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Queen Dispersal Strategies in the Multiple-Queen Form of the Fire Ant *Solenopsis invicta*

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abstract: Newly produced queens in the multiple-queen (polygyne) form of the fire ant *Solenopsis invicta* show dramatic variation in dispersal patterns, and this variation is influenced by genotypic variation at a single locus associated with the genetic marker *Gp-9*. Heavy, homozygous $Gp\text{-}9^{BB}$ queens exhibit the highest vagility among polygyne queens and are strongly attracted to the open, disturbed-habitat patches that characteristically attract queens of the single-queen (monogyne) form (all of which possess genotype $Gp\text{-}9^{BB}$). Intermediate weight, heterozygous $Gp\text{-}9^{Bb}$ queens exhibit a mixed dispersal strategy: some remain in the area near their natal nest, while others disperse to land in the same disturbed-habitat patches as $Gp\text{-}9^{BB}$ queens. Light, homozygous $Gp\text{-}9^{bb}$ queens appear to lack the energy reserves needed to take part in mating flights in substantial numbers. Most queens that disperse from their natal nest site apparently fail to infiltrate mature nests to reproduce. However, consistent with the expectations of game-theoretical models for the evolution of dispersal, the low realized success of dispersing queens does not prevent relatively large numbers of them from dispersing. Furthermore, the results presented here are consistent with the hypothesis that the reproductive syndrome that characterizes polygyny in *S. invicta* is largely controlled by a single locus.

Keywords: alternative reproductive strategies, dispersal, social organization, gene flow, polygyny, fire ants.

Dispersal is a trait that has far-reaching repercussions on the ecology and evolution of organisms at nearly every level of biological organization. Not only is knowledge of dispersal strategies important for understanding the reproductive strategies of individuals (Julliard et al. 1996; O'Riain et al. 1996; Olsson et al. 1997), but it also plays a critical role in understanding the distribution and abundance of organisms (Price 1984) and the genetic divergence between populations that can lead to population differentiation or speciation (Slatkin 1985; Latta et al. 1998). Dispersal may take on additional significance in social systems, where the decision to forgo dispersal leads to opportunities for interaction with close relatives. Thus, in cooperatively breeding birds it is the philopatric offspring that become helpers at the nest, and in multiple-queen insect societies it is predominantly the philopatric queens that are recruited into nests as additional reproductives (Bourke and Franks 1995; Keller 1995; Crozier and Pamilo 1996).

An important goal in the study of dispersal is to understand the proximate causes of differences in dispersal behavior (Harrison 1980; Roff 1986; Nunes and Holekamp 1996; Lurz et al. 1997; Zera and Denno 1997), as this may provide insights into how individuals or populations respond to changing ecological selection pressures. In ants, variation in the dispersal strategies of newly produced queens is relatively common and is often associated with variation in the social organization of colonies. Single-queen (monogyne) colonies of ants produce new queens that tend to have large energy reserves and strong flight capabilities (Keller and Passera 1989; Passera and Keller 1990; Stille 1996). These new queens disperse from their natal nest during mating flights, after which they mobilize stored energy reserves to initiate reproduction independent of worker assistance (Hölldobler and Wilson 1977). In contrast, multiple-queen (polygyne) colonies tend to produce new queens with few energy reserves and weaker flight capabilities (Keller and Passera 1989; Passera and Keller 1990; Stille 1996). These queens not only tend to mate in or close to their natal nest (Ross and Keller 1995) but also generally initiate reproduction within their natal nest, as evidenced by the generally significant relatedness values among nest mate queens (Bourke and Franks 1995;

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Keller 1995; Crozier and Pamilo 1996), or perhaps within nests in the local subpopulation, as suggested by significant population viscosity often found in polygyne populations (Pamilo 1983, Chapuisat et al. 1997). Although the addition of supernumerary queens results in the lowering of average relatedness among nest mates, the adoption of related queens into nests can be favored under some selection regimes, particularly when queens that disperse away from their natal nest are rarely successful in founding their own nest (Herbers 1993; Bourke and Heinze 1994; Seppä et al. 1995). Since the adoption of supernumerary related queens into the nest must be linked to the adoption of alternative dispersal strategies by newly produced queens, understanding the proximate forces that lead to changes in queen dispersal strategies might lend insights into how ant populations change fundamental aspects of their colony social organization.

In this study, we investigate the dispersal strategies of new queens in a North American population of the polygyne form of the fire ant *Solenopsis invicta*. Until recently, most population genetic and behavioral data from this ant had given few indications that polygyne *S. invicta* queens exhibit dispersal strategies any different from their monogyne counterparts, in contrast to theoretical expectations. Like monogyne queens, polygyne queens appear to mate on the wing in massed mating flights (Glancey and Lofgren 1988), and nest mate reproductive queens are, on average, unrelated to one another (Ross 1993; Ross and Keller 1995; Goodisman and Ross 1997). Neither of these observations suggest that newly produced queens might exhibit philopatry toward their natal nest or subpopulation. However, Porter (1991) documented, using mark-recapture techniques, that at least some new queens from polygyne colonies reproduce in their natal nest, and recent studies using mitochondrial DNA (mtDNA) markers, which are especially useful for detecting limited female dispersal, revealed strong differentiation between subpopulations of an extensive polygyne population of *S. invicta* (Shoemaker and Ross 1996; Ross and Shoemaker 1997; Goodisman and Ross 1998). These two observations indicate that colonies predominantly recruit new queens from either their own (Porter 1991) or nearby nests (Goodisman and Ross 1998). Thus, there is good reason to believe that polygyne queens of *S. invicta* exhibit philopatry toward either their natal nest or their local subpopulation, but conclusive evidence of this is currently lacking.

Although the significant relatedness, and thus limited dispersal, of polygyne queens in many other ant species is predicted by kin-selection models for the evolution of polygyny (Nonacs 1988, 1993; Bourke and Franks 1995; Crozier and Pamilo 1996), game-theory models for the evolution of dispersal suggest that a strategy of pure philopatry might not be evolutionarily stable. Indeed, most models that explore the evolution of dispersal have found that even when dispersing individuals have extremely low reproductive success, high levels of dispersal may still be favored under a fairly wide range of ecological conditions (Hamilton and May 1977; Frank 1986; Holt and McPeek 1996). These results suggest that some queens from polygyne ant colonies should disperse, even if dispersing queens stand little chance of reproducing. Such dispersal is especially likely to occur whenever many more new queens are produced than the colony would likely recruit as new reproductives (Nonacs 1993). We therefore might expect queens from many polygyne ant populations to exhibit dispersal polymorphisms, and behavioral data from several studies indicate that these polymorphisms may be fairly common (Briese 1983; Rosengren et al. 1993; Heinze and Tsuji 1995; Sundström 1995).

Solenopsis invicta provides an ideal system to examine dispersal strategies in polygyne queens for several reasons. Not only are the population genetics and basic biology of the system particularly well studied (Ross and Keller 1995), but we have reason to expect a priori the existence of a dispersal polymorphism based on the striking variation in the weights of newly produced queens (Keller and Ross 1993*a*, 1995). Since weight variation among new queens in other ants appears to be a strong predictor of their reproductive strategies (McInnes and Tschinkel 1995; Sundström 1995; DeHeer and Tschinkel 1998), the weight polymorphism found in polygyne *S. invicta* might also correlate with dispersal tendencies. Significantly, queen weights appear to be determined largely by genotype at a single locus, for which we have found a marker gene designated as *Gp-9*. Previous work attributed this weight variation to the enzyme locus *Pgm-3* (or a linked gene) (Keller and Ross 1993*a*, 1995), but subsequent analyses indicate that *Gp-9* is a much better predictor of queen weight in our study population (L. Keller, K. Ross, M. Goodisman, and C. DeHeer, unpublished data).

