Research article

A newly-discovered mode of colony founding among fire ants

W. R. Tschinkel

Department of Biological Science, Florida State University, Tallahassee, FL 32306-3050, USA
e-mail: tschinkel@bio.fsu.edu

Summary

Queen ants start new colonies either unassisted by workers (independent founding), assisted by workers from their natal nest (dependent founding), or assisted by the workers of other species (dependent, socially parasitic). The monogyne form of the fire ant, *Solenopsis invicta*, founds independently in summer, but in the fall it also produces a few sexuals some of which overwinter, then fly and mate in early spring. These overwintered queens lack the nutritional reserves and behaviors for independent colony founding. Rather, they seek out unrelated, mature, orphaned colonies, enter them and exploit the worker force to found their own colony through intraspecific social parasitism. Success in entering orphaned colonies is higher when these lack overwintered female alates of their own. When such alates are present, orphaning causes some to dealate and become uninseminated replacement queens, usually preventing entry of unrelated, inseminated replacement queens. Such colonies produce large, all-male broods. Successful entry of a parasitic queen robs the host colony of this last chance at reproductive success. Only overwintered sexuals take part in this mode of founding.

Introduction

When Wheeler wrote his classic book *Ants* in 1910, he noted that ants start new colonies either unassisted by workers (independent founding), assisted by workers from their natal nest (dependent founding) or assisted by workers of other species (dependent, temporary social parasitism) (Hölldobler and Wilson, 1990). Queens which found independently usually do so by sealing themselves in a chamber and, without feeding, draw on large nutritional reserves to rear the first worker brood (claustral founding) (Hölldobler and Wilson, 1990). Queens that found dependently lack large amounts of body reserves (Keller and Passera, 1989). After mating, such queens are adopted back into their natal nest (or rarely, into an unrelated nest), which subsequently fissions to form a new daughter nest. In temporary social parasites, the newly-mated queen invades the nest of another species and exploits these workers to found her own colony.

In the 80 years that have elapsed between Wheeler's *Ants* (1910) and the modern compendium by Hölldobler and Wilson, *The Ants*, (1990) many details of these modes of founding have been illuminated (Hölldobler and Wilson, 1990; Tschinkel, 1993 and references therein), but no additional modes of founding have been clearly recognized. Some authors have suggested that queen replacement can occur in mature colonies, even in monogyne species (Buschinger 1970; Elmes 1973, 1980; Seppa 1992), but these suggestions have usually been in the context of colony longevity rather than colony founding. In following up a study on queen replacement in the fire ant, *Solenopsis invicta* (Tschinkel and Howard 1978), it became apparent that fire ants practice alternate strategies of colony founding, one the familiar independent one, and the other a previously undescribed form of dependent founding.

The fire ant, *Solenopsis invicta*, is typical of independently-founding species. In early spring, it rears large numbers of sexual alates, and these participate in mating flights during late spring and early summer (Markin et al., 1972; Tschinkel, 1993a). Newly mated queens dealate, dig chambers and rear the first workers either by themselves or in cooperation with other newly mated queens (Markin et al., 1972; Tschinkel and Howard, 1983; Tschinkel, 1993b). After a mid-summer hiatus, some colonies produce small numbers of sexual alates in the fall (Tschinkel, 1993a). Many of these overwinter in the nest, and fly on the very first warm days in early spring before most spring alates eclose as adults (Fletcher and Blum, 1983).

When queens were removed from *S. invicta* colonies, about one-third of these orphaned colonies had an inseminated replacement within 2 months (Tschinkel and Howard, 1978). In the remainder of the colonies, female alates shed their wings to become uninseminated replacement queens which produced all-male broods. In attempting to repeat this earlier study, I found that replacement with mated queens occurred only if the orphaning took place between January and late March. Because the mating flights of overwintered sexuals took place during this period, it seemed possible that queen replacement in orphaned colonies was connected with overwintered sexuals. This connection was explored through a series of observations and experiments on orphaned colonies, and led to the discovery of a previously undescribed from of colony founding.

Methods

Orphaning

All colonies in the Tallahassee area are monogyne. Colonies were orphaned on cool, sunny days by scooping soil and ants from the warm parts of the mound into a large tray and searching visually for the queen. The queen was recognized by her distended abdomen (physogastry) and high degree of attraction to workers, and was always surrounded by a swarm of excited workers.

