Behav Ecol Sociobiol (1995) 36: 367–375

Donald A. McInnes · Walter R. Tschinkel

Queen dimorphism and reproductive strategies in the fire ant *Solenopsis geminata* (Hymenoptera: Formicidae)

Received: 30 April 1993/Accepted after revision: 22 February 1995

Abstract Alate trapping studies of a monogyne population of the fire ant *Solenopsis geminata* indicate that two sizes of gynes are produced. Macrogynes, which participate in late spring and summer mating flights, are larger, fattier, and more than twice as heavy as microgynes, which participate in fall mating flights. Three patterns of gyne production were observed in 51 colonies studied: 35 produced macrogynes only, 9 produced microgynes only, and 7 produced both morphs, contributing to both summer and fall mating flights. Behavioral evidence and rearing studies suggest that macrogynes found new colonies independently, whereas microgynes achieve colony queen status by infiltrating or being adopted by established colonies. Of the total number of female alates collected from the trapped colonies, 56% were microgynes. However, because of their smaller size and lower fat content, microgynes made up only one-third of the caloric investment in female alates. By measuring the thorax lengths of queens from mature colonies, we determined that at least 56% were macrogynes and 35% or more were microgynes. These results indicate that as a reproductive strategy, colony investment in microgyne production may have at least as high a payoff as investment in macrogyne production.

Key words Fire ant · *Solenopsis geminata* · Queen polymorphism · Microgyny · Reproductive strategies

This is publication #24 of the Fire Ant Research Team

D.A. McInnes (✉)[1] · W.R. Tschinkel
Department of Biological Science, Florida State University, Tallahassee, FL 32306, USA

Present address:
[1] Department of Biology, University of Rochester, Rochester, NY 14627, USA

Introduction

Recently, the number of queens per social insect colony has attracted a great deal of interest among sociobiologists (see review by Keller 1993). The distribution of polygyny across diverse ant taxa indicates that it has evolved independently several times, but the factors that favor its evolution remain unclear (Rosengren and Pamilo 1983; Nonacs 1988; Herbers 1993). The difference between species with monogyne (single queen) and polygyne (> 1 queen) colonies is fundamental, with the number of queens per colony generally indicative of a number of basic colony traits relating to life cycle and social structure. Among the most remarkable differences between monogyne and polygyne populations are those in the degree of offspring dispersal and methods of colony founding (Hölldobler and Wilson 1977, 1990; Keller 1991).

Ants employ two primary strategies in establishing new colonies: dependent founding and independent founding (Wheeler 1933; Brian 1965). In the former, young queens receive the help of workers; often new colonies are formed by budding or fission following the adoption of one or more newly inseminated queens (e.g., Rosengren and Pamilo 1983; Vargo and Porter 1989). Dispersal of young queens in dependently founding species may be minimal; in some species, mating occurs in or on the natal nest (e.g., Kasugai et al. 1983; Markin 1970; review by Passera and Keller 1990). During independent founding, a queen starts a new colony without worker aid; dispersal may be distant and the first brood is nourished by the queen's body reserves, histolysis of her wing muscles, and, in some species, by any foraging she may do (Wheeler 1933). It could be argued that parasitic species also exhibit dependent founding, but in their case, the young queens infiltrate or are adopted into nests of and receive the help of workers of different species (reviews by Buschinger 1986, 1990; Sudd and

Franks 1987; Hölldobler and Wilson 1990; Bourke and Franks 1991).

Most polygyne species employ (at least occasionally) a dependent method of colony foundation, whereas monogyne species generally initiate new colonies in an independent fashion (Keller 1991). Only a small number of monogyne ants are known to found colonies in a dependent manner. These include *Cataglyphis cursor* and army ants, such as *Eciton burchelli*. Except for a brief period preceding colony fission, colonies of these species contain only one inseminated queen. In both *C. cursor* and *E. burchelli*, gynes (whereas "queen" denotes a mated and egg-laying individual, "gyne" here refers to any member of the queen caste, regardless of reproductive state) mate at their natal nest, which then divides one or more times to restore monogyny (Franks and Hölldobler 1987; Lenoir et al. 1988).

Multiple reproductive tactics within single species have been documented several times in ants (e.g., Briese 1983; Fortelius et al. 1987; Cherix et al. 1991). Alternative tactics of reproduction and dispersal often have morphological correlates in insects (Harrison 1980). Among ants, gynes which may be adopted back into mature nests after mating are less fatty (Keller and Passera 1989), often have a lower capacity for flight (see Buschinger and Heinze 1992; Rosengren et al. 1993), and may be considerably smaller than their independently founding and widely dispersing counterparts. Intraspecific co-occurrence of smaller-than-usual queens (microgynes) and normal queens (macrogynes) has been reported in several ants (Wheeler 1937; Bourke and Franks 1991), but in only a few is there any functional information about the two queen types.

Janzen (1973) found a queen dimorphism in the polygyne acacia ant *Pseudomyrmex venefica*. Microgynes were observed to return to thorns on their maternal tree after mating. Though the evidence is limited, Janzen believes that macrogynes seek out sapling acacias on which to establish new nests.

