

The success of alternative reproductive tactics in monogyne populations of the ant *Solenopsis invicta*: significance for transitions in social organization

Christopher J. DeHeer^a and Walter R. Tschinkel^b

^aDepartment of Entomology, University of Georgia, Athens, GA 30602–2603, USA, and ^bDepartment of Biology, Florida State University, Tallahassee, FL 32306, USA

Newly produced queens from monogyne (single-queen) colonies of the ant *Solenopsis invicta* usually initiate reproduction independently, that is, without worker assistance. However, some recently mated queens attempt to bypass this risky phase of new colony foundation by entering established nests to reproduce, although it is unclear how often these queens are successful in natural populations. We surveyed a mature monogyne population of *S. invicta* in both 1995 and 1996 for colonies headed by queens incapable of independent colony founding (diploid-male-producing queens) in order to estimate the frequency of colonies that are headed by queens that initiated reproduction within established nests (adopted queens). Using the frequency of diploid-male-producing queens among the recently mated queens in this population, we estimated that the overall rate of queen replacement by adopted queens is about 0.7% per colony per year. Although theory suggests that a change to a novel queen reproductive tactic could be associated with a fundamental change in social organization (queen number), this does not appear to be the case in monogyne *S. invicta*. However, the evolution of nest-infiltrating reproductive tactics by queens in a monogyne population and the evolution of multiple-queen societies may result from similar ecological pressures facing newly mated queens. We therefore incorporate this strategy into an existing theoretical framework that was developed to explain the evolution of alternative social organizations in ants, providing testable predictions regarding the distribution and frequency of queen adoption in other single-queen ant societies. *Key words*: alternative reproductive tactics, fire ants, polygyny, *Solenopsis invicta*. [*Behav Ecol* 9:130–135 (1998)]

Biologists have shown considerable interest in alternative reproductive strategies because of the critical tests these strategies provide for evolutionary theory (e.g., Sinervo and Lively, 1996) and because of their possible role in generating diversity (West-Eberhard, 1986). Alternative reproductive strategies take on additional significance for social insect biologists because of their importance in the evolution of multiple-queen (polygyne) societies (Heinze, 1993; Heinze and Tsuji, 1995; Herbers, 1993; Rosengren et al., 1993; Sundström, 1995). The existence of such societies has presented a challenge to behavioral ecology since the birth of kin selection theory (Hamilton, 1964; Hölldobler and Wilson, 1977) because an apparent paradox arises during the transition from monogyny to polygyny: workers that allow additional queens to enter the colony to reproduce are generally more related to their mother's offspring than to those of newly recruited queens. Ants provide particularly useful systems for studying the evolution of polygyny because this system is both common (Crozier and Pamilo, 1996) and highly variable within (e.g., Keller, 1993) and between taxa (Ross and Carpenter, 1991). The ecological constraints model for the evolution of polygyny posits that the apparent paradox may be resolved by simultaneously considering not only the long-term interests of workers but also the reproductive tactics of newly produced queens. In some habitats, such as those saturated with mature nests, ecological conditions may prevent lone queens from founding new nests. When this occurs, selection may favor strategies or tactics that permit the recruitment of related queens into the nest because this not only provides reproduc-

tive opportunities for related queens but also ensures that the nest site remains inhabited by related individuals (Bourke and Heinze, 1994; Herbers, 1993; Keller, 1995; Nonacs, 1988; Pamilo, 1991a).

Under the ecological constraints model, one or more of the three parties within monogyne nests (functional queen, workers, and newly produced queens) may play a role in facilitating a change in queen number (Nonacs, 1988, 1993). The reproductive queen and the workers may directly facilitate this change in queen number simply by permitting newly mated queens to enter the colony (Nonacs, 1988), and the power of each of these parties might depend on their relative size and (for workers) abundance. Newly produced queens may facilitate a change in queen number by attempting to enter an established nest to reproduce instead of founding a new colony independently (Elmes, 1973; Nonacs, 1993; Sundström, 1997). Additionally, because the reproductive tactic adopted by new queens depends on their physiological status (queens with greater energy reserves tend to be those that attempt independent colony founding; Keller and Passera, 1989; Ross and Keller, 1995; Sundström, 1995), workers are in a position to indirectly facilitate a change in queen number by producing underweight queens that are inclined to enter established nests to reproduce (Nonacs, 1993). Surprisingly, variation in the strategies or tactics of workers and queens within single-queen ant societies that could lead to a change in social organization has received little attention (but see Briese, 1983; Sundström, 1995, 1997).

Recently, Tschinkel (1996) described variation in queen colony-founding tactics within a monogyne population of the fire ant *Solenopsis invicta*. Spring- and summer-reared queens from monogyne populations typically attempt independent

Received 7 May 1997; accepted 26 August 1997.