Insemination of dealates

The spermatheca of dealated females was exposed by dissection. When inseminated, the spermatheca was opaque and milky-white, when uninseminated, it was clear and transparent (Tschinkel, 1987a).

Brood checks

On sunny spring days, much of the brood, especially pupae, could be found in the mound. A trowelful of mound was scattered in a large plastic tray and inspected for several minutes to assess the type and approximate relative amount of brood present. Scored categories included small larvae (which could be worker or sexual), sexual larvae, worker pupae, male alate pupae, and female alate pupae. Worker and female alate pupae can be produced only by inseminated queens, and are evidence of the presence of such a queen in the colony.

Colony identity

It could be argued that between checks, an orphaned colony could have abandoned its nest and another, perhaps queenright colony taken its place. This is extremely unlikely because (1) colony movement averages only once or twice a year, predominately during the summer rainy season; (2) it would require the coordinated movement of two neighboring colonies within a short space of time, a very unlikely event; (3) when colonies move, they typically move within their own territory. The abandoned nest is therefore not available to other colonies without changes in the typically stable territory boundary (Adams and Tschinkel, unpublished data).

Results and discussion

In both 1994 and 1995, groups of colonies were orphaned on 3 dates during the spring – before, during and after the flight of overwintered sexuals. Six to 9 weeks later, the brood contained in these colonies was checked. By this time, any worker brood of the original queen had eclosed. Because workers in *S. invicta* are completely sterile, the presence of worker pupae at this time indicated that the colony had an inseminated replacement queen. The presence of only male pupae indicated an uninseminated queen, and the absence of brood indicated queenlessness. Table 1 shows several patterns – when colonies were orphaned before the late winter mating flights, all queens were replaced, but only 17% of these were inseminated. Orphaning during March, when the mating flights were taking place, again resulted in almost 100% replacement, but almost 40% of these were inseminated. When colonies were orphaned after most of the overwintered sexuals had flown, no replacement queens were inseminated, and many colonies remained queenless. These results suggested that the overwintered gynes might be the source of the inseminated (and probably the uninseminated) replacement queens.

Table 1. Frequency and type of replacement queen for colonies orphaned before, during and after the mating flights of overwintered alates. Results for 1994 and 1995 were combined. Percent values = no./row total × 100

Date of orphaning in relation to mating flights	No. (%) of Colonies that had					
	inseminated replacement queen		uninseminated replacement queen		no replacement queen	
	No.	(%)	No.	(%)	No.	(%)
Before (Jan-mid-Feb)	4	(17%)	20	(83%)	0	(0%)
During (Feb. 17-late March)	15	(39%)	23	(59%)	1	(3%)
After (April to May)	0	(0%)	29	(83%)	6	(17%)

In 1995, mating flights of overwintered alates occurred between Feb. 17 and the end of March. These late-winter flights were on a much smaller scale than typical spring flights, and differed in triggering factors and timing as well (Table 2). Inspection of the mounds of mature colonies during March mating flights revealed dealated overwintered queens on mature mounds, often in the act of digging an entry into the colony. An average of about 1 in 20 mounds (n = 795) had such dealates. This is probably an undercount because some dealates could have been obscured by vegetation or could have slipped into openings or crevices, and each mound was inspected only once during an afternoon. Because there were more than 15 flights between Feb. 17 and the end of March, the probability that a newly-mated queen attempted entry into any given mound was quite high. There was no difference in the frequency of queens captured on orphaned or queenright colonies (ANOVA, $F_{1,29} = 0.27$, N.S.), suggesting that queens landed on randomly-chosen colonies, and did not detect queenlessness in advance. Most of these queens were under attack by workers at the time of capture. Dissection of dealated queens captured on mounds revealed that 85% of them were inseminated (n = 24).

Adoption of newly-mated, overwintered queens into orphaned colonies was tested directly in mid-March. Six colonies were orphaned. Newly-mated queens were marked by tying a fine wire around the petiole. Two marked queens were released each day for 5 days on each of the six orphaned colonies, beginning one day after orphaning. A different color wire was used every two days. Seven weeks later, these colonies were excavated. Two lacked brood and were probably queenless, two had all-male brood indicating uninseminated queens. The remaining two colonies produced worker pupae, and from each of them I recaptured a wire-marked queen in fully physogastric condition and highly attractive to workers. The wire color in both cases indicated that the queens were released on the first or second day after orphaning. This is direct evidence that overwintered female alates were the source of inseminated replacement queens.