Microgyny is best known from the genus *Myrmica*, in which the relationship of macrogynes and microgynes ranges from intraspecific and intracolonial coexistence to obligate parasitism (reviewed by Sudd and Franks 1987; Bourke and Franks 1991). In *M. ruginodis*, macrogynes and microgynes occur together in polygyne nests or separately in nests with queens of one type or the other (Brian and Brian 1949, 1955; Elmes 1991). In *M. rubra*, microgynes are rarely found separately from macrogynes. The microgynes, which produce mostly sexual offspring, are socially parasitic on *M. rubra* macrogynes, which produce mostly workers (Elmes 1978; Pearson 1981), and will likely come to be recognized as a separate species (Pearson 1981; Elmes 1991). The trend toward interspecific parasitism is complete in *M. subuleti*/*M. hirsuta*. Queens of *M. hirsuta*, once thought to be microgynes of *M. sabuleti*, are now recognized as parasites and placed in their own species (Elmes 1978).

In this paper we present our observations on a queen dimorphism in the fire ant *Solenopsis geminata*. We believe this to be the first record of a non-parasitic ant which founds colonies dependently and yet does not undergo colony fission nor budding, and the first record of microgyny in a monogyne ant population.

Methods

Study site and ants

All field work was performed in the Munson Sandhills region of the Apalachicola National Forest, 3–20 km south of Tallahassee, Florida. The Munson Sandhills are characterized by sandy well-drained soil and gently rolling topography. *S. geminata* seems to be resisting displacement by the exotic fire ant *S. invicta* in this habitat, although *S. invicta* dominates certain components of the sandhills region (Tschinkel 1988; McInnes 1994). *S. geminata* can be found here at various densities (Tschinkel 1988), up to approximately 200 colonies per hectare (D.A. McInnes unpublished work). The Apalachicola National Forest population of *S. geminata* is monogyne (see below).

Alate trapping

In the early spring each year 1988–1990 approximately 20 mature *S. geminata* colonies were selected for alate trapping. Colonies were monitored weekly until sexual pupae were present in some of the nests (circa late April/early May) at which time a "teepee" trap of fiberglass window screen supported by a tripod of laths was erected over each mound. Like those used in previous studies (e.g., Morrill and Whitcomb 1972), the traps funneled alates (gynes and males) flying from the nest into a collection chamber. The collection chamber of our trap consisted of a 2-l soda bottle coated with fluon, which held the alates alive until removal for transport to the laboratory. The output of sexuals was quantified on a daily basis by checking traps each evening within an hour after all alate emergence had ceased. At the time of collection, mound activity was verified. The daily checks allowed the colonies to be tracked if they moved, and new nest sites were covered with additional traps. If the locations or identity of any of the trapped colonies became ambiguous, those colonies were eliminated from the present analyses. Trapping continued until early December, when the surface activity of the colonies diminished to near zero for winter hibernation.

Collected alates were taken back to the lab and immediately killed by freezing at $-10°$ C for a minimum of 12 h and then dried at 50° C to constant weight. For each collection of a colony's daily reproductive output, the numbers of males and females and the total dry weight for each sex were determined. In those instances where more than a few hundred ants of either sex were collected from a colony, the statistics were determined from samples of 100–200 ants and the composition of the entire collection estimated.

Fat analysis

Fat content was determined for gynes collected at or near the beginning of each month, June to November. Six gynes were selected at random from each of six colonies for each month. Colonies were used for 1 month only; in total 216 gynes from 36 colonies were analyzed. Selection of colonies was not entirely random because all colonies were not reproductively active each month. Fat content

was determined gravimetrically after extraction by diethyl ether. Methods were similar to those of Peakin (1972). Each alate was contained in a perforated gelatin capsule (Eli Lilly and Co., Indianapolis) and extracted in a Soxhlet extractor to constant dry weight (40–48 h). Both the dry weight of gynes prior to extraction and the percent fat (after angular transformation) were analyzed by ANOVA of the dependent variable on month, with colony nested within month.

Mature colony queens

Queens of mature colonies were collected by thinly spreading a shovelful or two of soil and ants from the top of a nest onto a sheet of plastic. Attempts were made to collect queens from more than 200 colonies, including those trapped in 1990. Insemination was verified either by dissection or the rearing of eggs in the laboratory. Most collecting was done in the early spring of 1990 and 1991. For collections during the mating season, the presence or absence of reproductives in the nest was noted.

Newly mated queens

Newly mated queens were collected on the ground following mating flights. Insemination was verified as for colony queens. Newly mated queens not dissected or used for other purposes were allowed to rear brood individually in test tubes in the laboratory at 27–30° C. A census of the developmental stages beyond the third larval instar was taken within 24 h after eclosion of the first minims.

Linear measurements

Head width, at the eyes, and thorax length, from pronotum to mesosternum, were measured to the nearest 0.024 mm for the queens collected from mature colonies and those gynes selected for fat extraction. An ocular micrometer was used on a dissecting scope at 25.2 × magnification. ANOVA of head width and thorax length on month (with colony nested within month) was performed on the data from the trap-collected gynes.

Results

Mating flights occurred from late May or early June until the end of November. The number of colonies releasing alates peaked in mid-summer and steadily declined thereafter (Fig. 1). Despite the smaller number of reproductively active colonies in the fall, alate production was bimodal each year, with peaks in June (1990) or July (1988, 1989) and again in October (Fig. 2A). On average those colonies active in the fall released a greater number of alates than did those colonies active in the summer (Fig. 2B).

