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ECOLOGY AND EVOLUTION OF SOCIAL ORGANIZATION: Insights from Fire Ants and Other Highly Eusocial Insects

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ABSTRACT

Social organisms exhibit conspicuous intraspecific variation in all facets of their social organization. A prominent example of such variation in the highly eusocial Hymenoptera is differences in the number of reproductive queens per colony. Differences in queen number in ants are associated with differences in a host of reproductive and social traits, including queen phenotype and breeding strategy, mode of colony reproduction, and pattern of sex allocation. We examine the causes and consequences of changes in colony queen number and associated traits using the fire ant *Solenopsis invicta* as a principal model. Ecological constraints on mode of colony founding may act as important selective forces causing the evolution of queen number in this and many other ants, with social organization generally perpetuated across generations by means of the social environment molding appropriate queen phenotypes and reproductive strategies. Shifts in colony queen number have profound effects on genetic structure within nests and may also influence genetic structure at higher levels (aggregations of nests or local demes) because of the association of queen number with particular mating and dispersal habits. Divergence of breeding habits between populations with different social organizations has

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the potential to promote genetic differentiation between these social variants. Thus, evolution of social organization can be important in generating intrinsic selective regimes that channel subsequent social evolution and in initiating the development of significant population genetic structure, including barriers to gene flow important in cladogenesis.

INTRODUCTION

Social organization refers to the number of individuals in a social group, their behavioral and genetic relationships, and the way in which reproduction is partitioned among them. Social organization comprises the most fundamental defining features of animal societies, forged by ecological and social selection acting over the history of a population, and creating social and genetic environments that govern the course of subsequent social evolution (1, 80, 97, 143, 177).

It has become increasingly evident over the past decade that social organization varies not only among species but also within species or even populations. Striking variation in group composition and in the partitioning of reproduction among group members is proving to be the rule rather than the exception in a wide array of social vertebrate and insect species (74a, 75, 148, 150, 183). Such variation raises two sets of issues with broad ecological and evolutionary implications. The first set relates to the underlying causes. Variation in social organization is the product of diverse extrinsic selection pressures generated by the local ecology that interact with intrinsic selection pressures related to competitive and cooperative interactions among group members (1, 75, 121, 123). Thus, studies of variation in social organization may shed light on how ecological and social factors jointly influence the course of social evolution.

The second set of issues relates to the consequences of variation in social organization for the evolution of individual phenotypes and patterns of gene flow. Alternative phenotypes associated with variation in social organization differ in fitness according to ecological and social context. The mechanism for regulating their production may include a genetic component (18, 51, 182), or it may involve phenotypic plasticity (151), with the social environment inducing expression of the appropriate phenotype (77, 78, 107). In either case, differing reproductive habits of the alternative phenotypes may incidentally inhibit interbreeding between them, allowing accumulating genetic differentiation and the eventual incorporation of a genetic basis to phenotypic expression. Thus, studies of variation in social organization are relevant to understanding how phenotypic responses to ecological and social selection mediate population genetic divergence (176, 178, 179).

Eusocial insects exhibit enormous variation in virtually all elements of social organization (11, 35, 37a, 74a, 80, 148, 180) and thus are ideal subjects for studying the causes and consequences of its evolution. Variation in colony queen number, one conspicuous element of social organization, assumes special significance with respect to the issues raised above. Queen number apparently responds to variation in local ecological selection pressures and, in turn, influences the intrinsic selective milieu of a society by shaping within-nest genetic structure (e.g. 7, 11, 12, 68, 75, 120, 123, 143, 157). Moreover, variation in queen number often is associated with parallel variation in other reproductive traits, illustrating concerted phenotypic responses to ecological and social selection (66). For instance, in ants, the presence of a single queen per colony (*monogyny*) typically is associated with colony reproduction by the emission of sexuals, mating away from the nest following flight, extensive queen dispersal, and independent colony founding by queens (no assistance from workers). In contrast, the presence of several queens per colony (*polygyny*) often coincides with loss of the mating flight (with mating sometimes occurring in the nest), limited dispersal, and dependent colony founding (workers assist queens) (11, 12, 61, 65, 72, 73). These different reproductive strategies are associated with particular queen phenotypes. Monogyne ant queens tend to have larger body sizes (70), higher nutrient reserves (69, 102), longer life spans (71), higher fecundity (55, 64, 88, 170), and a later first age of sexual production (71) than do their polygyne counterparts.