Other aspects of the natural history of this genetic polymorphism suggest a possible role for *Gp-9* in dispersal polymorphisms. The *Gp-9* genotype of a new queen determines whether or not she can successfully reproduce within a polygyne nest. Polygyne workers execute new queens of the heaviest class (those with genotype $Gp\text{-}9^{BB}$) if these attempt to initiate reproduction within polygyne nests, and many of these queens actually are killed before they can leave the nest on mating flights (Ross 1992; Keller and Ross 1993*a*; Ross and Shoemaker 1993). However, since these queens are close in weight to those produced in monogyne nests (Keller and Ross 1993*a*, 1995), they likely have sufficient energy reserves for dispersal and independent nest founding if they depart from the parent nest before workers attack them. In contrast, the lighter queens (those with genotypes $Gp\text{-}9^{Bb}$ and $Gp\text{-}9^{bb}$), which

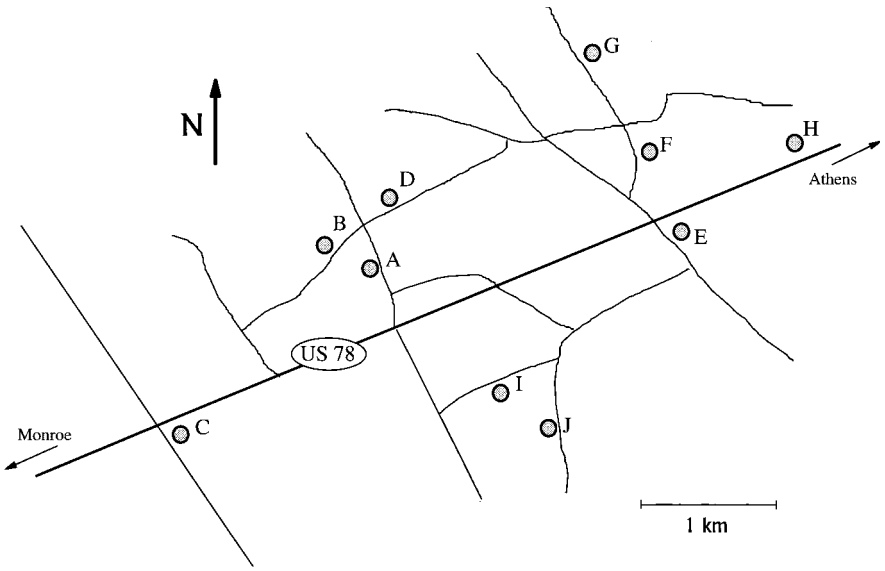

Figure 1: Map of the 10 sites within the polygyne study population in Walton County, Georgia, from which queens of *Solenopsis invicta* were collected. The numbers of queens collected at each site are given in the appendix, table A1.

make up the majority of new queens produced in polygyne nests, probably lack sufficient energy reserves for independent colony founding (Ross and Shoemaker 1993; see also Porter et al. 1988) and must therefore seek adoption into mature nests to reproduce. Indeed, the fact that nearly every reproductive queen in the polygyne form bears genotype *Gp-9*^{Bb}, whereas only *Gp-9*^{BB} queens head monogyne colonies, is consistent with the hypothesis that the two genotypic classes of queens utilize divergent dispersal and colony-founding strategies (Ross 1997; C. DeHeer, D. Shoemaker, and K. Ross, unpublished data; *Gp-9*^{bb} queens appear to die before becoming reproductives). Finally, strong among-site differentiation in mitochondrial haplotype frequencies of polygyne reproductive *Gp-9*^{Bb} queens (Shoemaker and Ross 1996; Goodisman and Ross 1998) indicates that polygyne nests recruit queens predominantly from the local subpopulation, as expected if many *Gp-9*^{Bb} queens exhibit reduced dispersal tendencies.

Methods

Collection of Queens

We collected queens on days of mating flights from 10 different sites within a polygyne population of *Solenopsis invicta* in Walton County, Georgia, during the spring and summer of 1996 and 1997. In this area of northern Georgia, colonies of the two social forms have a predominantly allopatric or parapatric distribution. Thus, we collected from an area containing only polygyne nests, but most colonies beyond a relatively narrow transition zone approximately 5 km away from our study sights contained only a single queen per nest. No two sites were separated by more than 5 km, and many sites were within 1 km or less of another site (fig. 1). All of the sites contained both numerous polygyne nests and an exposed plot of ground on which recently flown fire ant queens could be easily spotted and collected. Whenever possible, we collected queens at each site during three different stages of flight-related activity: as they aggregated on the tops of nests just before flight (Markin et al. 1971), as they flew on extended low-level flights in the vicinity of polygyne nests (M. Goodisman, C. DeHeer, and K. Ross, unpublished data), and as they landed on the ground following flight. We refer to these queens as preflight queens, low-flight queens, and postflight queens, respectively. We made multiple collections at some sites on different days or years (appendix, table A1). We collected no more than five preflight queens from the surface of each nest. Although sampling multiple queens from single nests may artificially inflate sample sizes because of nonindependence of virgin-queen genotypes, this effect will be extremely modest given that the effective queen number in polygyne nests is high (Ross 1993). The low-flight queens flew for more than several seconds at altitudes low enough to be captured from the ground with insect nets. Such behavior has not been described previously in fire ants; queens and males from the monogyne form appear to fly almost exclusively at altitudes of at least 30 m and up to 250 m (Markin et al. 1971). We describe this behavior and its implications for

the breeding biology of polygyne fire ants more fully elsewhere (M. Goodisman, C. DeHeer, and K. Ross, unpublished data). Postflight queens were captured as they walked on the soil surface after shedding their wings, but before they attempted excavation of a potential nest site. After capture, all queens were kept on wet ice in the field until they could be placed in an ultracold freezer (−70°C). We collected a total of 1,539 preflight queens, 617 low-flight queens, and 1,645 postflight queens (see appendix, table A1).

The exposed plots of ground from which we collected postflight queens were variable in both their size and surface composition. Their size ranged from ca. 200 m^2 to over 2,000 m^2, and their surfaces varied from black pavement to packed earth with sparse vegetation. Importantly, these same disturbed habitat types are highly attractive to dispersing monogyne queens, probably because they present large, reflective surfaces visible to queens flying at high altitudes (Vinson and Greenberg 1986).

Laboratory Procedures

We obtained the whole-body (wet) mass of each queen to the nearest 0.1 mg using an analytical balance. We dissected the abdomens of low-flight and postflight queens and observed their spermathecae in order to determine mating status. An opaque, turgid spermatheca indicates the presence of sperm and successful mating. We dissected a subset of preflight queens ($N = 40$) in order to confirm that mating had not occurred before queens flew.

We determined *Gp-9* genotypes from thoracic tissue of all queens by means of electrophoresis on 14% horizontal starch gels with a continuous buffer system (pH 8.6 tris-borate-EDTA). Gels were run at 300 V for 1 h, at which point the *Gp-9* bands had migrated ca. 25 mm. Horizontal slices of the gel were stained for 1 h in a nonspecific protein stain (0.05% Nigrosin and 0.05% Naphthol Blue Black dissolved in destain solution [a 1 : 4 : 5 ratio of acetic acid, water, and ethanol]), after which background staining was removed with repeated soaks in destain solution. The protein product of *Gp-9* behaves as a monomer, with the product of the *B* allele having a greater anodal mobility than the product of the *b* allele. Since *Gp-9* stains only with a general protein stain, it appears not to represent the product of any identified enzyme.