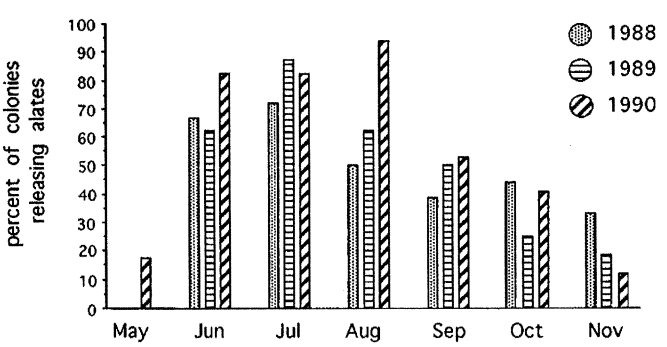

Fig. 1 Percent of trapped colonies releasing alates each month (sample sizes are 1988, $n = 18$; 1989, $n = 16$; 1990, $n = 17$ colonies). Each year the number of reproductively active colonies peaked midsummer and declined thereafter

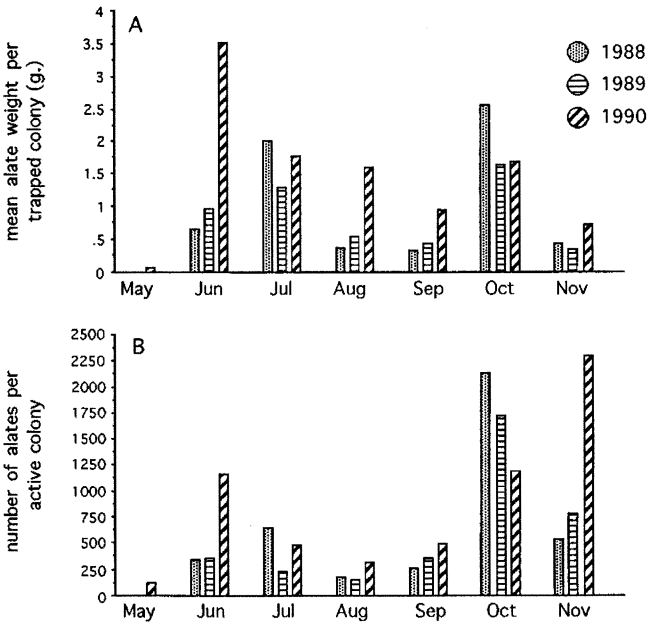

Fig. 2 A Total dry weight of alates collected per trapped colony–for each month the total dry weight of alates was divided by the number of colonies trapped (sample sizes are the same as in Fig. 1), **B** The number of alates collected per reproductively active colony–for each month the total number of alates collected was divided by the number of colonies releasing alates that month. Colonies active in the fall release more alates, but the overall population pattern is bimodal because more colonies are active in the summer

In all 3 years, the dry weight of males remained about 2 mg throughout the mating season. The weight of females, however, changed drastically in the fall (Fig. 3, Fig. 4A). Gynes collected in the late spring and summer averaged more than twice the weight of gynes collected October–December. The mean dry weight of spring/summer gynes was 9.9, 10.2, and 10.6 mg in 1988, 1989, and 1990 respectively. The fall gynes averaged 4.3, 4.4, and 4.8 mg the same years. Nested ANOVA indicated that both month ($F = 1016$, $df = 5$, $P < 0.001$) and colony ($F = 5.1$, $df = 28$, $P < 0.001$) had significant effects on gyne weight.

The pattern of alate production differed from one colony to the next, but each of the colonies from which alates were collected could be classified into one of three types. Most of the colonies (35/51) produced alates in the spring/summer only. The gynes produced by these colonies, macrogynes, all weighed more than 6 mg dry weight (mean = 10.5 mg ± 0.8 SD). Figure 5A shows the mean weights of gynes collected each day from a single colony representative of this type. Nine (18%) colonies did not release any alates

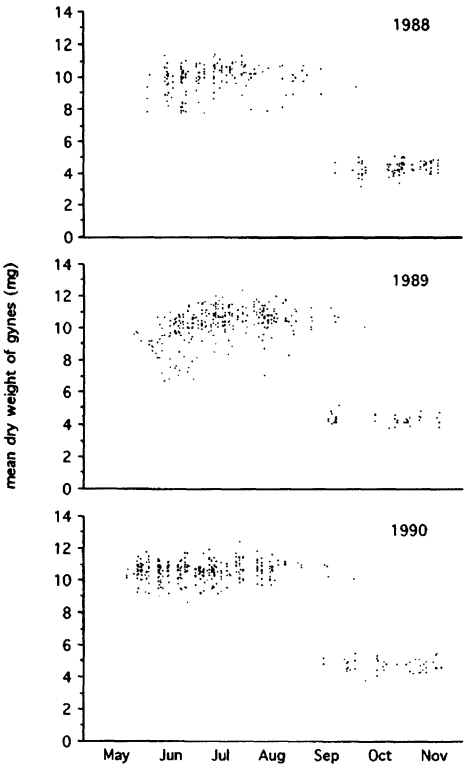

Fig. 3 The mean dry weight of gynes across the season – each *point* shows the mean weight of gynes collected on 1 day from a single colony (points represent from one to several hundred ants; number of colonies as in Fig. 1)

