into one half (monogyne half) and the other received the remaining queens (polygyne half). For the present experiments, only the monogyne halves were used and all virgin queens tested were reared in these colony fragments in the laboratory.

S. geminata from Gainesville consisted of two monogyne colonies of the "red form" (*sensu* Wilson, 1971; Wojcik et al., 1976) collected on 7 July 1991. Both of these were queenright and held in the laboratory until set-up on 28 August 1991. Both colonies contained numerous winged virgin queens at the time of collection; these field-reared alates were the individuals tested.

Voucher specimens of all species have been deposited in the Entomology Collection, Brackenridge Field Laboratory, University of Texas at Austin.

Colonies of all species were removed from the soil by flooding (Jouvenaz et al., 1977) and were maintained in the laboratory ($29 \pm 2^\circ\text{C}$) according to standard procedures (Vargo and Fletcher, 1989). Dealation and ovary development were studied using winged virgin queens placed in small colony fragments which either contained the mother queen or were queenless. Colony fragments were derived from dividing colonies into three portions of equal weight (Fletcher and Blum, 1981). There was one queenright fragment and two queenless fragments used for each colony. The number of colonies (N) used and the mean (\pm SD) weights of the fragments were the following: $N = 8$, weight = 4.8 ± 1.4 g for *S. richteri*; $N = 5$, weight = 14.8 ± 6.3 g for hybrid *S. invicta/richteri*; $N = 5$, weight = 4.8 ± 2.0 g for Austin *S. geminata*; and $N = 2$, weight = 5.0 ± 0.0 g for Gainesville *S. geminata*. One g of colony weight contained approximately 600 workers, 400 worker pupae, and 1000 larvae.

Each colony fragment received five virgin queens, all of which were at least 1 month old at the start of the experiment. The fragments were monitored once a day and the number of dealates present was recorded. In addition, any virgin queen corpses present were recorded and removed. Virgin queens observed being executed, i.e., held by the appendages and bitten by workers as described by Wilson (1971), were removed and dissected to assess ovary development (see below). After 1 week, each surviving virgin queen was isolated on damp plaster and subjected to a 5-hour oviposition test (Fletcher et al., 1980), and the number of eggs laid was recorded. In the case of *S. richteri* and the *S. invicta/richteri* hybrid, all virgin queens were then dissected in 70% ethanol under a dissecting microscope in order to assess ovary development. This was accomplished by counting the total number of chorionated eggs present in the ovarioles and common oviduct. The sizes of the chorionated eggs was $\geq 0.4 \times 0.28$ mm for *S. richteri* and the hybrid (also for *S. invicta*, see below) and $\geq 0.28 \times 0.17$ mm for Austin *S. geminata*, which has somewhat smaller eggs than the others (E. Vargo, unpublished data). At the beginning of each experiment, five virgin queens from each colony were weighed and dissected to assess ovary development.

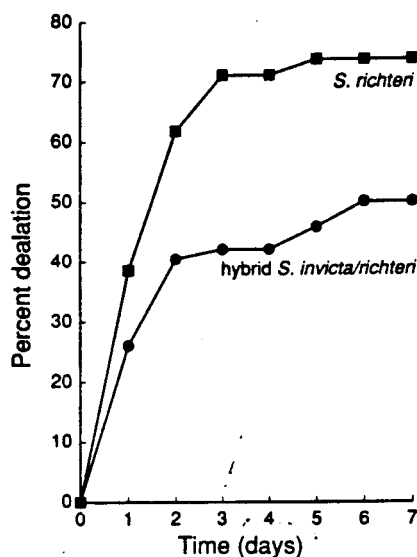


Figure 1. Frequency of dealation among virgin queens of *S. richteri* and hybrid *S. invicta/richteri* in queenless colony fragments. Shown are cumulative totals for 16 fragments of *S. richteri* and 10 fragments of the hybrid, each fragment containing five females

Results

Dealation and ovary development in S. richteri and hybrid S. invicta/richteri

In *S. richteri*, dealation occurred in all of the queenless fragments, beginning within 24 hours and reaching about 75% of the virgin queens by the end of 1 week (Fig. 1); no dealation occurred in any of the queenright fragments. Workers began executing dealates within 24 h and a total of 12 individuals in 8 of the 16 colony fragments (mean = 0.75 ± 0.9 per colony fragment, range = 0–3) were observed being executed. An additional 17 corpses were found, bringing the total of dead individuals to 29 (36.3%) for a mean of 1.8 ± 1.3 (range = 0–4) per colony fragment. Only a single virgin queen out of 40 died in the queenright fragments, strongly suggesting that all deaths in the queenless fragments were the result of execution by workers.