We isolated total DNA from queen heads with the Puregene DNA Isolation Kit using the protocol outlined in the manufacturer's instructions but excluding the RNase treatment step. A 4-kb portion of the mitochondrial DNA was PCR-amplified as in Ross and Shoemaker (1997), except that reactions were carried out in 15-μL volumes. We digested 10 μL of this PCR product with the restriction enzyme *Hin*fI, separated the digestion products on 1.5% agarose gels, stained them with ethidium bromide, and visualized the bands under UV light. Digestion with *Hin*fI discriminates the four haplotypes (A, B, C, and D) found in *S. invicta* populations from northern Georgia (Shoemaker and Ross 1996; Ross and Shoemaker 1997).

Table A1 in the appendix gives counts of queens with each *Gp-9* genotype and mtDNA haplotype for each sample.

Identification of Monogyne and Polygyne Queens

Although the nearest known monogyne colonies of *S. invicta* were several kilometers from our collection sites, this is not outside the potential dispersal distance of newly mated queens searching for landing sites (Markin et al. 1971). Therefore, some proportion of the postflight queens we collected may have been from monogyne colonies. We used the *Gp-9* and mtDNA genotypes to assign queens or groups of queens to either the monogyne or polygyne form. The marker *Gp-9* can be used to assign individual queens to one or the other social form because the $Gp\text{-}9^b$ allele is absent from the monogyne form locally but found in the majority of polygyne queens (Ross 1997). Any captured queen that has at least one copy of the $Gp\text{-}9^b$ allele must therefore originate from nests of the polygyne form.

The remaining low-flight or postflight queens, which bear the genotype $Gp\text{-}9^{BB}$, might originate from either the monogyne or the polygyne form (preflight queens were collected on the tops of polygyne nests). We used the strong mtDNA haplotype frequency differences found locally between the social forms (Shoemaker and Ross 1996; Ross and Shoemaker 1997) in conjunction with maximum likelihood methods to partition the postflight $Gp\text{-}9^{BB}$ queens at each site into those of monogyne and polygyne origin. We captured too few low-flight $Gp\text{-}9^{BB}$ queens to partition them in this manner, but the absence of diagnostic monogyne haplotypes among these queens suggests that most were from polygyne nests.

In essence, the maximum likelihood model estimates the migration rate of monogyne queens at each site independently of all other sites and independently of distance from the monogyne population. The estimated migration rate depended on the mtDNA haplotype frequencies in the nearby monogyne population, the haplotype frequencies in the surrounding polygyne population, and the observed haplotype frequencies in the $Gp\text{-}9^{BB}$ queens landing in the disturbed habitat patches. The model implicitly assumes that *Gp-9* genotype and mtDNA haplotype are independent within each social form.

We assumed that a proportion, m, of the postflight $Gp\text{-}9^{BB}$ queens in a given sample migrated into each collection site from the neighboring monogyne population, while the remaining fraction of queens, $1-m$, originated from po-

lygyne nests. If haplotypes A, B, C, and D are temporarily defined as haplotypes *1*, *2*, *3*, and *4*, then the frequency of haplotype *i* (*i* = *1* to *4*) in postflight queens from a given sample can be given by the expression $\bar{f}_i = mf_i^M + (1 - m)f_i^P$, where f_i^M and f_i^P correspond to the frequency of haplotype *i* in the monogyne and polygyne source populations, respectively. If N_i queens collected in a sample were of haplotype *i*, then the resulting likelihood equation is

$$L = C\prod_{i=1}^{4}(\bar{f}_i)^{N_i}, \tag{1}$$

where *C* is a multinomial constant. To find the maximum likelihood estimate (MLE) of *m*, first take the log of equation (1) to obtain the simpler log-likelihood equation, *S*. Taking the derivative of *S* with respect to *m* gives the equation

$$\frac{\delta S}{\delta m} = \sum_{i=1}^{4}\frac{N_i(f_i^M - f_i^P)}{\bar{f}_i}. \tag{2}$$

Setting equation (2) equal to zero and solving for the migration rate yields three real roots. The MLE for the proportion of *Gp-9*^{BB} queens that originated from the neighboring monogyne population ($\hat{m}$) equals the only root that lies in the interval (0, 1).

We used the program Mathematica to determine the MLEs of *m* for all samples using the above algorithm. We assumed f_i^M = 0.866, 0.114, 0, and 0.020 for *i* = *1*, *2*, *3*, and *4* (the frequencies of the four haplotypes in the local monogyne population [Shoemaker and Ross 1996; Ross and Shoemaker 1997]), and f_i^P = 0.240, 0.013, 0.747, and 0 for *i* = *1*, *2*, *3*, and *4* (the average haplotype frequencies found among preflight queens in this study). Other published values of f_i^P (e.g., Shoemaker and Ross 1996) yielded similar estimates of *m*. The number of *Gp-9*^{BB} queens that originated from the monogyne population was obtained by multiplying the unique MLE of *m* by the total number of *Gp-9*^{BB} postflight queens in each sample. Table A2 in the appendix gives the counts of *Gp-9*^{BB} queens that were assigned to each social form using the maximum likelihood model. Importantly, the model we used is conservative in the sense that it yielded the lowest proportion of *Gp-9*^{BB} queens that were assigned to the polygyne form.

General Predictions

The data that we generated allowed us to make two general types of comparisons that test the hypothesis that *Gp-9*^{BB} queens exhibit greater dispersal tendencies than *Gp-9*^{Bb} and *Gp-9*^{bb} queens. The first comparison relies on the observation that monogyne queens disperse relatively long distances (Markin et al. 1971) and become concentrated at landing sites that present large reflective surfaces to high-flying queens (parking lots, recently cleared land, etc. [Milio et al. 1988]). Their attraction to and concentration at these sites probably reflects both high vagility and habitat choice, since disturbed habitat is necessary for the successful establishment of new colonies. If polygyne *Gp-9*^{BB} queens exhibit reproductive strategies similar to monogyne queens, with both higher vagility than *Gp-9*^{Bb} and *Gp-9*^{bb} queens and attraction to disturbed habitat, then sites that characteristically attract the largest proportion of monogyne queens among all queens also should attract the largest proportion of polygyne *Gp-9*^{BB} queens among all polygyne queens. Furthermore, we expect polygyne *Gp-9*^{BB} queens to be overrepresented among postflight queens landing in the open, disturbed-habitat patches, relative to the proportion of queens with this genotype among preflight queens.

The second comparison to test the association between queen *Gp-9* genotype and dispersal tendencies relies on the observation that there is substantial among-site variation in the frequency of mtDNA haplotypes in the polygyne form (Shoemaker and Ross 1996; Ross and Shoemaker 1997; Goodisman and Ross 1998). Given this variation, we can reject the hypothesis of philopatry for any class of queens if their mtDNA haplotype frequency does not match that of preflight queens from the same site. Thus, if *Gp-9*^{Bb} and *Gp-9*^{bb} queens are strongly philopatric, we predict that the mtDNA haplotype frequencies of low-flight queens and postflight queens should match those of preflight queens from the same site. Unfortunately, we cannot use this same procedure to test for philopatry of *Gp-9*^{BB} polygyne queens since it is not possible to unequivocally assign individual queens with one of the common haplotypes (A) to the monogyne or polygyne form.

A related method of examining queen dispersal tendencies estimates the extent of mtDNA genetic structure using the analysis of molecular variance (AMOVA) approach developed by Excoffier et al. (1992) and implemented in the program WINAMOVA. This procedure yields an estimate of differentiation, Φ_{ST}, analogous to Wright's F_{ST}. Previous studies of differentiation in this polygyne population documented significant values of Φ_{ST} ranging from 0.503 to 0.136, depending on the spatial scale over which differentiation was studied (Shoemaker and Ross 1996; Ross and Shoemaker 1997; Goodisman and Ross 1998). Since the preflight queens are produced by reproductive queens that exhibit significant among-site haplotype differentiation, strong philopatry would be expected to maintain such differentiation in both the low-flight and postflight queens. Thus, if *Gp-9*^{Bb} and *Gp-9*^{bb}

queens exhibit strong philopatry, we should detect significant Φ_{ST} values for both low-flight and postflight queens with these genotypes.