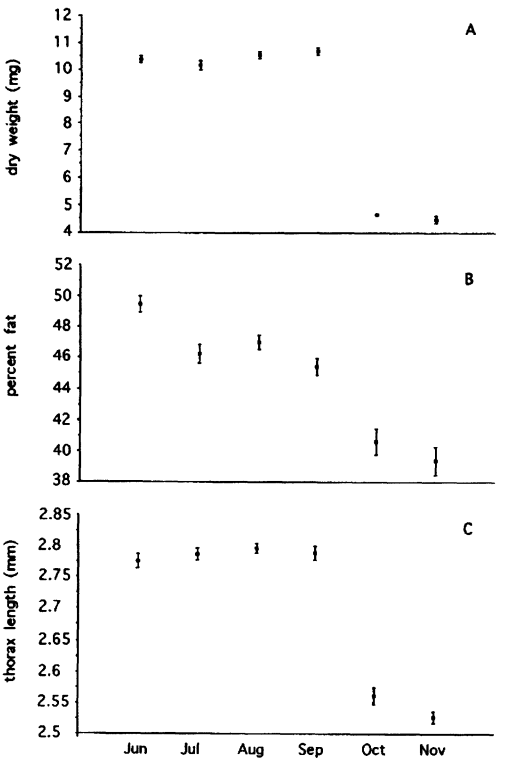

Fig. 4 The **A** dry weights, **B** thorax lengths, and **C** fat percentages of gynes collected on or near the 1st of each month (means and SEs; $n = 36$ for each month)

until the end of summer or the beginning of fall (e.g., Fig. 5B). The gynes produced by each of these colonies, microgynes, were all less than 6 mg dry weight (mean = 4.5 mg ± 0.4). Seven (14%) of the 51 colonies produced both spring/summer and fall alates. The gynes produced by these colonies were comparable to those produced by other colonies at the same time – spring/summer gynes weighed around 10 mg, while those collected in the fall weighed about 4–5 mg (Fig. 5C). The overlap in release of macrogynes and microgynes in late September (Fig. 3) occurred because some colonies of type A and B (Fig. 5) were simultaneously active. No colony released both macrogynes and microgynes concurrently. Each colony producing alates both in the spring/summer and fall underwent a period of several weeks in August and September when no alates were released. The gynes collected before this "dormant" period were all heavy, and those afterward all light. The same three temporal patterns were evident in male production. Colonies generally

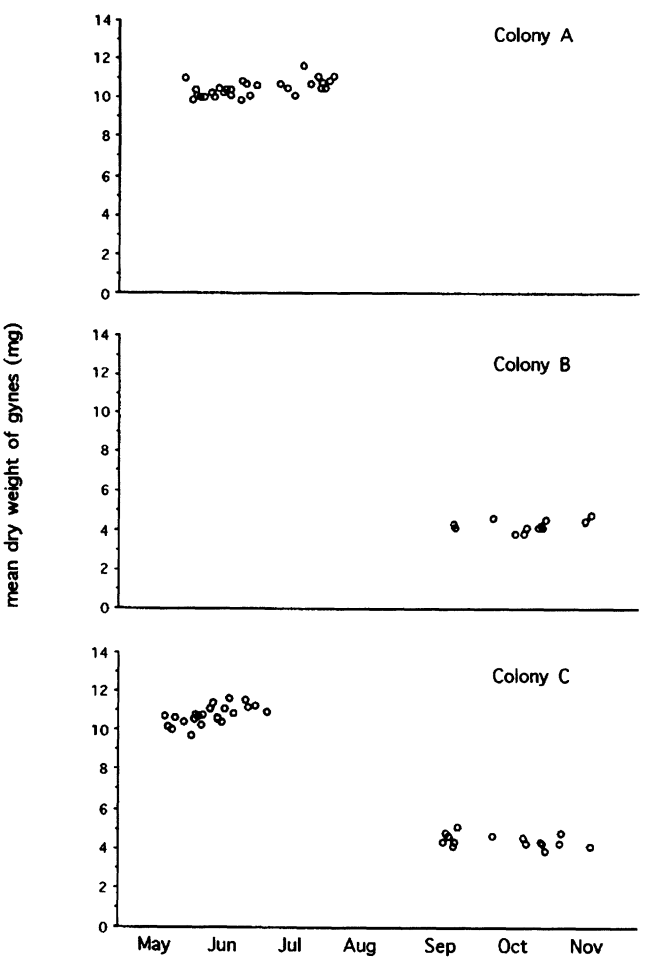

Fig. 5 The mean dry weights of gynes collected from three different colonies–**A** colony **A** participated only in late spring and summer mating flights and released only large gynes; **B** colony **B** participated only in fall mating flights and released only small gynes; **C** colony **C** participated in both summer and fall mating flights and released both types of gyne (*points* represent from one to several hundred ants)

released males at the same time (spring/summer, or fall, or both) as they released gynes. Two years of periodic examinations and observations during mating flights on ten non-trapped colonies indicated that *S. geminata* colonies exhibit the same pattern of alate production from one year to the next. One colony, observed during 4 consecutive years, released alates only in the fall.

Microgynes not only weighed less than macrogynes collected in the spring and summer, they were also smaller (Fig. 4B). Nested ANOVA indicated that both month and colony had significant effects on thorax length ($F = 104$, $df = 5$, $P < 0.001$ for month and $F = 6.9$, $df = 28$, $P < 0.001$ for colony). The distribution of thorax lengths is completely non-overlapping (Fig. 6A). Gyne head width produced a similar pattern – the distribution was strongly bimodal, although some overlap in size was evident between the smallest macrogynes and the largest of the fall microgynes.

The fat content of gynes produced a pattern similar to those for dry weight and thorax length (Fig. 4C). Macrogynes collected in the spring and summer averaged 47.1 ± 3.6% fat by weight, while fall microgynes were 40.0 ± 5.2% fat. ANOVA indicated that both month ($F = 67.3$, $df = 5$, $P < 0.001$) and colony (nested within month, $F = 8.2$, $df = 28$, $P < 0.001$) significantly affected fat content.