Similar results were obtained in the hybrid. Again, dealation occurred in all queenless fragments (Fig. 1), whereas no virgin queens dealated in any of the queenright fragments. Six dealates (0.6 ± 1.0 per fragment, range = 0–3) were observed attacked and being killed by workers. An additional four corpses were found, bringing to 10 (20%) the total number dead or being killed (mean = 1.0 ± 1.2 , range = 0–3). None of the 25 alates in the queenright fragments died, again suggesting that all individuals dying in the queenless fragments were killed by the workers.

There were significant differences in ovary development among the groups of virgin queens in both taxa (Table 1; $F_{4,139} = 166.4$, $P < 0.0001$ and $F_{4,89} = 37.3$,

Table 1. Ovary development (mean \pm SD, no. chorionated oocytes present) in relation to queenlessness, dealation and execution in virgin queens of *S. richteri* and the *S. invicta/richteri* hybrid. Number of individuals is given in parentheses. Within each column, groups having different letters differed significantly ($P < 0.05$) according to the Newman-Keuls test

Group	No. chorionated oocytes	
	<i>S. richteri</i>	hybrid <i>S. invicta/richteri</i>
<i>Queenless conditions</i>		
Dealates	28.4 \pm 8.7 (31) a	18.1 \pm 10.7 (16) a
Dealates being executed	14.8 \pm 11.8 (12) b	9.2 \pm 3.4 (6) b
Alates	1.5 \pm 1.7 (21) c	3.8 \pm 3.9 (22) c
<i>Queenright conditions</i>		
Alates at end of experiment	0.8 \pm 1.3 (40) c	1.4 \pm 1.4 (25) c
Alates at start of experiment	0.3 \pm 0.5 (40) c	0.8 \pm 1.1 (25) c

Table 2. Oviposition by virgin queens of *S. richteri* and hybrid *S. invicta/richteri* in relation to queenlessness and dealation. Individual females were subjected to a 5-hour oviposition test. Number of individuals is given in parentheses

Group	No. eggs laid (Mean \pm SD)	
	<i>S. richteri</i>	<i>S. invicta/richteri</i> hybrid
<i>Queenless conditions</i>		
Dealates	11.5 \pm 8.3 (31)	6.8 \pm 8.4 (16)
Alates	0 (21)	0.05 \pm 0.21 (22)
<i>Queenright conditions</i>		
Alates	0.03 \pm 0.16 (39)	0.04 \pm 0.20 (25)

$P < 0.0001$ for *S. richteri* and the hybrid, respectively). The pattern of ovary development was very similar in the two cases. The unattacked dealates had the most developed ovaries, while the dealates that were in the process of being executed by the workers had more developed ovaries than any of the alates. Although alates in the queenless units had more developed ovaries than those held with the queen, this difference was not significant. In addition, the alates held with the queen for the 1-week period of the experiment had more developed ovaries than did a representative sample of females examined at the beginning of the experiment, but this increase was not significant.

Ovipositional activity paralleled the degree of ovary development (Table 2). All of the *S. richteri* dealates and 75% of the hybrid dealates laid eggs, whereas only a single individual in each of three of the four alate categories laid eggs; these latter individuals laid only one egg each. Among the dealates, the number of chorionated oocytes was strongly related to the number of eggs laid in the hybrid ($R^2 = 0.64$, $F_{1,14} = 24.8$, $P < 0.0002$) but not in *S. richteri* ($R^2 = 0.09$, $F_{1,29} = 2.9$, $P > 0.09$).