© 1998 International Society for Behavioral Ecology

colony founding after mating flights, but behavioral observations indicate that virgin queens that overwinter in the nest seek adoption into mature nests to initiate reproduction (Tschinkel, 1996). The divergent reproductive tactics adopted by each class of queen are paralleled by striking physiological differences. Spring-reared queens weigh 8.5 mg (dry weight) at maturity (Tschinkel, 1993), whereas overwintered virgin queens weigh only 5.5 mg at the time of their mating flight and have far fewer fat reserves (Tschinkel, 1996). The ecological constraints model for the evolution of polygyny suggests that such a fundamental change in colony-founding tactics exhibited by new queens could be associated with a change in social organization. One purpose of this study was therefore to determine whether a switch in colony-founding tactics among monogyne *S. invicta* queens may lead to a durable change in colony queen number. Perhaps of more general interest, however, is determining how successful this alternative reproductive tactic is relative to independent colony founding. A critical parameter in addressing both of these questions is determining how often these overwintered queens succeed at adopting themselves into established nests. Thus, a second purpose of this study is to determine the proportion of nests that are headed by adopted queens in a natural population of monogyne *S. invicta*.

METHODS

Estimation of the frequency of queen replacement

As in most well-studied Hymenopteran systems that are characterized primarily by outbreeding (Cook and Crozier, 1995), sex in *S. invicta* is determined by genotype at one or a few loci (Ross and Fletcher, 1985). Assuming a single locus, heterozygotes develop into females, whereas hemizygotes (haploids) and homozygotes (diploids) develop into males. Thus, a queen that mates with a male who carries an allele at the sex-determining locus identical to one of her own will produce roughly half diploid males and half females from her fertilized eggs. Due to a population bottleneck during their introduction into the United States and subsequent loss of allelic diversity at the sex-determining locus, diploid-male-producing (DMP) queens are quite common among newly mated queens (Ross and Fletcher, 1985; Ross et al., 1993). However, the likelihood that DMP queens survive to maturity depends largely on the reproductive tactic that these queens adopt. During independent colony founding, DMP queens invest most of their resources trying to raise diploid males rather than workers, producing only a fraction of the workers that other queens can produce during this period (Ross and Fletcher, 1986). Because the number of workers reared in incipient nests founded by one or more queens is of critical importance to survival during this stage (Adams and Tschinkel, 1995; Tschinkel, 1992), it is unlikely that DMP queens can survive this period of intense competition (Ross and Fletcher, 1986). In contrast, DMP queens are just as successful as other queens at gaining acceptance into mature nests to reproduce (Ross and Fletcher, 1985, 1986). We can use the differential selection against DMP queens in different reproductive environments to infer the presence of adopted queens in monogyne colonies: a mature, monogyne colony headed by a DMP queen represents direct evidence for successful adoption into a mature nest.

Furthermore, because DMP queens produce few worker offspring, mature colonies headed by a DMP queen are unlikely to survive a full year in the field. Because roughly half the offspring of DMP queens are diploid males, which represent more than twice the energetic investment of even the largest worker, a colony headed by a single DMP queen will invest

more than two-thirds of its energy into sexual (diploid male) production throughout the entire reproductive season. It is unlikely that colonies investing this little in worker biomass can survive for an entire year (an assumption that is supported by our results; see Tschinkel, 1993). Thus, we can estimate the proportion of colonies that adopt a new queen per year (T , or the frequency of queen replacement) using the formula:

$$T = \frac{d}{\Theta}, \quad (1)$$

where d is the proportion of colonies that adopt a DMP queen per year, and Θ is the proportion of DMP queens among newly mated queens in the population (Ross et al., 1993). We estimated Θ using 400 newly mated queens collected from this population during a late spring mating flight, following the methods of Ross and Fletcher (1985) and Ross et al. (1993).

Field collections

We excavated and examined the contents of mature colonies from a monogyne population in Tallahassee, Florida, USA, during late May and early June of both 1995 ($n = 1022$ colonies) and 1996 ($n = 2350$ colonies) to search for those colonies containing diploid males. This is a well-studied population in which polygyny has never been observed (Porter, 1992; Tschinkel WR, personal observation). Based on laboratory studies, a colony headed by a DMP queen will produce a highly male-biased sex ratio, and roughly a 50:50 ratio of males to workers (Ross and Fletcher, 1985). During our first year of sampling, we conservatively identified potential DMP colonies as those containing either large males (diploids are noticeably larger than haploids; Ross and Fletcher, 1985) or a male-biased sex ratio (>5:1 ratio of male alates to female alates) and a relatively high investment in sexuals (>1:10 ratio of alate brood to worker brood). From these 225 colonies we collected at least eight males, eight large adult workers, and eight worker brood and immediately froze them in liquid nitrogen. Because male size proved to be a particularly useful indicator of ploidy level in the field (see Results), we relied more heavily on male size to identify DMP colonies during our second year of sampling. Thus, during 1996 we collected at least eight males, eight workers, and eight worker brood from 19 colonies containing especially large males or roughly a 50:50 ratio of male to worker brood.