Queens of ant species that found colonies independently have fat reserves in excess of 40% of their dry weight (Keller and Passera, 1989). The spring-reared, independently founding alates (n = 50) of *S. invicta* averaged 7.58 to 8.53 mg

Table 2. Comparison of colony founding by spring-reared and overwintered queens

	Spring-reared queens	Overwintered queens
Eggs laid (N. Florida)	Feb-May	Sept-Oct
Mating flights	April-July	late Feb.-early April
Alates emitted/colony/ flight	100's to 1000's	10's to 100's
Mating flight timing	> 30-35° days after rain	any day > 20-22 °C.
Flight time of day	Mid-day	Mid-late PM
Female alate weight	15-16 mg	8-11 mg
Percent fat, female	45-50%	35-40%
First eggs after mating	2-3 d	same day as mating
Do queens tend eggs?	always	usually not
Approx. % mated	100%	85%
Q. activity after mating	dig founding nest	seek out mature mounds
Founding type	independent, claustral	intraspecific parasitism

(dry wt.) and 45-50% (S.D. = 3.0) fat (Tschinkel, 1993b). By contrast, overwintered gynes (n = 120) averaged 5.57 mg (dry), and contained 37.0% (S.D. = 3.74) fat (Table 2). The gasters of these gynes were visibly thinner than those of spring-reared gynes.

When newly-mated queens were allowed to found a nest in the laboratory, spring reared queens laid eggs, tended brood and produced a mean of 10 to 35 workers (Tschinkel, 1992a). By contrast, fewer than 15% of overwintered queens tended brood at all (n = 64). Those that did produced an average of only 7.0 post-egg brood (S.D. = 4.5). Most overwintered queens stuck their eggs to the walls of the nest tube, willy nilly, unlike spring-reared queens who clumped them. Altogether, overwintered queens seemed to lack not only the reserves needed for independent founding, but also the behaviors.

Altogether, this is evidence of intraspecific, temporary social parasitism in which a newly-mated queen exploits the workers of an unrelated orphaned colony to found her own colony (the wire-marked, adopted queens were very unlikely to be related to the adopting colony, having been captured more than 15 km away). The ability to enter orphaned colonies is probably a special characteristic of overwintered gynes. The queen, once adopted, by-passes the very risky claustral stage (Hölldobler and Wilson, 1990; Wheeler, 1910) and can expect much higher survivorship through the protection and care of the host workers. Because they are not related to the parasitic queen, the host workers gain no fitness from this relationship. As the host workers rear the eggs laid by the parasitic queen, the colony will gradually come to consist of the new queen's own daughters.

Overwintered gynes not only provide an alternate mode of colony founding, but also protect against entry of such queens from other colonies (Table 3). In colonies that contained overwintered gynes at the time of orphaning, 14% of the replace-

Table 3. A replacement queen is more likely to be inseminated when the host colony lacks female alates at the time of orphaning. Data for 1995 only

Female alates present at orphaning?	Colonies with replacement-queens	
	Number of colonies	Percent replacement-queens inseminated
Present	46	11%
		$X^2 = 6.66$, df = 1, p < 0.01
Absent	18	39
Total	64	19

ment queens were inseminated parasitic queens and 86% were uninseminated sisters of the workers. By contrast, in colonies lacking such gynes, 62% were parasitic, and only 38% were related ($X^2 = 12.56$, d.f. = 1; p < 0.0004). This protective function may account for the strongly female-biased sex ratio among colonies with overwintered sexuals. About 63% of colonies (n = 46) with overwintered sexuals had only females, and 6% only males. When both sexes were produced (31%), females typically predominated. Lack of overwintered gynes occurred most commonly in colonies too small to produce sexuals. This effect of the presence of female alates was probably the cause of the association between small colony size and queen replacement noted by Tschinkel and Howard (1978). Nevertheless, 11% of larger colonies that produced sexuals in the spring failed to produce fall sexuals. Another 6% produced only males (n = 66) which probably offer no protection against invasion by a parasitic queen.