Microgynes made up 56% of the total number of gynes collected. Because of their smaller size, they made up only 35% of the total weight, and because they have a lower fat content, the energy investment in microgynes on a population level is likely to be somewhat less. If one uses the assumptions of Peakin (1972) concerning the relative caloric content of fat and non-fat constituents of ants, and if similar respiratory costs during development are assumed, microgynes accounted for 33% of the total investment in gynes.

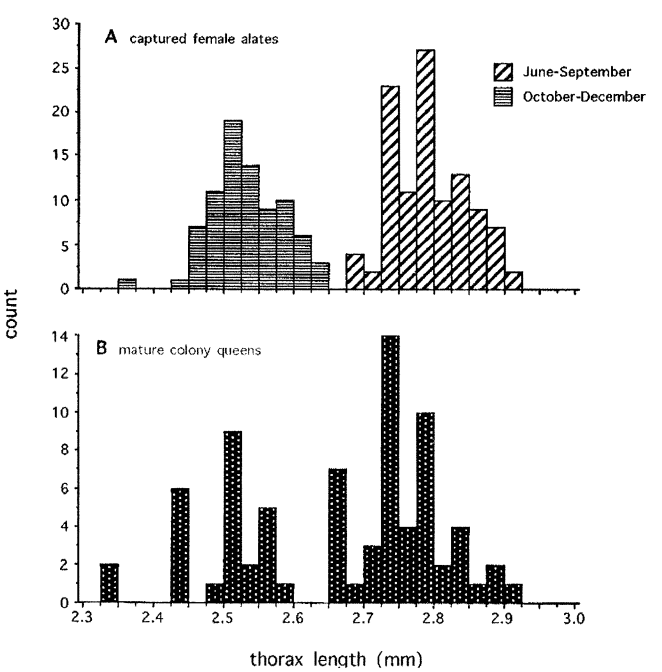

Fig. 6 The thorax lengths of **A** trap-collected gynes and **B** mature colony queens collected by partial nest excavation. The figure shows the natural distribution of mature colony queen thorax lengths, but the trap-collected gynes are the same portrayed in Fig. 4 and do not represent a random sample of the years' production; (captured female alates $n = 216$, colony queens $n = 75$)

In searching for newly-mated queens, the best strategy for finding macrogynes after a mating flight was to search along forest roads and firebreaks for queens walking or digging themselves a founding chamber. This method proved unsuccessful for finding microgynes. Newly mated microgynes were apparently attracted to existing colonies and were most easily collected by monitoring a mature nest and capturing alighting or dealate gynes on the mound or on the outside of the trap screening. On four occasions a microgyne was observed to alight on the mound of a mature colony, break off her wings and walk about on the surface of the mound. In each case, within 2 min, the microgyne was attacked and killed by resident workers. Insemination of these gynes was verified by dissection. Macrogynes were never observed to land on an existing nest or on the outside of an alate trap, despite hundreds of hours of observation.

Brood censuses were performed on 65 newly mated queens that established nests in the laboratory; 55 were from summer mating flights and 10 from fall flights. The mean brood count at the time of first minim eclosion (number of minims + pupae + 4th-instar larvae)of the summer macrogynes was 24.0 ± 9.9 (SD), but only 3.1 ± 3.1 for the fall microgynes (Mann-Whitney *U*-test: $U = 12.0$, $P = 0.0001$). Two incipient nests were detected in the field in October 1991. Both were headed by macrogynes and contained a few dozen workers (42 in one nest, 48 in the other).

Queens were collected from 75 mature colonies. All were attractive to workers and most exhibited some degree of physogastry (abdominal swelling due to ovarian development). The distribution of thorax lengths of colony queens (Fig. 6B) indicates that both macrogynes and microgynes are successful at becoming colony matriarchs. Using the distribution of thorax lengths of the trap-caught gynes (Fig. 6A) as a reference, 26 (35%) of the 75 colony queens were macrogynes and must have originally participated in fall mating flights. Of the colony queens 42 (56%) were macrogynes, originating from spring or summer flights. Determination could not be made for seven (9%) of the colony queens. These had thoraces of 2.67 mm, which was larger than the largest measured fall-caught alates and smaller than the smallest spring/summer alates.

Most of the queens collected from mature colonies were obtained in March and April, before any sexuals are produced, but we have some data on the repro-

ductive output of 26 colonies from which we collected the queen. Of these queens 18 were macrogynes and the other 8 were microgynes. Of the 18 nests in which the queen was a macrogyne, 17 produced sexuals in June or July. The other macrogyne colony released only fall sexuals (i.e., microgynes and males). The queen from this colony was not collected until March following the mating season for which we have data. It is therefore possible that during the intervening fall and winter a change in queens occurred, or that colony movement caused a misidentification of the nest. None of the eight colonies with microgyne queens contained any sexuals, nor sexual brood in July, when the queens were collected. No further information on their reproductive output is available, although based on our trapping studies, colonies of similar size invariably produce alates, suggesting these colonies would have done so in the fall. These results are significantly different from what would be expected if no relationship existed between queen and daughter morph (Fisher's exact test, $P < 0.001$).

We attempted to verify if existing colonies will adopt microgynes. Following nuptial flights, twenty-four dealate microgynes were collected on the outside of alate traps or on nest mounds. These were paint-marked in the field at the time of collection and released on the mounds of 12 mature nests (two per nest). In most cases the marked ants entered the colony, either by walking down a nest entrance or by being dragged in by the resident workers. All 12 colonies were subject to the queen-searching procedures described above one or more times, 1–4 weeks later. A single queen was found in each of 9 of the 12 colonies, but in no instance was a marked gyne recovered.