Colony queen number and associated elements of social organization can vary dramatically at a hierarchy of levels. Queen number often is labile across populations, among colonies within a population, and even during the ontogeny of single colonies in many ants and wasps (31, 34, 44, 58, 67, 74, 117, 125, 129–131). Similarly, the way in which reproduction is divided among nestmate queens (15, 54, 62) and the strategies employed by queens to become active reproductives (44, 125) can vary geographically or even within local populations in these insects.

In this review we discuss the ecological and social factors that promote shifts in social organization and the consequences of such shifts for reproductive strategies, phenotypic evolution, and genetic structure. We focus on the "highly eusocial" Hymenoptera, which generally have clear morphological differences between queens and workers and form large perennial colonies (35). We use the fire ant *Solenopsis invicta* as a principal subject because variation in its social organization has been studied extensively. We focus on colony queen number because it is central to the variation in social organization found in fire ants and many other eusocial insects.

VARIATION IN COLONY QUEEN NUMBER

Association of Colony Queen Number with Other Properties of Social Organization

The biology of *Solenopsis invicta* has been studied extensively in the southeastern United States, where the species was introduced from South America

Table 1 Major differences between the monogyne (M) and polygyne (P) social forms of the fire ant *Solenopsis invicta* in the United States.

	Monogyne (M) form	Polygyne (P) form
Number of wingless (reproductive) queens per nest[a]	1	2 to more than 200
Relative fecundity of wingless (reproductive) queens[b]	High	Low
Unmated wingless (reproductive) queens in nests[c]	Absent (or rare)	Frequent
Mode of colony founding[d]	Independent	Dependent
Relative weight of winged (nonreproductive) queens[c]	High	Low
Relative worker size[f]	Large	Small
Relative next density[g]	Low	High
Connections between nests[h]	No	Yes
Genetic relatedness of nestmate workers[i]	Close to 0.75	Variable and often close to 0
Diploid males[j]	Absent	Frequent
Relative number of new sexuals produced[k]	Many	Few

[a] Includes mated and unmated queens in the P form. See section on "Within-nest genetic structure."

[b] (34, 166, 167, 170).

[c] See section on "Within-nest genetic structure."

[d] M queens start new colonies independently after a mating flight by raising brood without the help of workers; P queens return to or remain within an established P nest after shedding their wings and initiating oogenesis (41, 77, 86, 108, 114, 165). P colonies reproduce dependently through fissioning, a process in which wingless queens leave their nest with workers to initiate a new nest in close proximity to and in continuing contract with the parent nest (172).

[e] Mature winged queens of the M form weight on average 48% more than their counterparts in the P form, mainly as a result of their greater fat reserves (77, 79).

[f] (42).

[g] (109, 111).

[h] P workers and brood are transported from one nest to another (172), and P workers have a high tolerance of non-nestmate workers (92). M colonies are territorial (181), and M workers have a low tolerance of non-nestmate workers (92).

[i] (129, 133, 141).

[j] See section on "Production of diploid males."

[k] See section on "Sex allocation."

earlier this century (81). Two distinctive social forms exist in *S. invicta*: the monogyne (M) form, in which colonies have a single egg-laying queen, and the polygyne (P) form, in which colonies have multiple queens. The two forms often occur in distinct populations in which nests of one form predominate (83, 129, 135, 139), yet the P form is normally found in geographical association with the M form (42, 109, 110, 139). The forms differ in a number of traits besides colony queen number (Table 1); most important among these are the breeding habits of queens. Monogyne queens mate in aerial swarms and found new nests without the help of workers, that is, independently (86, 165), whereas P queens mate in the nest or during swarming but always initiate egg-laying in established P nests, that is, dependently (41, 77, 108). Polygyne nests multiply by fissioning (172) (Table 1).

Colonization of the United States by *S. invicta* has resulted in a unique opportunity to view selection in progress (41a) by comparing the social biology of this ant in the introduced range with that in its native range. Although the biology of the ant in South America is not yet well known, available data indicate that both social forms occur there and that, as in the United States, queen number is associated with other properties of the social organization. The native P form is known to differ from this form in the United States in some important social attributes, however, a point discussed more fully below.