The ability to invade another colony and to resist that invasion decline together. In October and January, 70 to 77% of colonies had gynes (n = 26, 30). The mating flights that began in late February caused this to decline to 58% in early March and 28% at the end of March (n = 33, 29) when most gynes had flown.

Although dealation by uninseminated gynes in the orphaned colony spells its eventual doom through the cessation of worker production, the resulting large all-male brood gives the colony one last chance in the reproductive game. Entry of an unrelated, inseminated parasitic queen robs the colony of this last chance, reducing its fitness. *It is this feature that makes this mode of colony founding parasitic.*

The relative success of these alternate modes of colony founding probably depends on the population density of mature fire ant colonies. Spring-reared gynes that land in territory occupied by mature fire ant colonies are practically always killed (E.S. Adams and W.R. Tschinkel, unpublished data). Thus, spring-reared queens are more likely to succeed in areas from which fire ants are absent, or present at low densities. On the other hand, as an area becomes saturated with mature colonies, and as these colonies age, mortality of the queen-mothers must increase, creating increased opportunity for colony founding via the socially-parasitic mode. Although colonies always invest less in fall sexuals than in spring sexuals, investment in fall sexuals may increase in pay-off as populations become saturated.

Colonies can be expected to evolve ratios of investment in spring and fall queens that maximize their reproductive success. I estimated the success rate of these alternate strategies as follows. The success of independent founding will depend upon whether the newly-mated queen lands in habitat occupied by mature fire ant colonies or not. In occupied territory (pasture land), we found approximately 130 mature colonies per ha (Tschinkel and Adams, unpublished). Their total annual production of female alates was 265,000 per ha (Tschinkel and McInnes, unpublished) (Morrill, 1974 reported 230,000 female alates per ha). If the population is stable and the mean colony life span is 7 yr (Tschinkel, 1987), approximately 19 colonies/ha will die every year, and their space will become available for recolonization by a newly-mated queen. If all the queens landed on occupied territory, their success rate would be approximately 19/265,000, or 7×10^{-5}. On the other hand, the success rate of queens landing in vacant habitat was about 10^{-3} (Tschinkel, 1992b), or about 1500 fold better.

Overwintered alates flying in early spring make up about 8% of the annual production (Morrill, 1974), or about 14,000 female alates/ha. If the deaths of colony queens is not seasonal, there will be approximately 3 orphaned colonies/ha available for parasitic colony-founding during Feb.–March when the overwintered gynes fly. This means that the average chance of successful founding by intraspecific social parasitism is about 3/14,000 or 2×10^{-4}, or about 285-fold better than independent founding in the same area, but only about one-fifth that of founding in vacant habitat.

Using these conditional success rates, I estimated the mean success of an average colony under varying investment in independent vs. dependent queens, and varying proportions of occupied vs. vacant habitat. I used 15 g as the average colony's annual production of female sexuals, and 7.5 mg and 5 mg as the mean dry weight of independent and parasitic female alates, respectively (thus, for a given investment of biomass, the number of parasitic female alates will be about one-third larger). The greatest success went to colonies that invested 100% of their production in independent queens and that had access only to vacant habitat. A reduction in the proportions of independent queens and vacant habitat both caused a decline in success. When vacant habitat fell below about 20%, increased investment in parasitic queens actually increased, rather than reduced total success.

The observed investment in parasitic queens was about 8–10% of the total annual female alate biomass (Morrill, 1974). My calculations indicate that when the habitat is completely occupied, parasitic queens contribute about 35% of the numerical reproductive success. At 80% occupation, this is about 5%. These figures could be considerably higher if the mortality of queen mothers occurs predominately during winter and early spring, creating greater opportunities for parasitic founding. An additional point of interest is whether colonies can regulate their production of parasitic queens in relation to the degree of habitat saturation. No data are available.