Microgynes were also introduced to six colonies which had been laboratory maintained for 6–18 months, including one in which the queen had died five to seven days earlier. The microgynes were collected following a mating flight, 1–2 h before the experiment was performed. Only one gyne was presented to each colony. These microgynes were not marked, and the laboratory colonies were chilled at 4° C for 15 min prior to the introductions. In all six colonies, workers killed the introduced microgyne within 45 min.

Discussion

Together, the apparent attraction of newly mated microgynes to existing nests and their lesser ability to rear brood claustrally (i.e., without foraging) suggest that microgynes are adapted to assume the role of matriarch after adoption by existing nests, rather than to initiate new colonies independently. Supportive evidence comes from the fat extraction results. In ant species that initiate new nests independently, gynes have a higher fat content at the time of mating than do gynes of species that found nests dependently (Keller and Passera 1989). Fat content measurements place *S. geminata* macrogynes near the center of the range of independently founding species. Microgynes contain less fat than species that found independently, but more than reported for those employing dependent founding (Keller and Passera 1989). In *S. invicta*, gynes released in the fall also contain less fat than earlier gynes (Tschinkel 1993; McInnes, 1994). In this species though, fall gynes have a normal capacity to found viable colonies under laboratory conditions (W.R. Tschinkel, unpublished work).

Despite our failure in introducing microgynes, the microgyne-adoption hypothesis cannot be discounted. The success rate may be so low that there was little chance of observing an adoption. The rate of adoption does not need to be very high for microgynes to be as successful as independently founding macrogynes. Although alternative reproductive tactics need not be equally successful to coexist (Austad 1984), the success rate of macrogynes is a reasonable starting place to estimate the success rate of microgynes. In a stable population producing only independently founding macrogynes, the expected success rate for any one gyne would be the reciprocal of the average number of gynes produced over the lifetime of a colony (i.e. the replacement rate). For a crude estimate, we assume that a colony produces no sexuals during its first 2 years and the average number of macrogynes in the years following, until the death of the colony queen. Of the trapped colonies that produced only macrogynes and males, the mean number of macrogynes captured by our traps was 320 per year. No data exist on the longevity of *S. geminata* queens. Based on the rate of sperm depletion, Tschinkel and Porter (1988) estimated successful *S. invicta* queens live an average of about 7 years. Using the same per worker sperm depletion rate and adjusting for the smaller colony size of *S. geminata* (McInnes 1994) produces an estimate of total colony lifetime production of 3200 macrogynes. This corresponds to an expected success rate of 3.13×10^{-4} for any individual macrogyne. If investment in the production of microgynes has a payoff equal to investment in macrogynes, microgynes would be expected to have an even lower success rate since they are cheaper to produce.

That queens produce daughters of the same morph as themselves suggests production of macrogynes and microgynes may be have a genetic basis. The production of both queen morphs (eg., Colony C, Fig. 5) by nearly one in seven colonies remains enigmatic. It seems unlikely that a change in colony queen can be responsible for a switch from production of macrogynes to microgynes in the same year. A mated microgyne would have to be adopted and immediately effect the production of microgyne alates, or she would have to

survive in the adopting colony for many months in order to take over the role of queen from the macrogyne matriarch during one of the succeeding summers. There is evidence against both of these hypotheses.

The timing of mating flights in the colonies of type C (Fig. 5) precludes replacement of the macrogyne colony queen by a newly adopted microgyne to explain the production of both morphs in some nests. There was not sufficient time for the earliest-flying microgynes to have been adopted and have produced a brood of microgyne offspring. For instance, the first microgynes to be caught in 1989 came from a colony which had released macrogynes earlier that year.

When Tschinkel and Howard (1978) removed queens from functionally monogynous *S. invicta* colonies, a second inseminated queen took over the matriarch role in one-third of the orphaned colonies. Because they observed no mating flights in the intervening period, the authors concluded that the new queens were most likely present in the nests prior to orphaning. In searching for queens of mature *S. geminata* colonies, we collected more than one inseminated gyne from four colonies (containing 2, 2, 3, and 6 mated gynes). In each of the four, only one gyne was attractive to workers or laid eggs during the first 24 h after collection, indicating the study population of *S. geminata* studied is functionally monogynous *sensu* Buschinger (1968). All four queens and all nine reproductively inactive gynes were macrogynes. It seems unlikely that colonies contained microgynes as replacement queens since none were observed as supernumerary queens. The nine supernumerary macrogynes may represent potential replacement queens, but they shed little light on the phenomenon of *S. geminata* microgyny.

If no switching of queens occurred, as these observations suggest, another hypothesis, that macrogynes and microgynes belong to different species, is also eliminated (at least they do not belong to two species with an effective barrier to hybridization).

If macrogyne and microgyne production are alternative reproductive strategies determined by a genetic polymorphism, it is possible that a queen producing both macrogyne and microgyne daughters is a heterozygote, or she may have been inseminated by a male carrying the alternative allele(s). Unless there is discrimination while the ants are airborne, opportunity exists for offspring of colonies of the two types to mate in late September (Fig. 3).

It appears microgynes need to be adopted by mature colonies, but not necessarily by macrogyne-headed ones. Some of the nests on which microgynes were observed to alight following a mating flight were reproductively active at the time, implying they were headed by microgynes. It does not seem likely that *S. geminata* microgynes are adopted back into their natal nest, as in *Cataglyphis cursor* (Lenoir et al. 1988), since we failed to find more than one inseminated microgyne per nest. Also, in more than 7 years of working with this population, we have never observed a case of colony fission. Colonies frequently occupy more than one nest site, but these instances are associated with nest relocation and are always of short duration (usually only 1 or 2 days).