Confirmation of male diploidy and determination of queen number

We determined the genotypes of eight males from each putative DMP colony at six polymorphic enzyme loci (*Acoh-1*, *Acoh-5*, *Est-4*, *G3pdh-1*, *Pgm-1*, *Pgm-3*) using horizontal starch gel electrophoresis (Shoemaker et al., 1992). All loci have two common alleles in the United States, with the frequency of the most common allele in males at each locus 0.91, 0.78, 0.74, 0.72, 0.84, and 0.82, respectively. Diploid males were identified by the presence of heterozygote genotypes at any one of these six loci. Diploid males may be misidentified if they are homozygous at all loci but, combined, these loci gave us a 99.4% certainty that we did not misclassify a DMP colony as a normal, worker-producing colony.

Because DMP queens are commonly found in polygyne colonies (Hung et al., 1974; Ross et al., 1993), it was necessary to confirm that the Tallahassee colonies found to contain diploid males were in fact monogyne. We therefore determined the genotypes of large, mature adult workers at the same six loci as above, the genotypes of both males and adult workers at two additional loci (*Aat-2* and *Gp-9*), and the genotypes of

Table 1

Genotype distributions of old workers, diploid males, and worker brood from four colonies that contained diploid males

Year	Colony	Caste	<i>Aco1-1</i>			<i>Aco1-5</i>			<i>Est-4</i>			<i>G3pdh-1</i>			<i>Pgm-1</i>			<i>Pgm-3</i>			<i>Aat-2</i>		
			aa	ab	bb	aa	ab	bb	aa	ab	bb	aa	ab	bb	aa	ab	bb	AA	Aa	aa	aa	ab	bb
1995	6-225	Old workers	8	0	0	4	4	0	5	3	0	8*	0	0	8	0	0	5	3	0	8	0	0
		Males	8	0	0	3	4	0	5	3	0	0	8	0	8	0	0	3	5	0	7	0	0
		Worker pupae	8	0	0	4	4	0	3	5	0				8	0	0	2	6	0			
1995	E-262	Old workers*	23	0	0	14	8	0	9	0	0	22*	1	0	22	1	0	1	22	0	21	0	0
		Males	14	0	0	0	6	8	13	0	0	0	14	0	14	0	0	0	14	0	14	0	0
		Worker pupae	8	0	0	3	4	0	8	0	0				8	0	0	0	8	0			
1996	CD-10	Old workers	12	0	0	5	7*	0				0	5	7*	12	0	0	4	8	0	12*	0	0
		Males	8	0	0	8	0	0	4	3	0	4	4	0	8	0	0	0	1	3	0	6	0
		Worker pupae	8	0	0	8	0	0	2	6	0				8	0	0	8	0	0	0	4	0
		Worker larvae	3	0	0	3	0	0							3	0	0	0	3	0	0	3	0
1996	CD-17	Old workers	8*	0	0	8	0	0	8*	0	0	0	8	0	8	0	0	0	0	8*	8	0	0
		Males	0	14	0	14	0	0	0	14	0	0	14	0	14	0	0	0	14	0	14	0	0
		Worker larvae	0	2	0	2	0	0	0	2	0				2	0	0	0	2	0	2	0	0

Numbers followed by an asterisk indicate genotypes that are present in old workers but entirely absent from both newly produced males and worker brood, thus implicating queen turnover.

* Some small, younger workers were included that may have been the offspring of the new queen(s).

worker brood (pupae or late instar larvae) at six of the eight loci (*Aat-2*, *Aco1-1*, *Aco1-5*, *Est-4*, *Pgm-1*, and *Pgm-3*). These data not only allow us to support or reject monogyny, but they should allow us to demonstrate that queen turnover has occurred in the monogynous nests that contain diploid males. Because queen replacement occurs during February or March, the offspring of both the old queen and the new replacement queen(s) should coexist in the colony during the time of year that we made our collections. Most of the large, older workers (as signified by their dark cuticle) eclosed in the previous summer or fall, whereas alates and worker brood must have originated from eggs laid in the spring. Therefore, in monogynous colonies that contain a recently adopted queen, genotypes within age cohorts should be consistent with one singly mated queen, whereas genotypes between age cohorts will be inconsistent with monogyny (*S. invicta* queens mate only once; Ross, 1993).