These calculations emphasize that a shift from independent to parasitic founding is driven by the degree of habitat saturation to which the species is typically exposed. For *S. invicta* in its natural home, the low investment in parasitic queens suggests that this is a weedy species represented mostly by young populations founded by independent queens in ephemeral habitat. Only occasionally does the habitat

become saturated enough for parasitic founding to contribute substantially to reproductive success. The congener *S. geminata* presents an interesting contrast because it practices similar alternate modes of founding (McInnes and Tschinkel, 1995), with much greater specialization for parasitic founding. Like *S. invicta*, this species produces a brood of sexuals in the fall, with gynes that are lighter and leaner than those produced in spring. Like the fall-queens of *S. invicta*, these queens are probably incapable of independent founding. Unlike those of *S. invicta*, fall queens of *S. geminata* are also smaller in dimensions (microgynes) than the spring queens (macrogynes) and fly in the fall without overwintering. After mating flights, micro-gynes were captured on the mounds of mature *S. geminata* colonies, where, like the overwintered queens of *S. invicta*, they probably attempt entry as colony-founding, social parasites (McInnes and Tschinkel (1995) suggested that successful entry required the host colony to be orphaned, but did not confirm this hypothesis). The queen-mothers of about one-third of mature colonies were microgynes. Although the success of independent founding in *S. geminata* is unknown, it is clear that, in contrast to *S. invicta*, parasitic founding contributes heavily to reproductive success. This suggests that *S. geminata* populations are less ephemeral and typically saturate the habitat to a much greater degree than do *S. invicta* populations. The "weedy" nature of *S. invicta* has been argued on other grounds by Tschinkel (1987b).

Because this mode of colony founding results in the replacement of a colony queen with another of the same species, it is difficult to detect. Its detection requires methods such as described in this paper, genetic methods or serendipitous morphological differences as in *S. geminata*. Widespread occurrence is thus possible. Among polygyne species, queen adoption, and therefore replacement, has commonly been reported, such colonies being potentially immortal (Bourke and Franks 1995). Evidence for queen replacement in monogyne species is much less common. By comparing theoretical calculations with field data, Elmes (1973) concluded that queen replacement must occur throughout the genus *Myrmica*, even in primarily monogyne species, and that monogyne and polygyne species differed primarily in monogyne longevity and queen adoption rates. Tschinkel and Howard (1978) demonstrated experimentally that inseminated queens were replaced in orphaned colonies of the monogyne form of *S. invicta*. Seppa (1992) found that in some colonies of the mostly monogyne *M. ruginodis*, the queen and workers were unrelated, and suggested that this was the result of queen turnover and was part of the normal life cycle. In the current context, the point of emphasis is that *queen replacement in monogyne colonies amounts to colony founding for the new queen*.

What social factors might pre-adapt a species to such means of founding? In *S. invicta*, colony identity is produced in part by the queen (Hölldobler and Carlin, 1987; Morel et al., 1990). In her absence, colony identity weakens, making orphaned colonies vulnerable to invasion by a parasitic queen. Thus, requeening of orphaned colony fragments is a standard laboratory technique for producing queenright experimental colonies (Tschinkel, 1988). During their long tenure in their natal colonies, fall gynes begin to lay eggs long before their early-spring mating flight (Fletcher and Blum, 1983). Most laid eggs on the same day they mated (unlike spring-reared queens) (Table 2). Because queen attractiveness increases with fecundity (Tschinkel, 1988), adoption by orphaned host colonies is thus facilitated.

Buschinger (1970) recognized that the acceptance of an unrelated, mated queen by a polygyne colony amounted to social parasitism. This definition applies equally well to the monogyne *S. invicta* invaded by an unrelated, overwintered queen. Colony founding by *intra*specific social parasitism, be it in monogyne or polygyne colonies, is a likely candidate for the starting point of the evolution of *inter*specific social parasitism for the purpose of colony founding (Buschinger 1970). This origin would help to explain why most hosts of social parasites are closely related species (Hölldobler and Wilson, 1990) – the extra-specific host represents only a broadening of the host range of an intraspecific parasite. The more similar a species is to the intraspecific parasite, the more readily this mode is transferred to the related species. It would be interesting to determine if interspecific temporary parasites sometimes also parasitize their own species as well.

Socially parasitic colony founding may also be the starting point for the evolution of polygyny. At least in the USA, the queens in colonies of the polygyne form of *S. invicta* are not related to one another. Failure by workers of orphaned colonies to recognize when the colony contained more than one replacement queen would lead directly to a polygyny of unrelated queens.

Acknowledgements

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