In our opinion, *S. geminata* microgynes are unlikely to be successful unless they are adopted by orphaned colonies. This hypothesis best explains the results of our rearing studies and behavioral observations on *S. geminata*. Adoption by orphaned colonies is thought to be the mechanism employed by queens of some species of temporary parasites (reviewed by Sudd and Franks 1987). Although our single trial with a newly mated microgyne proved unsuccessful, orphaned nests of *S. geminata*, in both the laboratory and the field, often accept replacement queens from other colonies (D.A. McInnes, unpublished work).

The occurrence of more than one egg-laying queen (functional polygyny) has been reported in *S. geminata* (Adams et al. 1976; McKay et al. 1991; Vargo 1993), but no data exist on the relationship of polygyny and queen size. Vargo (1993) reported head widths for gynes of a polygyne population of *S. geminata* Texas, but these data cannot be usefully compared to our data because the shape of *S. geminata* gynes differs in Texas and Florida. Texas gynes have smaller heads relative to their thorax lengths than do Florida gynes (D.A. McInnes, unpublished work). Worker allometry also differs between Texas and Florida (S. Porter, personal communication). In polygyne populations of *S. invicta*, newly mated queens are adopted by mature colonies, but no difference exists in the head widths (Porter 1992) nor in the thorax lengths (Keller and Ross 1993a) of queens of polygyne and monogyne colonies in this species. Differences in queen size relating to polygyny though, have been reported in other species (e.g., *Camponotus nawai*, Satoh, 1989). In order for polygyny to evolve in the Apalachicola National Forest population of *S. geminata*, it is necessary that the mechanisms prohibiting the acceptance and coexistence of additional reproductively active queens break down. Though a major change in social structure, studies of *S. invicta* suggest that such an evolutionary step may not be genetically complex (Keller and Ross 1993a, b).

Microgyny has been proposed as an intermediate step in the evolution of workerless, socially parasitic ants known as inquilines. In hypotheses proposed by Sudd and Franks (1987), Bourke and Franks (1991), and Buschinger (1991), polygyny is prerequisite and miniaturization evolves after the parasitic relationship has been established. More information is required to determine the extent to which the relationship of *S. geminata* microgynes and macrogynes are parasitic, but our observations clearly intimate the evolution of microgyny is possible in the absence of polygyny.

Acknowledgements This work was supported in part by an National Science Foundation research grant (#BSR8920710) to W.R.T. For field and lab assistance we are grateful to C. Adams, E. Adams, J. Carter, D. Cassill, S. Clark, M. Doms, N. Furman, M. Law, T. Macom, M. Morgan McInnes, and K. Moegling. The patience of those who helped search for newly mated queens was often tested and always appreciated. Thanks to E. Vargo for sending Texas specimens, and to S. Porter for demonstrating his queen collection technique. E. Adams, M. Balas, D. Cassill, L. Keller, M. Kulhmann, D. Simberloff, and two anonymous reviewers provided helpful criticism of an earlier draft.

References

Adams CT, Banks WA, Plumley JK (1976) Polygyny in the tropical fire ant, *Solenopsis geminata* with notes on the imported fire ant, *Solenopsis invicta*. Fla Entomol 59:411–415

Austad SN (1984) A classification of alternative reproductive behaviors and methods for field-testing ESS models. Amer Zool 24:309–320

Bourke A, Franks NR (1991) Alternative adaptations, sympatric speciation and the evolution of parasitic, inquiline ants. Biol J Linn Soc 43:157–178

Brian MV (1965) Social insect populations. Academic Press, London

Brian MV, Brian AD (1949) Observations on the taxonomy of the ants *Myrmica rubra* L. and *M. laevinodis* Nylander (Hymenoptera: Formicidae). Trans R Entomol Soc Lond 100:393–409

Brian MV, Brian AD (1955) On the two forms *macrogyna* and *microgyna* of the ant *Myrmica rubra* L. Evolution 9:280–290

Briese DT (1983) Different modes of reproductive behaviour (including a description of colony fission) in a species of *Chelaner* (Hymenoptera: Formicidae). Insectes Soc 30:308–316

Buschinger A (1968) Mono- und Polygynie bei Arten der Gattung Leptothorax Mayr (Hymenoptera Formicidae). Insectes Soc 15:217–226

Buschinger A (1986) Evolution of social parasitism in ants. Trends Ecol Evol 1:155–160

Buschinger A (1990) Sympatric speciation and radiative evolution of socially parasitic ants – heretic hypotheses and their factual background. Z Zool Syst Evolut Forsch 28:241–260

Buschinger A, Heinze J (1992) Polymorphism of female reproductives in ants. In: Billen J (ed) Biology and evolution of social insects. Leuven University Press, Leuven, Belgium, pp 11–23

Cherix D, Chautems D, Fletcher DJC, Fortelius W, Gris G, Keller L, Passera L, Rosengren R, Vargo EL, Walter F (1991) Alternative reproductive strategies in *Formica lugubris* Zett. Ethol Ecol Evol Special Issue 1:61–66

Elmes GW (1978) A morphometric comparison of three closely related species of *Myrmica* (Formicidae), including a new species from England. Syst Entomol 3:131–145

Elmes GW (1991) Mating strategy and isolation between the two forms, *macrogyna* and *microgyna*, of *Myrmica ruginodis* (Hym. Formicidae). Ecol Entomol 16:411–423