Estimation of the frequency of queen replacement

We calculated the frequency of mature colonies headed by a DMP queen (*d*) separately for each year and generated 95% confidence intervals around each value using a resampling technique (bootstrapping; Efron and Tibshirani, 1986). We also calculated an overall value of *d* by pooling the data sets and generating confidence intervals using bootstrapping on the combined data set. We used equation 1 to calculate *T*, the rate of queen replacement per colony per year, for each year and for the combined data set.

RESULTS

Diploid males

We considered 4 out of the 225 colonies from which we collected males in 1995 to be likely candidates for containing a DMP queen based on our field identifications. Using electrophoresis we confirmed that two of the four contained diploid males, compared to zero out of the remaining 221 nests, suggesting that our field ID's were likely to have correctly classified colonies with respect to the presence of diploid males. Thus, out of the 1022 colonies that we surveyed in 1995, 2 were headed by DMP queens. Similarly, out of the 2350 col-

onies that we surveyed in 1996, we confirmed that 2 contained diploid males on the basis of electrophoresis.

Within-colony genetic structure of DMP colonies

The genotype distributions of mature workers, diploid males, and worker brood from the four colonies confirmed to contain diploid males are presented in Table 1. With the exception of one odd genotype in colony E-262, in all four colonies the cohort of workers produced in the previous fall showed genotype distributions consistent with monogyny. Because some smaller workers were included in the genetic analyses for colony E-262, the inconsistent genotype probably represents a young worker that eclosed sometime in the spring. Indeed, a larva from the same colony (almost certainly laid during the spring) has the same genotype at *Pgm-1* as this odd worker. These results suggest that all four colonies were monogynous during the previous fall. However, only two of these colonies (6-225 and CD-17) exhibited genotype distributions within the new cohort of ants that were consistent with monogyny. The other two colonies contained both homozygous genotypes at one locus within the new cohort of ants (males and worker larvae and pupae), a genotype distribution that could not be generated by one, singly mated queen. Thus, these colonies either accepted multiple replacement queens or have experienced sequential queen replacement over a relatively short period of time.

Significantly, a comparison of genotypes between age cohorts of ants within each of the four DMP colonies suggests that neither of our assumptions about the fate of DMP queens has been violated. To utilize the frequency of DMP queens in mature colonies to estimate the annual rate of queen replacement, we must assume that the DMP queens we find do not represent either (1) the exceptional case when DMP queens may succeed at independent colony founding, or (2) replacement DMP queens from the previous year(s) that survived longer than a year. The older workers from all four colonies have a genotype at one or more loci that is entirely absent from the new cohort of ants (see Table 1), thus implicating recent queen turnover.

Table 2

Proportion of monogyne colonies that adopt a diploid-male-producing (DMP) queen per year (d) and proportion of colonies that adopt a new queen per year (T)

Year	Proportion of colonies that adopt	
	A DMP queen (d)	A new queen (T)
1995	0.00147 [0–0.0039]	0.011 [0–0.030]
1996	0.00064 [0–0.0017]	0.005 [0–0.013]
Overall	0.00089 [0–0.0015]	0.007 [0–0.012]

The 95% confidence intervals are shown in brackets.

Rate of queen replacement

We estimated the frequency of DMP queens among newly mated queens, Θ , as 0.13, a value similar to estimates from previous studies of introduced populations (Ross and Fletcher, 1985; Ross et al., 1993). When calculating d , the frequency of mature colonies headed by a DMP queen, we weighed the two colonies with the offspring of (probably) two replacement queens half as much as those with a single replacement queen because multiple replacement events double the chance that these colonies will contain diploid males (and thus be detected using that method). We estimate the rate of queen replacement per year (T) to be 1.1% in 1995, 0.5% in 1996, and 0.7% overall. We present the estimates and the 95% confidence intervals of both d and T in Table 2.

DISCUSSION

We have demonstrated that DMP queens are rarely found reproducing in mature, monogyne colonies of *S. invicta* and that in each case these queens have replaced the original queen during the year in which we sampled them. Knowledge of the proportion of DMP queens among newly mated queens in this population allows us to estimate the proportion of colonies per year that adopt replacement queens (both DMP and worker-producing queens). During 1995 and 1996, we estimate that the rate of queen replacement per colony was 1.1% and 0.5%, respectively, yielding an overall rate of queen replacement per colony of 0.7%. If the worker-producing replacement queens survive until their sperm is depleted (conservatively about five years for a fire ant queen that initiates reproduction in a mature colony; those queens that initiate reproduction independently of workers spend the first few years of their life at a much lower fecundity and are likely to have viable sperm for a longer period; Tschinkel, 1987b), roughly 3% of the mature nests in our study population are headed by adopted queens.