Results

Phenotypic Effects of Gp-9

The weights of various classes of queens captured during flight-related activities are shown in figure 2. The *Gp-9*^{BB} queens with haplotype B were classified as monogyne queens since this haplotype is very rare in the polygyne form. Similarly, *Gp-9*^{BB} queens with haplotype C and queens with at least one copy of the *Gp-9*^{b} allele were classified as polygyne queens since these variants are absent in the local monogyne form. Although *Gp-9*^{BB} queens from the two social forms were relatively similar in weight, the monogyne queens weighed slightly but significantly more than the polygyne queens with this genotype (ANOVA; $P < .001$). Queens with genotype *Gp-9*^{Bb} weighed markedly less than *Gp-9*^{BB} queens of either social form, and *Gp-9*^{bb} queens weighed markedly less than queens of all other classes (ANOVA, Scheffé's test; $P < .001$). Because of the strong correlation between queen phenotype and reproductive strategy in other ants (Keller and Passera 1989; Rosengren et al. 1993; Sundström 1995), the phenotypic similarities between monogyne queens and polygyne *Gp-9*^{BB} queens suggest that they might show similar dispersal and reproductive strategies.

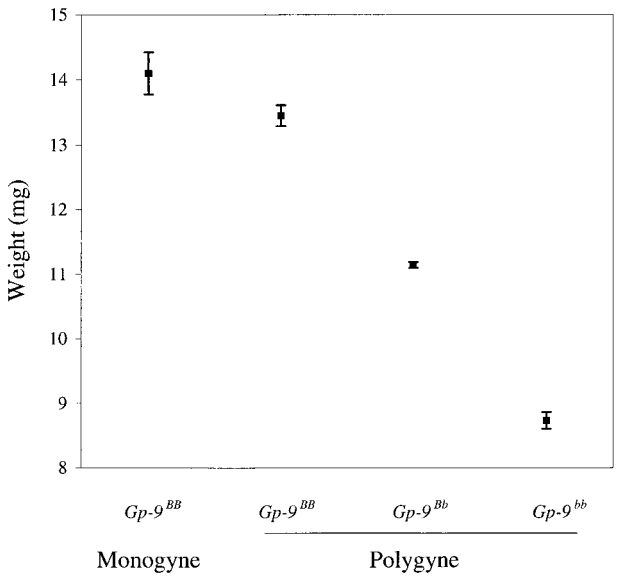

Figure 2: Weights of queens with different *Gp-9* genotypes (bars represent 95% confidence intervals about the mean). Only queens with diagnostic haplotypes were used in calculating the weights of *Gp-9*^{BB} queens from each social form (haplotype B for monogyne and haplotype C for polygyne queens).

Gp-9 *Genotypes of Queens in Flight-Related Activities*

Preflight Queens. The frequency of genotype *Gp-9*^{BB} among preflight polygyne queens was consistently low, never exceeding 0.070 and with a season-long average of 0.023 (e.g., fig. 3). This genotype is considerably underrepresented among preflight queens compared with its frequency in workers (0.407) and younger virgin queens (0.202) (Ross 1997). Although this low frequency is consistent with the hypothesis that polygyne workers kill many *Gp-9*^{BB} queens before they have the opportunity to leave the nest on mating flights (Keller and Ross 1993*a*; Ross et al. 1996*a*; Ross 1997), it also indicates that some do leave and thus have some prospect of reproductive success.

We found a surprisingly high frequency of *Gp-9*^{bb} queens leaving the nests on days of mating flights; almost one-fifth (0.187) of the total preflight queens possessed this genotype, and this value was not less than 0.042 for any sample (e.g., fig. 3). In contrast, a previous study from the same population found a frequency of this genotype of no more than 0.002 for any class of females (Ross 1997). We discuss possible reasons for this discrepancy below.

Low-Flight Queens. Virtually all low-flight queens (95.0%) possessed the genotype *Gp-9*^{Bb}, with this percentage varying only from 84% to 98% among the four samples of such queens. The average frequency of *Gp-9*^{BB} among low-flight queens is marginally significantly lower than the frequency of *Gp-9*^{BB} among preflight queens (considering only *Gp-9*^{BB} and *Gp-9*^{Bb} queens; *G*-test of heterogeneity: $G_1 = 3.70$, $P = .054$). It is unclear whether these low-flight *Gp-9*^{BB} queens represent rare *Gp-9*^{BB} queens that may attempt independent nest founding or nest infiltration close to home, or if they are simply queens that we captured soon after taking off from nests. Furthermore, the average frequency of *Gp-9*^{bb} among low-flight queens is highly significantly lower than among preflight queens (*G*-test: $G_1 = 99.59$, $P < .001$).

Postflight Queens. The open-habitat patches constituting each collecting site attracted large numbers of *Gp-9*^{Bb} (polygyne) queens and *Gp-9*^{BB} queens of both social forms (e.g., fig. 3; appendix, table A2). The *Gp-9* genotype distributions for each site on different days of the same year showed no significant heterogeneity and, therefore, were combined. Curiously, the *Gp-9* genotype distributions of postflight queens differed significantly between years for the two sites in which collections were made in multiple years (site A: *G*-test, $G_1 = 34.66$, $P < .001$; site E: *G*-test,