At the end of the experiment, two of the hybrid queenright fragments lacked worker brood, and so it was suspected that the functional queens present were

Table 3. Change in ovary development of female alates of Austin *S. geminata* during the course of the 2-week experiment. Each of the 5 original colonies was divided into three fragments; one received the queen and the other two were queenless. Each fragment started with 5 virgin queens but some of these died during the course of the experiment. A sample of 5 virgin queens from each colony was dissected at the start of the experiment. Different letters indicate significant differences ($P < 0.05$) among groups according to the Newman-Keuls test

Group	N	Mean (\pm SD) no. chorionated oocytes
Queenless	41	6.1 \pm 4.8 a
Queenright	16	2.9 \pm 3.1 b
Start	25	0 c

uninseminated. These queens were dissected along with five of the *S. richteri* queens; the remaining queens were kept for other experiments and all had normal quantities of worker brood, indicating they were inseminated. The two dissected hybrid queens were found to be uninseminated, whereas all five *S. richteri* queens were inseminated. Apparently, the mother queens of the two hybrid colonies escaped collection. Based on the above results, it appears that reproductive function was taken over by a virgin who dealated after collection and other females which may have dealated were executed by the workers, leaving only a single functional virgin replacement queen. Interestingly, these virgin replacement queens were apparently as capable as mated queens of preventing dealation and oogenesis in other virgins, a situation much like that found in *S. invicta* (Willer and Fletcher, 1986).

Dealation and ovary development in S. geminata

Austin, Texas colonies. There was no dealation among the virgin queens of *S. geminata* from Austin. Females were subjected to an oviposition test at the end of one week and again at the end of 2 weeks. Following the second oviposition test all females were dissected to assess ovary development. There was a significant difference in ovary development among the virgin queens at the start of the experiment and those under both queenright and queenless conditions (Table 3). Virgin queens under queenless conditions had more developed ovaries than those in held in the presence of the queen. Like the virgin queens of *S. richteri* and the hybrid, those kept with the queen for the duration of the experiment had more developed ovaries than did those at the start, but unlike the former two taxa, this difference was significant in *S. geminata*. Although a higher frequency of females in the queenless fragments laid eggs than did those in the presence of a queen during both oviposition tests (Tab. 4), this difference was not significant (both $\chi^2_1 \leq 2.72$, $P > 0.05$), nor was there a significant difference in the mean number of eggs laid (both $t \leq 1.72$, $P > 0.05$).

Mortality was rather high in both the queenright and queenless groups. A total of 17 (23%) of the 75 females died, nine (36%) in the queenright fragments and eight

Table 4. Oviposition by virgin queens of Austin *S. geminata* in relation to the presence or absence of a queen

Week	Treatment	<i>N</i>	No. individuals laying eggs	No. eggs laid (mean \pm SD)
1	Queenright	25	2 (8%)	0.2 \pm 0.7
	Queenless	47	13 (28%)	0.7 \pm 1.5
2	Queenright	19	3 (16%)	0.3 \pm 0.6
	Queenless	41	12 (29%)	0.4 \pm 0.6

Table 5. Ovary development and ovipositional activity of virgin queens of Gainesville *S. geminata*. This experiment lasted 2 weeks. Q+ : queenright fragments; Q- : queenless fragments

Colony	Mean (\pm SD) weight (mg) of virgin queens at start (<i>N</i> = 5 of each)	Mean (\pm SD) no. chorionated oocytes (<i>N</i>)			Mean (\pm SD) no. eggs laid in 5-h oviposition test (<i>N</i>)	
		Start	End		Q+	Q-
			Q+	Q-		
1	13.8 \pm 1.4	0 (5)	0 (4)	0 (10)	0 (4)	0 (10)
2	17.1 \pm 0.7	0.6 \pm 1.3 (5)	0 (5)	3.2 \pm 4.8 (9)	0 (5)	4.2 \pm 9.4 (9)

(16%) in the queenless fragments. The frequency of mortality in the two groups did not differ significantly ($X^2 \leq 2.74$, $P > 0.05$). No instances of execution of virgin queens by workers was observed.

Gainesville, Florida colonies. These fragments were observed over a 2-week period. Three virgin queens, one in each of three queenless fragments lost three of four wings within 2 days from the start of the experiment, although none of these lost the remaining wing during the course of the experiment. One virgin queen in one of the queenright units was being attacked on day 6, but no other signs of execution were observed. However, one other virgin queen (from a queenless fragment) was found dead on day 14.