A central question that is often raised by studies of alternative reproductive tactics concerns the nature of the fitness consequences of adopting the novel tactic. Because the system of interest is a social system with potential conflicts of interest among the different parties involved, we discuss the fitness consequences for each party separately. From the perspective of overwintered queens, seeking adoption into mature nests is probably the best reproductive option available as long as there are opportunities to gain acceptance (Nonacs, 1988). Although infiltration is a risky tactic (see below), our data indicate that these queens do occasionally succeed at infiltrating mature nests to initiate reproduction. In contrast, their low weight and fat reserves make them unlikely candidates for successful independent colony founding (Tschinkel, 1996).

Indeed, the weight of these queens is similar to that of newly produced queens from the multiple-queen (polygyne) form of *S. invicta* (Keller and Ross, 1993), most of which are poor independent colony founders (Porter et al., 1988; Ross and Keller, 1995).

The fitness consequences of accepting an infiltrating queen into one's nest are less clear. Field data indicate that infiltrating queens are only accepted into colonies whose own queen has been lost, and that many such colonies lack their own overwintered virgin queens (Tschinkel, 1996). This has two consequences. First, any queen that is adopted would be a non-nest mate and, thus, probably an unrelated queen, as fire ant workers that are queenless for even a short period of time lose their ability to discriminate related from unrelated queens (Fletcher, 1986). Second, because little brood is present in the colonies at this time of year (Markin and Diller, 1971) and workers lack functional ovaries (Fletcher and Ross, 1985), groups of workers without functional or virgin queens have little opportunity to raise related brood to sexual maturity. Thus, adopting an unrelated replacement queen may entail little gain or loss for these individuals (see Herbers, 1993 for a more detailed discussion). However, infiltrating queens are occasionally accepted into orphaned colonies that contain virgin queens (Tschinkel, 1996). Unless the infiltrating queens exhibit philopatry, workers in these colonies will also accept an unrelated replacement queen, and their sister virgin queens lose the opportunity to dealate and produce a final flush of male offspring (Fletcher and Blum, 1981; Vargo and Porter, 1993), making this queen tactic parasitic.

We can approach the fitness consequences to workers that produce queens that seek adoption into mature nests like the problem of optimal sex investment. Like optimal sex investment, there is frequency-dependent selection against the most common class of new reproductives, in this case because each class of queens exploits a different but relatively fixed number of reproductive opportunities. For spring- and summer-reared queens that found colonies independently, natural colony death will always open up new habitats for colonization, while for overwintered queens that enter established nests to reproduce, orphaning of mature colonies during the winter will always provide opportunities for infiltration. Thus, like Fisherian sex ratio theory (Bourke and Franks, 1995), the population investment ratio in the two classes of queens is at equilibrium when the fitness payoff per unit of investment in each class of queen is equal. In a mature, stable population such as our study site, about 19 colonies/ha will die each year [assuming a 7-year life span for colonies (Tschinkel, 1987a) and 130 colonies/ha (Tschinkel WR and Adams ES, unpublished data)], and their territories will become available for colonization by newly mated queens. The annual production of independent colony founding queens during the same period is about 250,000/ha (excluding those that overwinter; Tschinkel WR and McInnes DA, unpublished data), and thus, the rate of successful independent colony founding is about 7.6×10^{-3} nests per queen. Because 1 g of investment in independent colony founding queens will produce roughly 120 virgin queens (female alates leaving the nest on mating flights weigh roughly 8.5 mg dry weight in the peak reproductive season; Tschinkel, 1993), monogyne colonies in a mature population can expect 9.1×10^{-3} new colonies/g of investment in independent colony founding queens.

If the annual rate of queen replacement by adopted queens is 0.007 (this study) and there are about 130 colonies/ha, these queens will establish themselves in about 0.91 colonies/ha. Although we have no data on the proportion of queens that overwinter in the nest from this population, Morrill (1974) reports that about 14,000 queens/ha fly during the early spring. Although these data were collected from a dif-

ferent population in northern Florida more than 20 years ago, they give us at least a rough estimate of the rate of successful reproduction by overwintered queens. Based on these data, the rate of successful acceptance into mature nests by overwintered queens is about 6.5×10^{-3} nests per queen. Because 1 g of investment in adoptive queens will produce roughly 140 virgin queens (female sexuals produced in the fall weigh about 7 mg dry weight on average; Tschinkel, 1993), monogyne colonies in a mature population can expect about 9.1×10^{-3} new colonies/g of investment in overwintered, infiltrating queens.

Although these calculations should be viewed with caution as they are based on estimates with fairly large standard errors, they give virtually identical estimates of the expected fitness payoffs per unit of investment in each tactic. At the least we can conclude that selection will probably not operate to drastically alter the current level of investment in overwintered, infiltrating queens, and it raises the possibility that selection may be responsible for the current level of investment in each class of queen.