Differences in properties of social organization associated with variation in queen number have been reported in several ant species and tend to be similar to those found in *S. invicta*. For example, queens and workers produced in polygyne colonies are smaller than those produced in monogyne colonies in *Formica truncorum* (158) and several *Myrmica* species (27). In the fire ant *S. geminata*, polygyne colonies produce fewer new queens, rear smaller workers, contain more unmated reproductive queens, and occur at higher densities than monogyne colonies (84, 168). Lower fecundity of queens in polygyne than in monogyne nests has been reported for a considerable number of species (55, 64, 88, 168), as has a tendency for polygyne colonies to reproduce through fissioning, while monogyne colonies produce queens that initiate nests independently (12, 65, 174). Finally, polygyny and colony reproduction via fissioning commonly are associated with persistent connections between nests (11, 12, 157).

Intraspecific variation in colony queen number in *S. invicta* and other ants, and associated differences in other properties of social organization, often parallel the variation seen between related monogyne and polygyne ant species. This suggests that variation at both levels stems from similar causes and that identification of the ecological and social factors influencing queen number within species may shed light on some features of cladogenesis in these insects.

Causes of Variation in Colony Queen Number

Solenopsis invicta has spread rapidly throughout the southeastern United States during the 60 years since its introduction (81). Entomologists have studied colonies throughout this period, yet it was not until 1973 that polygyny was first reported (39). Since this initial report, the frequency of polygyny apparently has increased throughout the introduced range, with many areas originally colonized by the M form now occupied by the P form (109, 110). Indeed, polygyny is now more common than monogyny in some large regions, such as east-central Texas (111).

The distributions of the two forms apparently are not associated with specific habitat types in the United States (111), and colonies of the two forms are intermingled at very localized scales in Argentina (KG Ross, EL Vargo, & L Keller, unpublished). This suggests that variation in queen number in fire ants is not a response to habitat differences, as has been suggested for other ants (60), and that another explanation for the gradual increase in the incidence of polygyny in the introduced range must be sought. Nonacs (91) suggested that polygyny arises as newly colonized habitats become increasingly saturated. Suitable habitats are widely available for colonization when *S. invicta* first enters an area, so the independent-founding strategy of the M form is highly successful at this point (114, 161). However, the success of dispersing M queens probably decreases as appropriate nesting sites become filled, and as predation and brood raiding by workers from existing colonies increase (162, 163). The diminished founding success of dispersing queens may generate strong selection on queens to attempt to remain in or reenter their natal colony (e.g. 12, 58, 124, 125), a behavior commonly associated with polygyny. Workers may be selected to accept such queens, some of which may be their sisters, once the probability of successful independent founding falls below a certain threshold (68, 144). Moreover, fissioning, the mode of colony reproduction associated with polygyny, may be more successful than independent colony founding in saturated habitats because queens are tended by workers during this process and thus are less vulnerable to predation and raiding (83, 162). Suggestive evidence for a link between a low success rate for independent founding and the inception of polygyny comes from the apparent correspondence of high nest densities in the monogyne form with high frequencies of occurrence of polygyny in Texas (111).

Constraints on independent founding may select for polygyny in other ant species as well (68). Herbers (56) showed that the availability of empty nest sites and degree of polygyny are inversely correlated across populations of *Leptothorax longispinosus*, and Bourke & Heinze (12) concluded from a comparative study of lepothoracine ants that polygyny is associated with limited nest sites, cold climate, and patchy habitats, factors that decrease the success of queen dispersal and independent founding.

A significant and unresolved issue is whether shifts from monogyny to polygyny generally are accompanied by important genetic changes (e.g. 178). If the alternative reproductive phenotypes have some genetic basis, then genes encoding the "polygyne phenotype" will increase in frequency when polygyny is favored, given some limitations on gene flow from the monogyne form. If alternative phenotypes are "inherited" by virtue of the social environment in which an individual is reared (as a result of phenotypic plasticity), then the polygyne phenotype will increase in frequency when and where polygyny becomes favored regardless of patterns of gene flow. Current evidence suggests that such "cultural inheritance" underlies the distinctive reproductive phenotypes of the two forms of *S. invicta*.