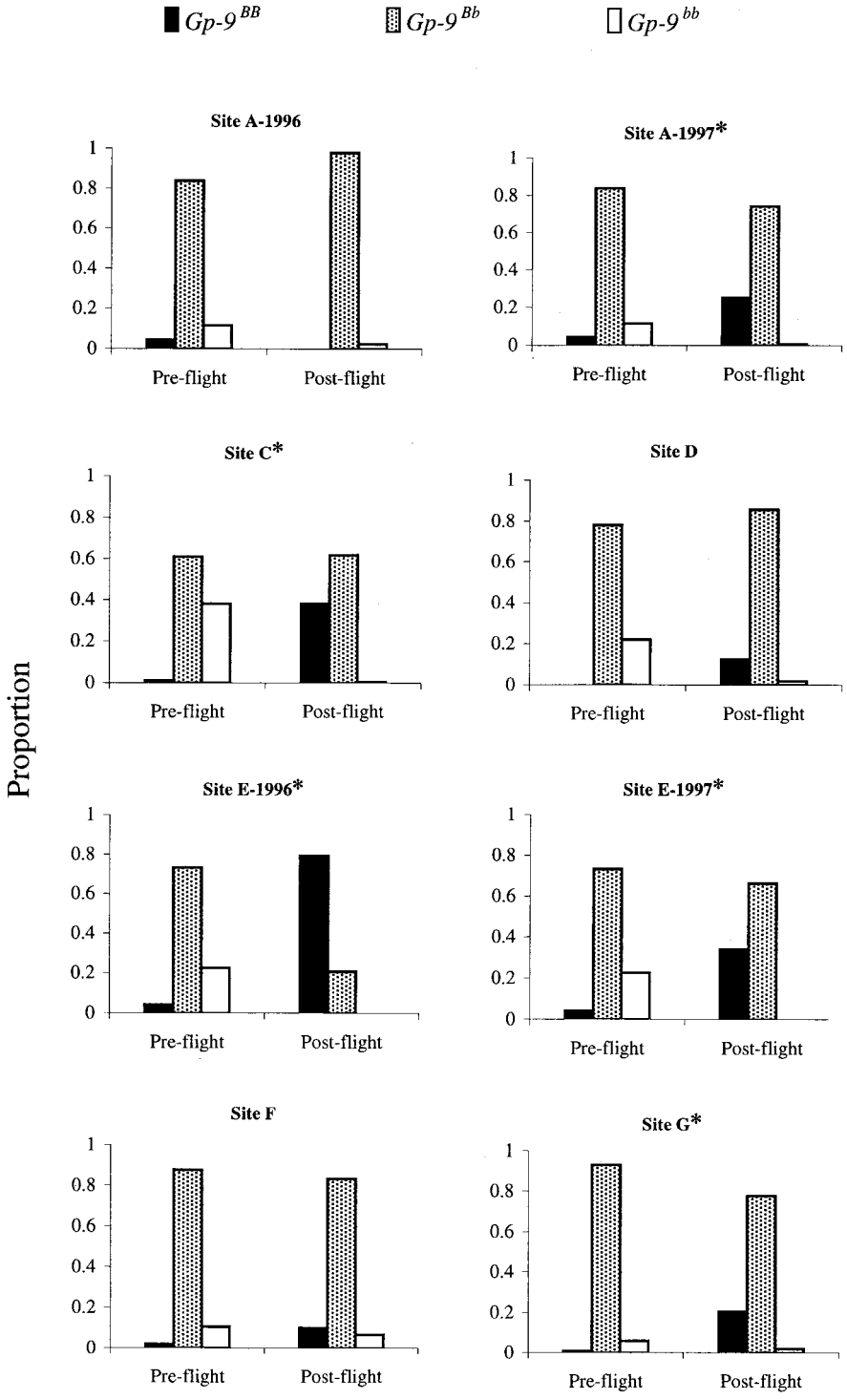

Figure 3: *Gp-9* genotype distributions for polygyne queens from eight samples in which both preflight and postflight queens were obtained. An asterisk indicates a sample with significant differences in *Gp-9* genotype distributions between preflight queens and postflight queens (considering only queens with genotypes $Gp\text{-}9^{BB}$ and $Gp\text{-}9^{Bb}$).

$G_1 = 14.62$, $P < .001$). We therefore separately considered data collected in different years from the same site.

If *Gp-9*^{BB} queens of the polygyne form disperse from their nest and attempt colony founding independent of workers (like monogyne queens), then we might expect polygyne *Gp-9*^{BB} queens to be attracted to the same open habitat patches that attract monogyne queens. We found strong support for this prediction. The proportion of *Gp-9*^{BB} queens among all polygyne queens was significantly correlated with the proportion of queens originating from the monogyne form in each sample (Spearman's rank correlation: $r_s = 0.9524$, $N = 8$, $P < .001$; fig. 4).

More importantly, the frequency of genotype *Gp-9*^{BB} among postflight polygyne queens landing on disturbed-habitat patches was substantially higher than among preflight queens. On average, 31.4% of polygyne postflight queens possessed genotype *Gp-9*^{BB}, more than an order of magnitude greater than the percentage of preflight queens with this genotype (average 2.3%). Although the excess of genotype *Gp-9*^{BB} among polygyne postflight queens can be partially explained by a deficit of *Gp-9*^{bb} postflight queens (ca. 0.9%, compared with 18.7% among preflight queens), *Gp-9*^{BB} polygyne queens are still greatly overrepresented among postflight queens, even when only the *Gp-9*^{BB} and *Gp-9*^{Bb} queens are considered (see fig. 3). Because preflight and postflight queens were collected on different days in some sites, the relevant frequency of *Gp-9*^{BB} among preflight queens may not have been obtained if there were temporal changes in its frequency. We therefore obtained the significance levels of the observed changes in *Gp-9*^{BB} frequency by comparing the frequency in postflight queens with the most conservative (highest) estimate of the frequency in preflight queens (0.070, from site A). Genotype *Gp-9*^{BB} showed a significant increase in frequency from preflight to postflight queens for five samples (site A, 1997: $G_1 = 11.1$, $P < .001$; site C: $G_1 = 30.7$, $P < .001$; site E, 1996: $G_1 = 45.3$, $P < .001$; site E, 1997: $G_1 = 21.3$, $P < .001$; site G: $G_1 = 6.9$, $P = .008$), although not for three other samples (site A, 1996: $G_1 = 5.1$, $P = .024$ [a deficiency of *Gp-9*^{BB} queens]; site D: $G_1 = 0.99$, $P = .32$; site F: $G_1 = 0.28$, $P = .60$). We suggest that this pattern results from both the greater vagility of polygyne *Gp-9*^{BB} queens and their greater attraction to open, disturbed landing sites, compared with *Gp-9*^{Bb} and *Gp-9*^{bb} queens. An alternate explanation is that *Gp-9*^{BB} queens are concentrated during postflight because they are more likely than *Gp-9*^{Bb} queens to take flight from the nest. However, this alone cannot explain the highly significant correlation in the percentage of monogyne and polygyne *Gp-9*^{BB} postflight queens in the same samples (fig. 4). This correlation suggests that *Gp-9*^{BB} polygyne queens exhibit dispersal tendencies comparable to those of monogyne *Gp-9*^{BB} queens.

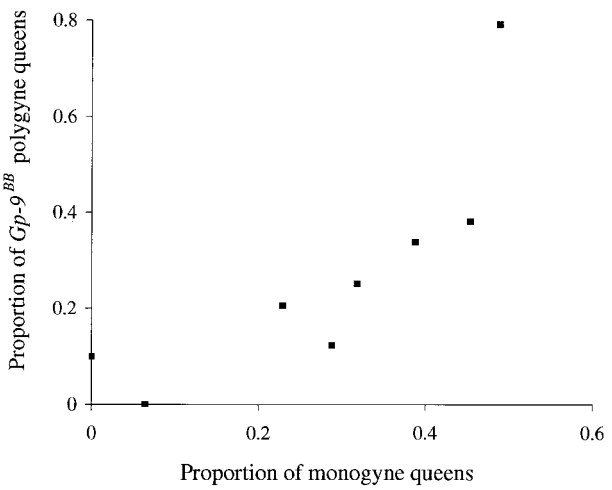

Figure 4: Relationship between the proportion of postflight monogyne queens and the proportion of postflight polygyne queens that possess genotype *Gp-9*^{BB} in a given sample.

mtDNA Haplotypes of Queens in Flight-Related Activities

Preflight Queens. We detected substantial variation in haplotype frequencies of preflight queens across sites (e.g., fig. 5). This among-site differentiation is highly significant using both a *G*-test of heterogeneity ($G_9 = 196.3$, $P < .001$) and an AMOVA ($\Phi_{ST} = 0.145$, $P < .001$).

Low-Flight Queens. As expected if low-flight queens exhibit philopatry, we also detected among-site differentiation in the haplotype frequencies of these queens using both a *G*-test of heterogeneity ($G_3 = 9.26$, $P = .026$) and an AMOVA ($\Phi_{ST} = 0.016$, $P = .016$). A direct comparison of haplotype distributions for low-flight queens and preflight queens from the same site provided further support for the hypothesis that low-flight queens often exhibit strong philopatry (fig. 5). In three of the four samples appropriate for testing (sites B, C, and D), no significant differences in haplotype distributions between preflight queens and low-flight queens were found ($G_2 = 2.68$, $P = .262$; $G_2 = 3.70$, $P = .157$; $G_2 = 0.06$, $P = .97$), although the difference was significant at site G ($G_2 = 8.37$, $P = .015$).

Postflight Queens. We combined the haplotype data from collections made at the same site within 10 d of one another. Although at one site (site C) there was significant heterogeneity in haplotype frequencies among days, pooling these samples did not alter the significance of our results. Because haplotype distributions are not significantly different between years at the same site (site A: $G_2 = 1.49$, $P = .475$; site E: $G_2 = 3.21$, $P = .200$), we combined these data for analyses of haplotype differentiation.