The willingness of *S. invicta* workers to accept unrelated, non-nest mate queens into their nest parallels the relatedness patterns seen in conspecific polygyne populations, where queens are usually unrelated to worker nest mates (Goodisman and Ross, 1997; Ross, 1993). This might suggest that the origin of polygyny in North American populations of *S. invicta* could be explained by the adoption of multiple replacement queens into orphaned monogyne colonies. Indeed, our discovery of two colonies that were previously monogyne yet apparently contained the offspring of more than one replacement queen raises the interesting possibility that we have detected colonies that have undergone the early stages of a change in social organization. Several lines of evidence, however, suggest that this is not the case. First, with the type of data available to us, we were unable to confirm that more than one queen simultaneously reproduced in these colonies. Second, we found one of these two colonies (E-262) during our first year of sampling, but based on both the relative location of this colony and the multilocus genotypes of the ants (see Table 1), the putative polygyne colony from 1995 (E-262) did not persist until the next year. Because polygyne nests do not appear to suffer greatly increased mortality due to the presence of DMP queens (because they contain some worker-producing queens; Ross and Fletcher, 1985), this suggests that the apparent polygyne nest we found in 1995 was either serially polygyne or did not retain multiple egg-laying queens for very long. Lastly, surveys from six polygyne populations in five southeastern states (Florida, Georgia, Louisiana, Mississippi, and Texas) indicate that social organization may in fact be constrained by the presence or absence of an allele that is linked to the protein encoding allele *Gp-9^b* (or is *Gp-9^b* itself). Every reproductive polygyne queen from these populations has the genotype *Gp-9^{ab}* (or rarely *Gp-9^b*) ($n = 2300$ queens), whereas nearly every reproductive monogyne queen has the homozygous genotype *Gp-9^{ab}* (Ross, 1997; DeHeer CJ, Ross KG, Shoemaker DD, unpublished data). Both of the putative polygyne colonies from this study were fixed for the *B* allele at *Gp-9*, suggesting that these colonies did not represent bona fide polygyne nests. Historical evidence also suggests that queen replacement in orphaned fire ant nests alone is insufficient to lead to a transition to polygyny: the process of queen replacement has probably been occurring in this population for more than 25 years (Tschinkel, 1996; Tschinkel and Howard, 1978), and yet polygyny is still apparently absent.

It is surprising that this reproductive tactic has only recently been characterized in what is one of the most extensively studied species of ants. We suggest that queen adoption in monogyne populations may be more widespread among ants than

is currently appreciated, but due to its rarity within species or its cryptic nature, it has largely escaped detection (but see Pamilo, 1991b; Seppä, 1994). Furthermore, although evidence suggests that the adoption of this novel reproductive tactic and the evolution of polygyny are not causally linked in *S. invicta*, we argue that they are linked in an ultimate sense. The evolution of infiltrating tactics by monogyne queens may, like the evolution of polygyny (Bourke and Heinze, 1994; Keller, 1995; Nonacs, 1988; Pamilo, 1991a), result from increasing constraints on independent colony founding. If habitat patches are sufficiently long lived (longer than the life of a typical queen) such that there are opportunities for new queens to enter established nests that have become orphaned and the constraints on independent colony founding are sufficiently high, then selection will favor new queens that attempt to exploit these opportunities. However, workers in queenright nests should generally be much less willing to allow even related queens into the nest, and only do so when there are strong ecological constraints on independent colony founding or very long-lived and/or valuable nest sites. We suggest that the frequency of queen replacement may vary continuously across monogyne species (or populations) and that these frequency differences should parallel the differences between monogyne and polygyne species (or populations). Thus, we hypothesize that the frequency of infiltrating tactics across monogyne species (or populations) will be positively correlated with nest-site longevity, the difficulty of founding a new nest independently, and opportunities for infiltrating established nests, but negatively correlated with queen longevity.

Comparative data for *S. invicta* and its congener *S. geminata* in the United States are consistent with these predictions. Mature *S. geminata* colonies have a relatively broad habitat tolerance, being readily found in both early- and middle-stage successional habitats. In contrast, *S. invicta* inhabits only highly disturbed, early-stage successional habitats (Tschinkel, 1987a). This means that without repeated disturbances, nest sites will be relatively short-lived for *S. invicta* when compared to those of *S. geminata*. The framework presented above predicts that queen replacement should be more common in monogyne *S. geminata* than in *S. invicta* and, as a corollary, that populationwide investment in queens that seek adoption into mature nests should be greater in *S. geminata*. Indeed, both of these predictions appear to be upheld. McInnes and Tschinkel (1995) found that approximately 35% of the mature nests in a *S. geminata* population were headed by adopted queens. In contrast, roughly 3.5% of the mature nests in our *S. invicta* study population are headed by adopted queens. Additionally, as predicted, the populationwide investment in infiltrating queens appears to be higher in *S. geminata* (33%; McInnes and Tschinkel, 1995) than in *S. invicta* (roughly 8% based on the numerical proportion of newly produced queens that fly during the early spring; Morrill, 1974). We suggest that other monogyne species (or populations) characterized by long-lived nest sites, short-lived queens, or extremely risky independent colony founding would be likely candidates for finding evidence of queen adoption.