Maintenance of Variation in Colony Queen Number

A geographically extensive survey by Porter (110) showed that most *S. invicta* populations in the United States remained predominantly monogyne or polygyne over a three-year period. This stability can be explained by the fact that the social environment in which queens mature influences their phenotype and reproductive opportunities, biasing them toward living in a colony with the same social organization as that in which they were reared. Newly emerged queens of the two forms are indistinguishable in weight, an important component of reproductive phenotype, yet M queens become 48% heavier than P queens during the period of adult maturation, mainly because of greater fat accumulation (77). Cross-fostering experiments showed that these differences are largely dependent on the number of reproductive queens present in the nest (77, 79). Young queens maturing in the presence of a single egg-laying queen develop the M phenotype, whereas those maturing in the presence of multiple queens develop the P phenotype, no matter which type of nest they developed in as brood.

In addition to this effect of social environment, maturation of P queens is influenced by their genotype at a single gene, designated *Pgm-3* (78, 79). Winged queens with the homozygous genotype $Pgm\text{-}3^{a/a}$ become 26% heavier than queens with the alternate genotypes in the P form. Significantly, there is no difference in weight among queens with different *Pgm-3* genotypes in the M form. The result of this interaction between genotype and social environment is the production of three phenotypic classes of queens: queens with extensive energy reserves (M queens), queens with minimal energy reserves (P queens with genotypes other than $Pgm\text{-}3^{a/a}$), and an intermediate class (P queens with genotype $Pgm\text{-}3^{a/a}$).

The phenotypic differences that develop between these three types of queens affect their reproductive options. The two types produced in P colonies apparently have insufficient reserves to found colonies independently. This conclusion is supported by the finding that most P queens attempting to found colonies alone in the laboratory produce either no workers or too few to give the colony a reasonable chance of survival (114). In contrast, queens from M nests have high success in producing the requisite number of workers to ensure colony survival (113, 164). Queens that cannot found colonies independently must be adopted into existing P colonies. Only small queens produced in P colonies are accepted by P workers; large P queens (all those with genotype $Pgm\text{-}3^{a/a}$) invariably are destroyed by workers during their attempts to become egg layers (78, 128). Understandably, P workers also seem not to accept newly mated M queens (137), which are even heavier than P queens with the genotype $Pgm\text{-}3^{a/a}$ (78, 79, 171).

Social organization in *S. invicta* thus is "culturally inherited" because the type of social environment in which a queen matures specifies her phenotypic characteristics, which, in turn, dictate the type of society in which she can survive and reproduce. Because of this mode of inheritance, populations retain their characteristic social organization in spite of extensive gene flow between the social forms (see below).

Occasional changeovers from one social form to the other have been documented in some fire ant populations (110). Polygyne nests, which multiply and expand their territory by fissioning, may replace M nests by outcompeting them or taking over their territories after their single queen dies (43). Monogyne nests may replace P nests when the latter are eliminated from an area by some catastrophe such as flooding (110), the vacant habitats thus created being colonized most readily by dispersing M queens.

Intraspecific variation in queen phenotypes associated with differences in social organization is known in other ants and can be of three types. First, queens from colonies differing in queen number can display modest but consistent phenotypic differences, as in fire ants. For example, queens of *Formica truncorum* produced in polygyne colonies are smaller and have less fat reserves than queens produced in monogyne colonies (158). These differences, which arise during adult maturation, are coupled with tendencies for monogyne queens to disperse on the wing and polygyne queens to mate and shed their wings in the nest. Thus, as in *S. invicta*, the social environment in which young *F. truncorum* queens mature affects their reproductive options.

The second type of variation involves distinct queen phenotypes (with size the principal difference), but the different morphs are not strictly associated with different social organizations (10, 87). As an example, *Myrmica ruginodis* has both "macrogyne" (normal) and "microgyne" (miniature) queen morphs. Colonies headed by macrogynes generally are monogyne and reproduce by independent founding, whereas those headed by microgynes are polygyne and reproduce by fissioning (13).