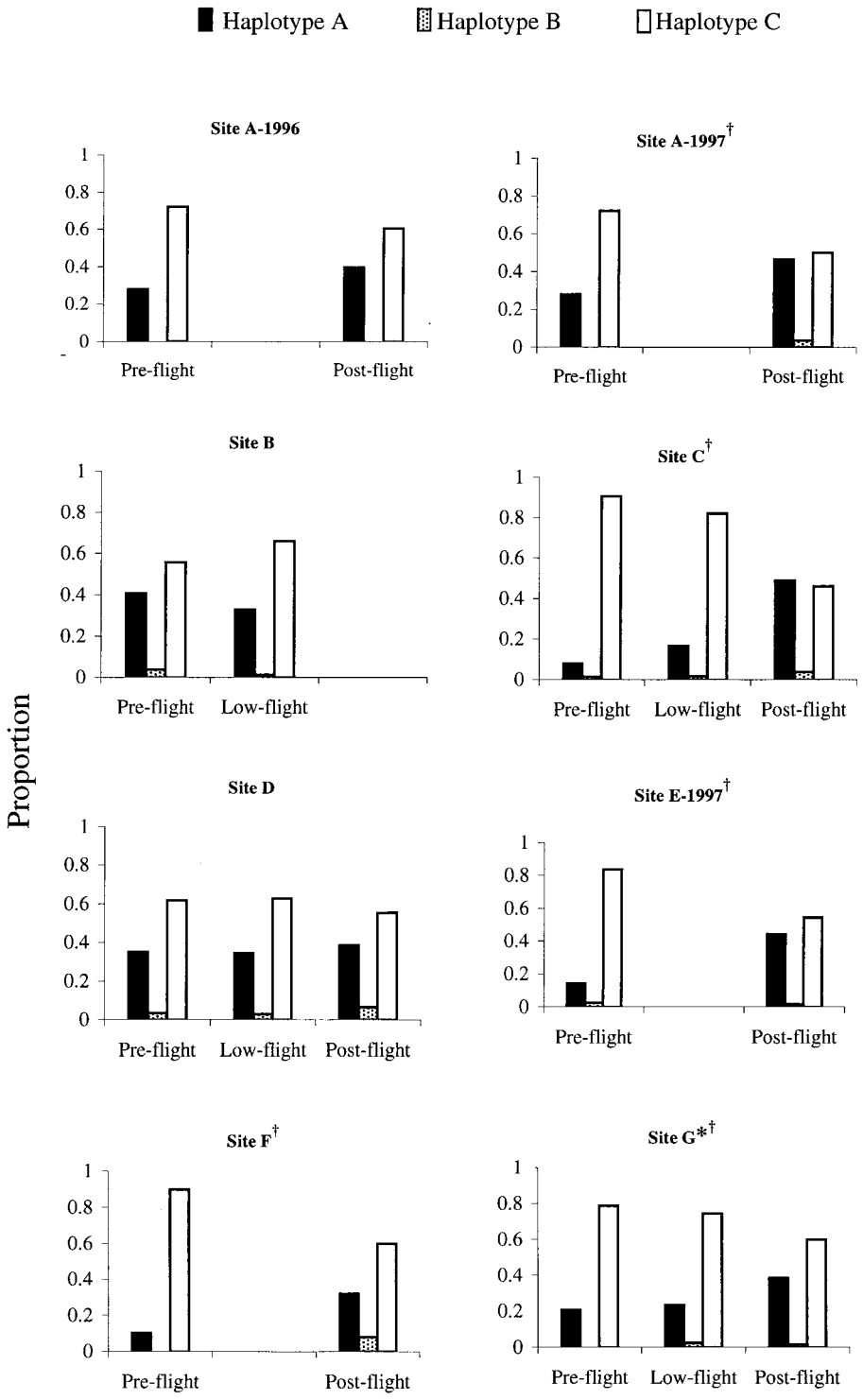

Figure 5: MtDNA haplotype distributions of *Gp-9*^{Bb} and *Gp-9*^{bb} queens for eight samples in which either low-flight or postflight queens were obtained in addition to preflight queens. An asterisk indicates a sample with significant differences in haplotype distributions between preflight queens and low-flight queens. A dagger indicates a sample with significant differences in haplotype distributions between preflight queens and postflight queens.

However, other analyses explicitly consider the mtDNA data from different years as independent data points because these sites attracted very different proportions of *Gp-9*^{BB} queens from one year to the next.

As expected if *Gp-9*^{BB} queens exhibit high vagility, they showed no among-site differentiation in haplotype frequencies ($G_{10} = 9.94$, $P = .446$; $\Phi_{ST} = 0.000$, $P = .381$). However, because many *Gp-9*^{BB} queens likely originated from monogyne nests, this lack of differentiation probably arises from the lack of genetic structure among mitochondrial haplotypes within the monogyne form (Shoemaker and Ross 1996; Ross and Shoemaker 1997). Unless dispersal was severely restricted among polygyne *Gp-9*^{BB} queens, we would likely have failed to detect significant mitochondrial structure using this approach because any signature of structure attributable to polygyne queens would be masked by immigrant monogyne queens.

Somewhat surprisingly, the *Gp-9*^{Bb} and *Gp-9*^{bb} postflight queens (pooled because of the rarity of *Gp-9*^{bb} queens) also showed no among-site differentiation ($G_{10} = 12.04$, $P = .282$; $\Phi_{ST} = 0.003$, $P = .220$). These results suggest that postflight polygyne queens with these genotypes landing on the open habitat patches usually immigrated from outside the site.

The hypothesis that all *Gp-9*^{Bb} and *Gp-9*^{bb} queens are philopatric also could be rejected by comparing the mtDNA haplotype frequencies of preflight and postflight queens with those genotypes (fig. 5). Haplotype distributions differ significantly between these queen classes in five samples (site A, 1997: $G_1 = 16.9$, $P < .001$; site C: $G_2 = 129.0$, $P < .001$; site E: $G_1 = 25.4$, $P < .001$; site F: $G_1 = 11.1$, $P < .001$; site G: $G_1 = 11.8$, $P < .001$), although not at two others (site A, 1996: $G_1 = 2.15$, $P = .143$; site D: $G_2 = 0.84$, $P = .657$). This pattern stands in contrast to the similarity in haplotype distributions between same-site preflight and low-flight queens (fig. 5). Curiously, deviations in haplotype frequencies between preflight and postflight queens are in the same direction at all six samples, with the C haplotype relatively underrepresented among postflight *Gp-9*^{Bb} and *Gp-9*^{bb} queens ($P = .008$; binomial test). However, this might be expected if many *Gp-9*^{Bb} and *Gp-9*^{bb} queens immigrated from outside the site, given that other sites in this polygyne population typically have lower frequencies of haplotype C than we observed at our sites (Ross and Shoemaker 1997).

If *Gp-9*^{Bb} and *Gp-9*^{bb} queens that land on open patches of ground were often, as we suggest, dispersing from outside the site, then we might expect these queens to be attracted to the same types of sites that attract dispersing monogyne and polygyne *Gp-9*^{BB} queens. We therefore predicted that samples that attract the greatest proportion of *Gp-9*^{BB} queens of both social forms should also attract a greater proportion of dispersing *Gp-9*^{Bb} and *Gp-9*^{bb} queens. We obtained a qualitative approximation of the latter value by calculating the *G*-statistic for haplotype differentiation between preflight and postflight queens in each sample. The *G*-statistic for this comparison (standardized to a single degree of freedom) should increase when the proportion of immigrating *Gp-9*^{Bb} and *Gp-9*^{bb} queens increases. As expected, the more attractive a site was to *Gp-9*^{BB} queens, the more the haplotype frequencies of postflight *Gp-9*^{Bb} and *Gp-9*^{bb} queens deviated from the haplotype frequencies of preflight queens (Spearman's rank correlation: $r_s = 0.893$, $N = 7$, $P = .003$). Thus, sites attractive to dispersing *Gp-9*^{BB} queens also were attractive to dispersing queens with the other genotypes.