Fortelius W, Pamilo P, Rosengren R, Sundström L (1987) Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera, Formicidae). Ann Zool Fennici 24:45–54

Franks NR, Hölldobler B (1987) Sexual competition during colony reproduction in army ants. Biol J Linn Soc 30:229–243

Harrison RG (1980) Dispersal polymorphisms in insects. Annu Rev Ecol Syst 11:95–118

Herbers JM (1993) Ecological determinants of queen number in ants. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 262–293

Hölldobler B, Wilson EO (1977) The number of queens: an important trait in ant evolution. Naturwissenschaften 64:8–15

Hölldobler B, Wilson EO (1990) The Ants. Belknap Press, Cambridge

Janzen DH (1973) Evolution of polygynous obligate acacia-ants in western Mexico. J Anim Ecol 42:727–750

Kasugai M, Takeda S, Sakurai H (1983) Observations on the microgyne form of ant *Myrmica ruginodis* Nylander (Hymenoptera, Formicidae) in Sapporo. Kontyu 51:73–79

Keller L (1991) Queen number, mode of colony founding, and queen reproductive success in ants (Hymenoptera, Formicidae). Ethol Ecol Evol 3:307–316

Keller L (1993) Queen number and sociality in insects. Oxford University Press, Oxford

Keller L, Passera L (1989) Size and fat content of gynes in relation to the mode of colony founding in ants (Hymenoptera; Formicidae). Oecologia 80:236–240

Keller L, Ross KG (1993a) Phenotypic plasticity and "cultural transmission" of alternative social organizations in the fire ant *Solenopsis invicta*. Behav Ecol Sociobiol 33:121–129

Keller L, Ross KG (1993b) Phenotypic basis of reproductive success in a social insect: genetic and social determinants. Science 260:1107–1110

Lenoir A, Querard L, Pondicq N, Berton F (1988) Reproduction and dispersal in the ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Psyche 95:21–44

MacKay WP, Porter SD, Gonzalez D, Rodriguez A, Armendedo H, Rebeles A, Vinson SB (1991) A comparison of monogyne and polygyne populations of the tropical fire ant, *Solenopsis geminata* (Hymenoptera: Formicidae), in Mexico. J Kansas Entomol Soc 63:611–615

Markin GP (1970) The seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae), in southern California. Ann Entomol Soc Am 63:1238–1242

McInnes DA (1994) Comparative ecology and factors affecting the distribution of north Florida fire ants. Ph.D. dissertation, Florida State University

Morrill WL, Whitcomb WH (1972) A trap for alate imported fire ants. J Econ Entomol 65:1194–1195

Nonacs P (1988) Queen number in colonies of social hymenoptera as a kin-selected adaptation. Evolution 42:566–580

Passera L, Keller L (1990) Loss of mating flight and shift in the pattern of carbohydrate storage in sexuals of ants (Hymenoptera; Formicidae). J Comp Physiol B Biochem Syst Environ Physiol 160:207–211

Peakin GJ (1972) Aspects of productivity in *Tetramorium caespitum* L. Ekol Pol 20:55–63

Pearson B (1981) The electrophoretic determination of *Myrmica rubra* microgynes as a social parasite: possible significance in the evolution of ant social parasites. In: Howse PE, Clément J-L (ed) Biosystematics of social insects (Systematics Association special volume no. 19). Academic Press, New York, pp 75–84

Porter SD (1992) Frequency and distribution of polygyne fire ants (Hymenoptera: Formicidae) in Florida. Fla Entomol 75:248–257

Rosengren R, Pamilo P (1983) The evolution of polygyny and polydomy in mound-building *Formica* ants. Acta Entomol Fenn 42:65–77

Rosengren R, Sundström L, Fortelius W (1993) Monogyny and polygyny in *Formica* ants: the result of alternative dispersal tactics. In: Keller L (ed) Queen number and sociality in insects. Oxford University Press, Oxford, pp 308–333

Satoh T (1989) Comparisons between two apparently distinct forms of *Camponotus nawai* Ito (Hymenoptera, Formicidae). Insectes Soc 36:277–292

Sudd JH, Franks NR (1987) The behavioural ecology of ants. Blackie, Glasgow

Tschinkel WR (1988) Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in northern Florida in relation to habitat and disturbance. Ann Entomol Soc Amer 81:76–81

Tschinkel WR (1992) Brood raiding and the population dynamics of founding and incipient colonies of the fire ant, *Solenopsis invicta*. Ecol Entomol 17:179–188

Tschinkel WR (1993) Sociometry and sociogenesis of colonies of the fire ant *Solenopsis* during one annual cycle. Ecol Monogr 63:425–457

Tschinkel WR, Howard DF (1978) Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. Behav Ecol Sociobiol 3:297–310

Tschinkel WR, Porter SD (1988) The efficiency of sperm use in queens of the fire ant, *Solenopsis invicta* Buren. Ann Entomol Soc Amer 81:777–781

Vargo EL (1993) Colony reproductive structure in a polygyne population of *Solenopsis geminata* (Hymenoptera: Formicidae). Ann Entomol Soc Amer 86:441–449

Vargo EL, Porter SD (1989) Colony reproduction by budding in the polygyne form of *Solenopsis invicta* (Hymenoptera: Formicidae). Ann Entomol Soc Amer 82:307–313

Wheeler WM (1933) Colony-founding among ants, with an account of some primitive Australian species. Harvard University Press, Cambridge

Wheeler WM (1937) Mosaics and other anomalies among ants. Harvard University Press, Cambridge