The third and most distinctive type of queen variation is similar to the second except that the smaller queens are wingless and resemble workers in other respects as well (5, 18, 48, 50, 53, 184). This pronounced dimorphism possibly has a simple genetic basis in some species (18), but in others the morphs appear to be environmentally induced (e.g. 184). Queens of the winged morph typically disperse and initiate new colonies independently, whereas wingless queens mate in the vicinity of their natal nest, in which they then remain. In one *Leptothorax* species, most wingless queens are accepted as reproductives by their natal colony, whereas winged queens generally are destroyed by workers if they fail to disperse (48).

In summary, variation in colony queen number in *S. invicta* and other ants frequently is associated with other important differences in the social biology, including distinctive queen behaviors and morphologies. We next review the consequences of these different syndromes for population genetic structure, production of diploid males, and sex ratios. We then consider how the suite of changes accompanying shifts in queen number may affect gene flow between socially divergent populations.

Consequences of Variation in Colony Queen Number

GENETIC STRUCTURE Changes in queen number affect genetic structure within the nest and at higher population levels, altering the focus of selection (3) and possibly setting in motion further social evolution (97). For instance, a shift from monogyny to polygyny alters the patterns of genetic relatedness that determine the extent of genetic conflict among nestmates, thus influencing such social traits as nepotism, the partitioning of reproduction, and sex allocation (7, 19, 75, 97, 118, 120, 123). At larger scales, modified breeding habits linked to a shift in queen number may impart local genetic structure within polygyne populations or even initiate genetic divergence between variant social forms.

Within-nest genetic structure The number of reproductive queens is a basic determinant of patterns of relatedness within nests, but its effects depend on other factors such as the apportionment of maternity among nestmate queens, their relatedness to one another, and numbers of matings by each (115, 129). Thus it is important to consider all of these features when evaluating how differences in queen number influence within-nest genetic structure.

Nests of the M form of *S. invicta* generally possess only a single reproductive female (86, 133, 141, 149, 165). Workers are incapable of laying eggs (35), and eggs laid by winged (virgin) queens in queenright colonies seem not to be viable (33, 133, 140). The number of wingless reproductive queens in P nests of *S. invicta* has been studied by direct counts and by indirect estimates based on within-nest genetic variation (relatedness). The number of mated queens per nest is highly variable, ranging from 2 to almost 200 in a well-studied Georgia population (Figure 1), with queen number highly predictive of the genetic variation measured among workers within a nest (129). The effective number of queens per nest in this population ($N_e = 4.9$), estimated indirectly from nestmate relatedness values, corresponds well to the harmonic mean number of queens actually collected from these nests ($N_h = 4.5$), as expected from the mathematical theory underlying relatedness estimation (115, 129, 173a). As is also expected when queen number varies substantially among nests, N_e is considerably less than the arithmetic mean number of queens per nest ($N_a = 25$). In native P populations, direct counts and indirect estimates both suggest that the number of mated queens per nest generally is lower than in introduced populations. For instance, estimates of N_e range from 4.0 to 6.1

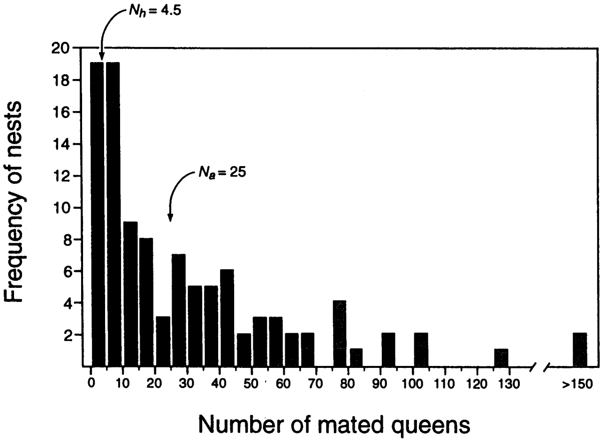

Figure 1 Frequency distribution of number of mated reproductive queens per nest in polygyne *S. invicta* from northern Georgia, United States (data from 129; EL Vargo, unpublished). The subset of 31 nests for which genetic data for estimating relatedness are available is indicated by black shading. The harmonic mean (N_h) and arithmetic mean (N_a) numbers of queens per nest are indicated for this subset.

for confirmed P nests in two Argentine populations, but estimates exceed 13 in the Georgia P population when nests with single queens are excluded (KG Ross, EL Vargo, L Keller, unpublished).