Discussion

Results from this study indicate that dispersal strategies of newly produced queens in the polygyne form of *Solenopsis invicta* are more diverse than previously thought and are strongly influenced by their genotype at a single locus marked by *Gp-9*. Heavy queens, which possess the genotype *Gp-9*^{BB}, are attracted to open, disturbed habitat patches in great numbers following mating flights. The proportions of *Gp-9*^{BB} queens landing on these disturbed habitats are commonly an order of magnitude greater than the proportions found exiting nests in the vicinity on days of mating flights. We suggest that the greater representation of *Gp-9*^{BB} polygyne queens landing at these patches results from the greater likelihood that these queens fly relatively large distances from their natal nest, compared with *Gp-9*^{Bb} and *Gp-9*^{bb} queens. This high vagility, combined with attraction to open, disturbed habitat, concentrates polygyne *Gp-9*^{BB} queens in landing areas that are also attractive to dispersing monogyne queens, all of which possess genotype *Gp-9*^{BB}. Indeed, habitats that attract the greatest proportion of polygyne *Gp-9*^{BB} queens also attract the greatest proportion of monogyne queens, suggesting that their dispersal and habitat selection tendencies are very similar.

The high dispersal tendencies of *Gp-9*^{BB} queens may be expected given their limited reproductive opportunities within polygyne nests and large energy reserves. Polygyne workers kill all *Gp-9*^{BB} queens as they initiate reproduction within established nests (Ross 1992; Keller and Ross 1993*a*, 1998), but the weights of these queens suggest that they may possess sufficient energy reserves to rear many workers and successfully begin their own nest (independent colony founding). Indeed, polygyne *Gp-9*^{BB} queens weigh nearly as much as the independent-founding queens of the monogyne form and substantially more than both *Gp-9*^{Bb} and *Gp-9*^{bb} polygyne queens (fig. 2).

Independent-founding of new colonies by polygyne *Gp-9*^{BB} queens after a dispersal flight is probably rare, given

the strong mtDNA differentiation between the monogyne and polygyne forms as well as the apparent absence of the most common polygyne haplotype (haplotype C) from a well-studied monogyne population in northern Georgia (Shoemaker and Ross 1996; Ross and Shoemaker 1997). However, the distribution of haplotype C among other fire ant populations suggests that this mode of colony founding by polygyne *Gp-9*^{BB} queens might be successful occasionally. Although absent from most monogyne populations, haplotype C does occur at a relatively low frequency in two monogyne populations that have an old (20 yr or more) association with nearby polygyne populations in which this haplotype predominates (in central Texas and southern Mississippi; C. DeHeer, D. Shoemaker, and K. Ross, unpublished data).

Results from this study also suggest that *Gp-9*^{Bb} queens exhibit a mixed dispersal strategy. We find evidence of philopatry among low-flight queens that we captured (virtually all of which bear genotype *Gp-9*^{Bb}), as shown by the significant among-site haplotype differentiation in these queens and the similarity in haplotype frequencies between preflight and low-flight queens from the same samples. Importantly, low-flight queens usually have mated (M. Goodisman, C. DeHeer, and K. Ross, unpublished data), so that many of these queens appear to return to or remain in their natal site during postmating flight activity. However, there is also a hint of some wider dispersal at this stage. Not only is the magnitude of the among-site differentiation of low-flight queens nearly an order of magnitude smaller than that found in preflight queens (Φ_{ST} = 0.016, compared with 0.145), but haplotype distributions at one site are significantly different between preflight and low-flight queens. Thus, it is probable that a portion of the queens that we captured in flight immigrated from outside the site at which they were collected. The signal of philopatry in *Gp-9*^{Bb} queens completely disappears when considering postflight queens. We did not detect a significant pattern of among-site haplotype differentiation among landing *Gp-9*^{Bb} queens, and their haplotype distributions differ markedly from preflight queens from the same site. We therefore conclude that a substantial proportion of postflight *Gp-9*^{Bb} queens must have immigrated from outside the site at which they were collected.

The dispersal patterns of polygyne queens as inferred by this study are very different from the dispersal patterns of polygyne *S. invicta* queens inferred by previous studies. Young queens collected during flight activity yield either weak (for low-flight queens) or nonsignificant (for postflight queens) mitochondrial genetic structure, suggesting that these queens exhibit relatively high levels of dispersal. In contrast, mitochondrial genetic structure among reproductive queens within established nests is quite strong and appears to be stable over time, indicating that gene flow within polygyne populations is quite low (Shoemaker and Ross 1996; Ross and Shoemaker 1997; Goodisman and Ross 1998). These contrasting patterns of genetic structure can be reconciled if dispersing queens are less likely to reproduce successfully than philopatric queens. We suggest that this pattern of relatively high dispersal coupled with relatively low gene flow may be more common in polygyne ants than is generally appreciated, because dispersal without gene flow is likely to go undetected in surveys of genetic structure. Thus, although many polygyne populations exhibit significant microgeographic genetic structure and high nest mate–queen relatedness (Bourke and Franks 1995; Seppä and Pamilo 1995; Crozier and Pamilo 1996; Ross et al. 1996*b*; Chapuisat et al. 1997; Ross and Shoemaker 1997), behavioral evidence indicates that polygyne queens commonly exhibit polymorphic dispersal behavior, with some queens flying away from their nest for matings and initiation of reproduction (Rosengren et al. 1993; Sundström 1995; Chapuisat et al. 1997). We have demonstrated that dispersal by new queens of *S. invicta* is, in fact, substantially greater than has been inferred from studies of genetic structure. Thus, even though effective dispersal (resulting in gene flow) is fairly low in this population, dispersal may nonetheless be a relatively common behavioral strategy. These results are in general agreement with models for the evolution of dispersal, which suggest that dispersal should be a common strategy under a wide range of ecological conditions, even when the expected reproductive success of dispersing individuals (and thus gene flow) is low (Hamilton and May 1977; Johnson and Gaines 1990).

The contrasting patterns of among-site mtDNA differentiation that we find between *Gp-9*^{Bb} queens engaged in different reproductive activities allow us to make inferences both about the recruitment of newly mated queens into mature nests of *S. invicta* and about possible variation in the reproductive strategies of *Gp-9*^{Bb} queens. Compared with mtDNA genetic structure among reproductive queens, structure among young queens potentially seeking adoption into nests is either weak (low-flight queens) or nonexistent (postflight queens). To maintain the observed level of among-site genetic structure in reproductive queens in the face of relatively widespread movement of queens during mating flights, workers must discriminate against non–nest mate queens or against queens from outside their subpopulation when they adopt newly mated queens into the nest. Although these findings are consistent with a mark-recapture study indicating that recruitment of newly mated nest mate queens must occur at least occasionally in North American populations (Porter 1991), several studies using both nuclear and mtDNA markers have failed to find the genetic signature (significant, positive nest mate queen relatedness) of nest mate

queen recruitment in these populations (Ross 1993; Goodisman and Ross 1997, 1998). These apparent discrepancies may result from either a combination of nest mate and non–nest mate (but mostly site mate) queen recruitment, or from the existence of additional mechanisms of queen recruitment in polygyne nests that lower relatedness among reproductive queens (such as movement of mature queens between nests or founding of new polygyne nests by cooperative groups of newly mated polygyne queens).