All virgin queens were dissected and their thoraxes examined in order to determine the condition of their alary muscles. All except a single queen had intact muscles. The one exception had partially histolyzed muscles and was one of the three virgin queens that had lost three wings.

The results of oviposition and ovary development assessment are summarized in Table 5. During the oviposition test, only three virgin queens laid eggs (range = 5–30), all from queenless fragments from colony 2. Five of the nine females from the queenless fragments of the same colony, including the three egg-layers, showed signs of ovary development (range of chorionated oocytes = 1–12), whereas none of the other experimental females showed signs of ovary development. Although only females from queenless fragments laid eggs and developed their ovaries, the

frequency with which they did so was not significantly greater than those from queenright fragments, either when the data from the two colonies were pooled (both $X_1^2 \leq 1.6$, $P > 0.25$, corrected for continuity) or when only colony 2 was considered (both $X_1^2 \leq 2.25$, $P > 0.25$, corrected for continuity). Of the 10 virgin queens dissected at the beginning of the experiment, one had some signs of ovary development, possessing three chorionated oocytes.

Discussion

Evidently, the response of virgin queens to queenlessness varies among fire ant species (subgenus *Solenopsis*) belonging to a single species group. Virgin queens of *S. richteri* respond to queenlessness very much like those of *S. invicta*, whereas virgin queens of *S. geminata* do not. The following comparison between *S. invicta* and *S. richteri* comes from the results of the present study and those of Fletcher and Blum (1981), which employed essentially the same experimental design. In both species, dealation began within 24 h of queenlessness. After 3 days the proportion of *S. richteri* females dealating was similar to the 84% reported for *S. invicta*. A higher proportion (36%) of *S. richteri* dealates was executed after one week than in *S. invicta* (16%) in the same period of time. In both species, ovary development is strongly tied to dealation, since dealates had significantly more developed ovaries than alates under both queenright and queenless conditions. All *S. richteri* dealates laid eggs, whereas only a single alate oviposited, a situation similar to that reported in *S. invicta*. Given that the phenomenon of reproduction by virgin queens in *S. richteri* so closely matches *S. invicta*, it is not surprising to find that their hybrid responds in the same manner.

The situation appears to be quite different in *S. geminata*. Admittedly, the small sample sizes used in this study together with the variable nature of the material used (viz., monogyne and polygyne colonies of origin) prevent firm conclusions from being drawn. Nevertheless, some clear differences between this species and the other taxa are evident. Firstly, virgin queens do not seem to dealate readily when removed from the mother queen, in striking contrast to monogyne *S. invicta* and *S. richteri*. Secondly, although virgin queens are more likely to develop their ovaries and exhibit greater degrees of ovary development when removed from an egg-laying queen (although not significantly more than in the presence of the queen), they do so more slowly than in *S. invicta* and *S. richteri*. Thirdly, dealation in *S. geminata*, when it occurs, does not appear to be complete and is not tightly connected to ovary development, in contrast to the situation in *S. invicta* and *S. richteri*. Fourthly, execution of ovary-developed virgin queens occurs less frequently, if at all, in *S. geminata*.

Why do the different species vary in their response to queenlessness? The rapidity with which virgin queens dealate and begin ovipositing once the queen is gone in *S. invicta* and *S. richteri* suggests that queenlessness may occur relatively frequently in these species. One possible reason for frequent queenlessness may be queen loss due to flooding. According to several authors (Allen et al., 1974; Buren et al., 1974; Trager, 1991), *S. invicta* and *S. richteri*, as well as most other members of the

S. saevissima species complex, are native to low lying grasslands that are often seasonally flooded in tropical to warm temperate South America. Periodic flooding could result in the death of the queen or splitting of the colony into one or more queenless fragments. It could pay some of the female alates in a queenless colony, or portion of a colony, to capitalize on the worker force and other colony resources present by laying eggs to produce males. In order to take full advantage of the colony's resources, the virgin queens would respond quickly by utilizing for rapid egg production the body reserves that are normally used during colony founding, thus foregoing the ability to found a colony independently.