A large proportion of reproductive queens in P nests (25–40%) are unmated in introduced populations (114, 135, 170); although reproductively active, these queens produce few viable eggs (170, 173). The proportion of unmated queens is lower in native P populations (2–12%), presumably because operational sex ratios are less female-biased than in introduced populations (see below).

Empirical measurements of within-nest relatedness also have been used to obtain reliable estimates of N_e in other ants (2, 9, 49, 59, 101, 126, 145, 146, 153, 156). For instance, Seppä (146) and Banschbach & Herbers (2) estimated N_e at 2.3 and 1.8 for polygyne *Myrmica ruginodis* and *M. punctiventris*, respectively, in good agreement with N_h values of 3.2 and 1.4. Sundström (156) estimated N_e at 16 in a population of *Formica truncorum* in which nests regularly contained more than 20 queens. The only other group of highly eusocial polygyne insects in which queen number and genetic structure have been studied jointly is the epiponine wasps. Observed colony queen numbers in four epiponine species were found to be variable and often low, with N_h between 3 and 10 (38, 116, 154, 155). Measured relatedness values in these wasps yielded estimates of N_e close to N_h in each case.

Fire ant queens of both social forms invariably mate only once (133, 140, 141, 149). Effective numbers of matings are low in most other ants (8a, 126) and in epiponine wasps (116) as well, with single matings apparently more common in polygyne than monogyne ant queens (76). Thus, variation in queen mating frequency plays a relatively minor role in altering within-nest genetic structure in most highly eusocial Hymenoptera with variable colony queen number, compared to the variation in queen number.

Variation in maternity apportionment among nestmate queens (reproductive skew; 75, 123) has been studied in the P form of *S. invicta* in the laboratory and field. Considerable skew was observed in the laboratory (127), with the result that relatedness of worker offspring was twice the value expected had all queens reproduced equally. Furthermore, greater skew was documented with respect to the maternity of new queens than the maternity of workers, resulting in consistently higher relatedness of queen offspring to one another than of worker offspring to one another. This difference in maternity apportionment according to offspring caste, which has been detected also in field studies (129), emphasizes that production of worker offspring may not always serve as a reliable indicator of skew in actual reproductive success in highly eusocial insects (66).

Few studies of other polygyne Hymenoptera have used genetic markers to quantify reproductive skew (see 47, 106, 127, 131 for behavioral studies). Pamilo & Seppä (100) obtained higher relatedness values for queen than for worker pupae in *Formica sanguinea*, consistent with greater skew in the maternity of sexual than of worker offspring. Seppä (146) concluded that skew among *Myrmica ruginodis* queens is minimal because worker relatedness values were such as would be expected had all captured nestmate queens reproduced equally. Skew appears minimal in epiponine wasps judging from oocyte counts (38, 116, 154, 155), a view supported by similarities between offspring relatedness values measured and those expected if equal maternity apportionment is assumed. Studies such as these can be useful not only because they illuminate one factor influencing within-nest genetic structure, but also because they can test theoretical predictions of how nestmate reproduction is partitioned in particular ecological and social settings (12, 75, 122, 123).

Relatedness of reproductive nestmate queens has been investigated in P populations of *S. invicta* in Argentina and the United States. Queens are closely related in native populations (r = 0.46; KG Ross, EL Vargo & L Keller, unpublished), implying that they usually are sisters recruited as egg-layers into their natal colony. In contrast, queen relatedness is essentially zero in the introduced ants (129, 133), which accords with mark-recapture evidence that at least some queens here are recruited from foreign nests after making mating flights (41, 108). The apparent breakdown in adoption of a colony's daughter queens as well as the increase in colony queen number in the United States may stem from the higher population densities characteristic of introduced populations (112) and consequent increased selection on young queens to seek adoption into existing colonies.

Nestmate queen relatedness in other highly eusocial species varies across the spectrum of possible values (58, 68, 126, 131). In those groups in which queens are moderately or highly related (2, 26, 38, 94, 99, 104, 116, 146, 153, 155), most new queens likely are derived from the parent nest. Low values reported for several ants (63, 104, 156) presumably result from recruitment of queens from foreign nests, acceptance of daughter queens in nests in which queen number consistently is high, and/or acceptance of daughter queens over several generations (68, 97).