Given that selection may favor relatively high levels of dispersal under many ecological conditions, even if the prospects for successful reproduction are low (Hamilton and May 1977; Johnson and Gaines 1990), it is not surprising that many *Gp-9*^{Bb} queens disperse to other sites even though they are unsuccessful at infiltrating mature nests. However, the correlation that we find between the proportion of *Gp-9*^{BB} queens attracted to a site and the inferred proportion of dispersing *Gp-9*^{Bb} queens attracted to the same site suggests that these *Gp-9*^{Bb} queens use the same rules as monogyne queens in choosing landing sites. The implication of this is that the large numbers of dispersing *Gp-9*^{Bb} queens attracted to open, disturbed habitats may disperse not to find mature nests to infiltrate but, rather, to found new colonies in the same manner as monogyne queens (independently of worker aid). Although their low weights suggest that most polygyne *Gp-9*^{Bb} queens are probably poor solitary (haplometrotic) nest founders (Porter et al. 1988), these queens might succeed more readily in cooperative (pleometrotic) colony-founding groups. Furthermore, although colonies cooperatively founded by multiple monogyne (*Gp-9*^{BB}) queens are invariably reduced to a single queen (Markin et al. 1972; Tschinkel and Howard 1983), colonies founded cooperatively by *Gp-9*^{Bb} queens may remain polygynous (primary polygyny) since colonies containing workers with at least one copy of the *Gp-9*^{b} allele are tolerant of multiple egg-laying queens (Ross and Keller 1998).

In contrast to queens of the other *Gp-9* genotypes, *Gp-9*^{bb} queens appear to only rarely fly from their natal nest. In spite of the relative abundance of such queens aggregating on top of nests on days of mating flights (18.7%), these queens were relatively rare both in low altitude flights (3.7%) and landing on the disturbed patches of ground (0.9%). Although the apparent lack of a mating flight by *Gp-9*^{bb} queens is characteristic of the extreme philopatry found in many polygyne ant societies (where mating occurs in or on natal nests), there is no evidence for this in polygyne *S. invicta*. Copulation has never been described in the immediate vicinity of nests, and *Gp-9*^{bb} queens are exceedingly rare as functional egg-laying queens (Ross 1997). The apparent incompetence of *Gp-9*^{bb} queens during mating flights and as reproductive queens might stem from their extreme phenotype. The *Gp-9*^{bb} queens weigh only 8.7 mg at maturity, significantly less than the average for all newly eclosed queens of the polygyne form (9.3 ± 0.02 mg; Keller and Ross 1993*b*) (*t*-test, $t = 3.961$, $N = 67$, $P < .001$). Since most maturing *S. invicta* queens gain substantial weight in the form of fat and glycogen reserves to support flight and oogenesis (Keller and Ross 1993*b*), the inability of *Gp-9*^{bb} queens to take flight or initiate reproduction might stem from their failure to acquire minimal threshold levels of these crucial energy reserves after eclosion.

The distribution of allele *Gp-9*^{b} within and between the social forms in *S. invicta* has led Ross and Shoemaker (1997) to hypothesize that either *Gp-9*^{b} or a linked allele is required for the expression of polygyny. The expression of polygyny manifests itself in two complementary ways: in the queen-recruitment strategies of workers and the reproductive strategies of new queens. Under the currently accepted ecological constraints model for the evolution of polygyny (Heinze 1993; Rosengren et al. 1993; Bourke and Heinze 1994; Keller 1995), monogyne colonies become polygyne when workers accept related supernumerary queens, a phenomenon that requires extremely limited queen dispersal. Both of these conditions for polygyny appear to be mediated by a simple genetic polymorphism in introduced *S. invicta* populations. Only colonies in which some workers possess at least one copy of the *Gp-9*^{b} allele will accept multiple queens (Ross and Keller 1998). The results from this study further suggest that dispersal strategies of queens are determined at least in part by *Gp-9* genotype, with many *Gp-9*^{Bb} queens showing limited dispersal, and *Gp-9*^{BB} queens generally showing high dispersal. Thus the genetic and reproductive differences seen between the two social forms of *S. invicta* are paralleled within the polygyne form, consistent with the hypothesis that genetic variation at *Gp-9* (or a linked gene) is necessary for the expression of polygyny.

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APPENDIX

Table A1: Numbers of queens collected at each site during each stage of flight-related activity

	BB			*Bb*			*bb*			
Site, behavior, and date	A	B	C	A	B	C	A	B	C	Total
A:										
Preflight:										
May 20, 1997	4	0	1	27	0	36	0	0	3	71
May 26, 1997	0	0	1	11	0	41	0	0	8	64
May 31, 1997	0	0	6	32	0	80	2	0	15	138
Postflight:										
July 14, 1996	3	0	0	15	0	23	0	0	0	47
May 26, 1997	69	11	34	53	4	57	1	0	0	233
B:										
Preflight:										
May 20, 1997	1	0	1	18	2	27	3	0	1	55
Low-flight:										
May 20, 1997	1	0	0	20	1	26	0	0	1	50
May 26, 1997	0	0	0	30	1	77	2	0	4	116
C:										
Preflight:										
May 31, 1997	0	0	3	12	3	146	9	1	83	257
Low-flight:										
May 26, 1997	0	0	0	4	1	12	0	0	0	17
June 3, 1997	0	0	0	6	0	37	0	0	1	44
Postflight:										
May 20, 1997	23	3	7	9	0	8	0	0	0	50
May 25, 1997	13	3	4	2	0	5	0	0	0	28
May 26, 1997	43	12	13	9	4	14	0	0	0	98
May 31, 1997	284	11	113	110	6	95	0	0	1	620
D:										
Preflight:										
June 3, 1997	0	0	0	21	3	43	9	0	10	91
Low-flight:										
May 26, 1997	3	0	2	19	2	38	2	0	4	70
Postflight:										
May 26, 1997	21	3	6	18	3	26	0	0	1	80
E:										
Preflight:										
June 2, 1997	0	0	1	0	0	17	0	0	15	33
June 3, 1997	0	0	9	23	3	126	7	1	26	208
Postflight:										
July 14, 1996	24	3	15	2	0	3	0	0	0	47
May 26, 1997	74	8	31	30	1	37	0	0	0	188
F:										
Preflight:										
June 3, 1997	1	0	1	8	0	84	2	0	9	105
Postflight:										
June 3, 1997	1	0	2	8	2	15	1	0	0	30
G:										
Preflight:										
June 13, 1997	0	0	1	18	0	70	1	0	3	105
June 19, 1997	0	0	3	26	0	85	3	0	10	135
Low-flight:										
June 19, 1997	2	0	0	64	7	214	3	0	5	314

Table A1 (*Continued*)

	BB			*Bb*			*bb*			
Site, behavior, and date	A	B	C	A	B	C	A	B	C	Total
Postflight:										
June 13, 1997	6	0	4	6	0	12	0	0	0	28
June 19, 1997	43	3	22	40	2	60	0	0	3	173
H:										
Preflight:										
June 13, 1997	0	0	0	41	1	5	6	0	0	56
I:										
Preflight:										
June 13, 1997	0	0	0	33	3	51	9	0	7	103
J:										
Preflight:										
June 13, 1997	0	0	0	22	0	45	10	0	12	90

Note: Broken down by *Gp-9* genotype (*BB*, *Bb*, *bb*), and mtDNA haplotype (A, B, C).

Table A2: Numbers of $Gp\text{-}9^{BB}$ postflight queens of the monogyne and polygyne forms

Site and date	Monogyne	Polygyne
A:		
July 1996	3	0
May 1997	74	40
C:		
May 1997	362	166
D:		
May 1997	23	7
E:		
July 1996	23	19
June 1997	73	39
F:		
June 1997	0	3
G:		
June 1997	46	32

Note: The maximum likelihood methods were used to estimate how many queens came from each social form.

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