We thank D. Cassill, J. Cooper, N. Daigle, and J. Poulton for their generous help in the field, and J. Smith, T. Varno, and J. White for their help in the laboratory. We also thank J. Evans, M. A. D. Goodisman, L. Keller, K. C. Ross, and D. D. Shoemaker for critical discussions that greatly improved the quality of this work. We are grateful to the St. Joe Land and Development Co., and its manager, Steve Lathrop, for access to the study site. C.J.D. was supported in part by a fellowship from the National Science Foundation and by a fellowship from the University of Georgia Graduate School. This work was supported by NSF grants DEB 8920710 (to W.R.T.) and IBN 9317853 (to W.R.T.), and by the Georgia Agricultural Experiment Station of the University of Georgia (to K. G. Ross).

REFERENCES

- Adams ES, Tschinkel WR, 1995. Effects of foundress number on brood raids and queen survival in the fire ant *Solenopsis invicta*. *Behav Ecol Sociobiol* 37:233–242.
- Bourke AFG, Franks NR, 1995. *Social evolution in ants*. Princeton, New Jersey: Princeton University Press.
- Bourke AFG, Heinze J, 1994. The ecology of communal breeding: the case of multiple-queen leptothoracine ants. *Phil Trans R Soc Lond B* 345:359–372.
- Briese DT, 1983. Different modes of reproductive behavior (including a description of colony fission) in a species of *Chelaner* (Hymenoptera: Formicidae). *Insect Soc* 30:308–316.
- Cook JM, Crozier RH, 1995. Sex determination and population biology in the Hymenoptera. *Trends Ecol Evol* 10:281–286.
- Crozier RH, Pamilo P, 1996. *Evolution of social insect colonies*. Oxford: Oxford University Press.
- Efron B, and Tibshirani R, 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat Sci* 1:54–77.
- Elmes GW, 1973. Observations on the density of queens in natural colonies of *Myrmica rubra* L. (Hymenoptera: Formicidae). *J Anim Ecol* 42:761–771.
- Fletcher DJC, 1986. Triple action of queen pheromones in the regulation of reproduction in fire ant (*Solenopsis invicta*) colonies. In: *Advances in invertebrate reproduction*, vol 4 (Porchet M, Andries JC, Dhainaut A, eds). Amsterdam: Elsevier; 305–316.
- Fletcher DJC, Blum MS, 1981. Pheromonal control of dealation and oogenesis in virgin fire ant queens. *Science* 212:73–75.
- Fletcher DJC, Ross KG, 1985. Regulation of reproduction in eusocial Hymenoptera. *Annu Rev Entomol* 30:319–345.
- Goodisman MAD, Ross KG, 1997. Relationship of queen number and queen relatedness in multiple-queen colonies of the fire ant *Solenopsis invicta*. *Ecol Entomol* 22:150–157.
- Hamilton WD, 1964. The genetical evolution of social behavior. II. *J Theor Biol* 7:17–52.
- Heinze J, 1993. Habitat structure, dispersal strategies, and queen number in two boreal *Leptothorax* ants. *Oecologia* 96:32–39.
- Heinze J, Tautz K, 1995. Ant reproductive strategies. *Res Popul Ecol* 37:135–149.
- Herbers JM, 1993. Ecological determinants of queen number in ants. In *Queen number and sociality in insects* (Keller L, ed). Oxford: Oxford University Press; 262–293.
- Hölldobler B, Wilson EO, 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften* 64:8–15.
- Hung ACF, Vinson SB, Summerlin JW, 1974. Male sterility in the red imported fire ant, *Solenopsis invicta*. *Ann Entomol Soc Am* 67:909–912.
- Keller L (ed), 1993. *Queen number and sociality in insects*. Oxford: Oxford University Press.
- Keller L, 1995. Social life: the paradox of multiple-queen colonies. *Trends Ecol Evol* 10:355–360.
- 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, 1993. Phenotypic plasticity and “cultural transmission” of alternative social organizations in the fire ant *Solenopsis invicta*. *Behav Ecol Sociobiol* 33:121–129.
- Markin GP, Diller JH, 1971. The seasonal life cycle of the imported fire ant, *Solenopsis saevissima richteri*, on the gulf coast of Mississippi. *Ann Entomol Soc Am* 64:562–565.
- McInnes DA, Tschinkel WR, 1995. Queen dimorphism and reproductive strategies in the fire ant *Solenopsis geminata* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 36:367–375.