Relatedness of mating pairs (inbreeding) interacts with colony queen number and other elements of social organization in complicated ways to determine within-nest relatedness patterns (89, 96). Extensive genetic studies of introduced and native *S. invicta* of both social forms employing many polymorphic allozyme loci indicate that these ants invariably are outbred (133, 137–139, 141). Similarly, genetic studies of other highly eusocial Hymenoptera seldom have found evidence of pronounced inbreeding (2, 9, 38, 63, 101, 116, 126, 131, 146, 153–156). Inbreeding might be anticipated in polygyne ants because of the association of restricted dispersal with polygyny. Although it has been detected in a few such ants (8, 59, 145), in others it has not (63, 99, 152, 153, 156), presumably because brood is moved between nests or adult males disperse widely (103).

Higher-level population genetic structure This refers to relatedness between nearby nests as well as genetic differentiation among very localized demes. Such structure may arise from mating near the natal nest, adoption of daughter queens, colony fissioning, and persistent interconnections between nests (23, 46, 94, 95, 131, 147), some or all of which are associated with polygyny in various highly eusocial Hymenoptera.

Higher-level genetic structure has been studied at scales relevant to the above processes in *S. invicta* from the native range only (KG Ross, EL Vargo & L Keller, unpublished). Both P but neither of the M populations studied in Argentina were significantly structured at scales of 10 m and 5 km. These results suggest more restricted dispersal in the P than the M form, consistent with the notion that queens are adopted by their natal colony and that colony reproduction occurs by fissioning in the native P populations. Among other highly eusocial Hymenoptera, higher-level structure has been detected in polygyne ants from six genera (2, 8, 24, 25, 45, 59, 95, 99, 147, 152, 156). Particularly interesting are cases in which it exists in the absence of local inbreeding (25, 99, 152, 156), presumably as a result of substantial dispersal by males but not queens or of single colonies occupying multiple nests. Pronounced higher-level structure in polygyne but not monogyne populations of single species or related species has been reported in *Formica* and *Myrmica* (99, 147, 156), as well as fire ants, and highlights the distinctive mating and dispersal strategies of the alternative forms. A major unresolved issue is whether these distinctive strategies commonly drive genetic differentiation between sympatric social forms (see below).

PRODUCTION OF DIPLOID MALES A unique consequence of variation in colony queen number in fire ants is the different distributions of diploid males in the two social forms. Although social Hymenoptera are characterized by a male-haploid genetic system, diploid (2N) males can be produced in some circumstances. Sex appears to be determined by heterozygosity at one or a few loci, with individuals heterozygous at such loci becoming females and individuals either hemizygous (haploid) or homozygous (diploid) becoming males (21). Diploid males have low viability and/or fertility and are produced at the expense of workers or fertile sexuals, so they constitute a cost to a colony. The resulting selection against their production acts to maintain many alleles and high heterozygosity at sex-determining loci. Production of 2N males is affected not only by sex-locus variation but also by the mating system (e.g. extent of inbreeding) and, importantly, by colony queen number (93, 101, 141).

Diploid males are common in P populations of *S. invicta* in the United States, representing 73–100% of all males produced (132, 141). In contrast, 2N males are absent from mature M nests. This pattern is not the result of greater inbreeding or smaller effective population sizes in the P than in the M form (132, 137, 139, 141), nor is it the result of M workers possessing and P workers lacking an ability to recognize and destroy 2N males early in development (134). Rather, it results from differential mortality of nests producing such males in the two forms. Colonies founded independently by M queens that produce 2N males invariably die early in development because resources are diverted from production of workers (the labor of which is crucial to early colony growth and survival) to production of males (132, 134). This source of mortality does not afflict the P form because colonies are founded by fissioning, during which a sizable worker force already is present to ensure sustained colony growth.

Production of 2N males constitutes a significant genetic load on *S. invicta* populations in the United States, with 15–20% of all newly founded colonies of the M form succumbing to this mortality factor. It is unlikely that such a load could persist in ecologically balanced communities, and indeed, male diploidy is uncommon in native populations (141). Diploid male production has increased in introduced populations because sex alleles were lost during a population bottleneck early in the colonization process (138, 141).