The reproductive option would payoff as long as the expected reproductive success of such virgin replacement queens is greater than those departing on mating flights and trying to establish their own independent colonies. The fact that very few of the virgin queens that become reproductively active in a nest will survive to produce large numbers of males due to execution by workers within days of dealation must also be taken into account when considering the payoffs. Whatever the source of queenlessness, virgin queens of *S. invicta* and *S. richteri* apparently are very sensitive to the presence of the queen and are primed to begin ovipositing soon after her loss; however, workers will execute most of these before they are able to lay significant numbers of eggs.

Thus workers are involved in reproduction by virgin queens in *S. invicta* and *S. richteri*. It should be noted that virgin queen reproduction in the case of queenlessness should also be favored by the workers. Because they are sterile, the loss of a queen means evolutionary death to the workers unless they adopt a new queen. By permitting a sister virgin queen to reproduce rather than adoption of a foreign mated queen workers ensure that the resulting sexual progeny will carry their genes.

In contrast to the native habitat of *S. invicta* and *S. richteri*, *S. geminata* is native to coastal areas from the southern U.S. to Central America and northern South America (Trager, 1991) and does not appear closely associated with flood plains. Thus queenlessness due to flooding may not have been frequent enough in the history of this ant to select for rapid dealation and laying of unfertilized eggs. As a result, there may have been no strong selection on virgin queens to begin reproducing immediately after queen loss; thus there was no significantly greater tendency of *S. geminata* virgin queens to lay eggs under queenless conditions than in the presence of the queen. Interestingly, egg-laying virgin queens did not shed their wings or histolyze their wing muscles, and so they apparently retain, for at least some period, the option of leaving the nest on a mating flight and attempting to found a colony independently. It is possible that dealation and/or histolysis of the wing muscles does eventually occur, but the present experiments may not have been carried out long enough to detect them. Another difference between *S. geminata* and the other fire ants was that workers did not execute the reproductively active virgin queens.

From a phylogenetic perspective, the most parsimonious scenario for the evolution of rapid dealation and oviposition in response to queenlessness in fire ants is that they arose once early in the *S. saevissima* species complex, the group to which both *S. invicta* and *S. richteri* belong. Based on an analysis of allozyme markers for 7 of the 12 species comprising the *S. saevissima* complex, an apparently monophyletic group (Trager, 1991), Ross and Trager (1990) found

S. invicta and *S. richteri* to be relatively distantly related, occurring in different sister lineages. Thus these traits, as well as the enforcement of monogyny through the execution of reproductively active queens by workers, most probably arose in some common ancestor, possibly in the ancestor of the complex. This phylogenetic analysis raises the possibility that the presence of these traits in different species within the *S. saevissima* species complex may be due to phylogenetic constraint rather than adaptation to current ecological conditions. Clearly, studies of virgin queen response to queenlessness in the other *S. saevissima* complex species as well as a more complete phylogenetic analysis of the group are needed to pin down the evolutionary origin of these traits and thereby shed light on the relative roles of phylogenetic constraint and ecological factors in their maintenance.

To our knowledge, dealation and oviposition by virgin queens in response to queenlessness have not been reported for other ants, quite possibly because this reproductive option has received little study. However, related phenomena have been reported in two ant species. In *Pheidole pallidula*, virgin queens lay eggs in the presence of the queen before they depart on a mating flight, but these eggs are nonviable (Passera, 1978). Virgin queens of this species normally fly within a few weeks of emergence, but if kept in the laboratory for a period of 6 months they will continue to lay nonviable eggs and many will shed their wings during this time (Passera, 1978). It is not known if these virgin queens will switch to laying viable eggs if the queen is removed, although virgin queens in isolation (without workers and brood) continue to produce only nonviable eggs (Passera, 1978). In the honey ant, *Myrmecocystus mexicanus*, virgin queens taken as they emerged from a nest for a mating flight laid eggs and physically broke off their wings when held without workers (Conway, 1983). It is not known whether *M. mexicanus* virgin queens would lay eggs in a queenless nest. Further study is needed to determine how widespread opportunistic reproduction by virgin queens is in queenless ant colonies.

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