- Morrill WL, 1974. Production and flight of alate red imported fire ants. *Environ Entomol* 3:265–271.
- Nonacs P, 1988. Queen number in colonies of social Hymenoptera as a kin-selected adaptation. *Evolution* 40:199–204.
- Nonacs P, 1993. The effects of polygyny and colony life history on optimal sex investment. In: *Queen number and sociality in insects* (Keller L, ed). Oxford: Oxford University Press; 110–131.
- Pamilo P, 1991a. The evolution of colony characteristics in social insects. II. Number of reproductive individuals. *Am Nat* 138:412–433.
- Pamilo P, 1991b. Life span of queens in the ant *Formica exsecta*. *Insect Soc* 38:111–119.
- Porter SD, 1992. Frequency and distribution of polygyne fire ants (Hymenoptera: Formicidae) in Florida. *Fla Entomol* 75:248–257.
- Porter SD, Van Eimeren B, Gilbert LE, 1988. Invasion of fire ants (Hymenoptera, Formicidae): microgeography and competitive replacement. *Ann Entomol Soc Am* 81:777–781.
- Rosengren R, Sundström L, Fortelius W, 1993. Monogyny and polygyny in *Formica* ants: the result of alternative dispersal tactics. In: *Queen number and sociality in insects* (Keller L, ed). Oxford: Oxford University Press; 308–333.
- Ross KG, 1993. The breeding system of the fire ant *Solenopsis invicta* effects on colony genetic structure. *Am Nat* 141:554–576.
- Ross KG, 1997. Multilocus evolution in fire ants: effects of selection, gene flow, and recombination. *Genetics* 145:961–974.
- Ross KG, Carpenter JM, 1991. Phylogenetic analysis and the evolution of queen number in eusocial Hymenoptera. *J Evol Biol* 4:117–130.
- Ross KG, Fletcher DJC, 1985. Genetic origin of male diploidy in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae), and its evolutionary significance. *Evolution* 39:888–903.
- Ross KG, Fletcher DJC, 1986. Diploid male production - a significant colony mortality factor in the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav Ecol Sociobiol* 19:283–291.
- Ross KG, Keller L, 1995. Ecology and evolution of social organization: insights from fire ants and other highly eusocial insects. *Annu Rev Ecol Syst* 26:651–656.
- Ross KG, Vargo EL, Keller L, Trager JC, 1993. Effect of a founder event on variation in the genetic sex-determining system of the fire ant *Solenopsis invicta*. *Genetics* 135:843–854.
- Seppä P, 1994. Sociogenetic organization of the ants *Myrmica ruginodis* and *Myrmica lobicornis*: Number, relatedness and longevity of reproducing individuals. *J Evol Biol* 7:71–95.
- Shoemaker DD, Costa JT III, Ross KG (1992) Estimates of heterozygosity in two social insects using a large number of electrophoretic markers. *Heredity* 69:573–582.
- Sinervo B, Lively CM, 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* 380:240–243.
- Sundström L, 1995. Dispersal polymorphism and physiological condition of males and females in the ant, *Formica truncorum*. *Behav Ecol* 6:132–139.
- Sundström L, 1997. Queen acceptance and nestmate recognition in monogyne and polygyne colonies of the ant *Formica truncorum*. *Anim Behav* 53:499–510.
- Tschinkel WR, 1987a. Fire ant queen longevity and age: estimation by sperm depletion. *Ann Entomol Soc Am* 80:263–266.
- Tschinkel WR, 1987b. Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in northern Florida in relation to habitat and disturbance. *Ann Entomol Soc Am* 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 invicta* during one annual cycle. *Ecol Monogr* 63:425–457.
- Tschinkel WR, 1996. A newly-discovered mode of colony founding among fire ants. *Insect Soc* 43:267–276.
- Tschinkel WR, Howard DF, 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. *Behav Ecol Sociobiol* 3:297–310.
- Vargo EL, Porter SD, 1993. Reproduction by virgin queen fire ants in queenless colonies: comparative study of three taxa (*Solenopsis richteri*, hybrid *S. invicta/richteri*, *S. geminata*) (Hymenoptera: Formicidae). *Insect Soc* 40:283–293.
- West-Eberhard MJ, 1986. Alternative adaptations, speciation, and phylogeny (a review). *Proc Natl Acad Sci USA* 83:1388–1392.