SEX ALLOCATION As is true for solitary organisms, colonies of social insects face the decision of how to allocate resources between growth (worker production) and reproduction (production of sexuals). However, eusocial Hymenoptera are unique because this decision depends on two parties, workers and queens, that have conflicting interests over such allocation of colony resources (98) as well as over the investment in each sex within the fraction allocated to reproduction (24a, 160). This conflict arises because of the differential relatedness between workers and brood of each sex that stems from male haploidy. Variation in colony queen number can affect this relatedness asymmetry and, thus, the preferred sex-investment ratio of workers (7, 98). Different dispersal strategies associated with variation in queen number also affect the preferred ratio, but for both parties (7, 20, 36, 91, 96a, 98).

The M and P forms of *S. invicta* differ in the amount of resources they allocate to production of workers and sexuals, with M colonies producing a higher proportion of sexuals among their offspring than do P colonies (114, 169, 169a). This difference in caste resource allocation reflects the different modes of colony reproduction of the two forms. Fissioning, characteristic of the P form, requires that a substantial number of workers accompany each queen inhabiting a new nest, whereas independent founding, characteristic of the M form, occurs in the absence of workers.

Estimates of the numerical sex ratio in the United States reveal a modest male bias in the M form (0.7 female:1 male) and female bias in the P form (1.4:1) (169). However, a high proportion of males produced in the P form are diploid and infertile (see above), and exclusion of such males results in an even stronger female bias (6.2:1) in the numerical ratio in the P form (only haploid males are present in the M form). This is important because it affects the operational sex ratio (OSR), the relative abundance of members of each sex available for mating. The OSR is equivalent to the numerical sex ratio for fertile sexuals in *S. invicta* because both sexes mate only once (see 129). Thus, the OSR is strongly female biased in the P form but moderately male biased in the M form in the United States, which may help explain why many P queens here remain permanently unmated, why, among those P queens that do mate, most mate with M males (see below), and why virtually all M queens become mated (40, 134).

Fire ant queens are larger and thus presumably require more investment than males. The M form produces larger queens and smaller males than does the P form, so that the sex-investment ratios estimated from the numerical ratios turn out to be equivalently biased toward females (1.5:1) for the two forms in the United States (169). Such female-biased investment, while lower than expected based on observed relatedness patterns (6, 90, 160), is in the direction predicted if there is at least partial worker control over colony investment. The identical investment by the two forms may be linked to the similar asymmetries in relatedness between workers and brood of each sex (which are similar between the forms because of low queen relatedness in the P form) and the correspondingly similar worker-preferred sex-investment ratios (7). This scenario assumes that workers regard 2N males as normal males, and indeed, the sex-investment patterns may be taken as evidence that this is the case. Investment ratios in native P populations, where nestmate queens are closely related and 2N males are rare, are expected to be less biased toward females than in the M form and to vary predictably with colony queen number, according to this scenario.

Variation in queen number is known to influence sex allocation in other highly eusocial Hymenoptera. Lower investment in reproductives in polygyne than in monogyne nests has been documented in several ant species (20, 157, 175), where it probably is associated with colony fissioning (20). Relative investment in each sex also commonly varies according to queen number. Polygyne colonies of several ants (20, 29, 31a, 55, 57, 157, 175) and epiponine wasps (117) are characterized by less female-biased sex-investment ratios than occur in conspecific monogyne colonies. This may be explained by the lower asymmetry of relatedness between workers and brood of each sex in polygyne colonies containing related queens compared to monogyne colonies. Female brood in such polygyne colonies are more closely related to workers than are male brood, but the difference diminishes with increasing queen number, so workers should prefer less female-biased sex ratios as queen number increases (7). Additionally, local resource competition may occur between daughter colonies when parent colonies adopt related queens and reproduce by fissioning, thus devaluing investment in queens and contributing to a less female-biased sex ratio in polygyne than in monogyne nests (7, 20, 36, 91, 96a, 97).

Differences in operational sex ratios between conspecific social forms such as occur in introduced *S. invicta* may influence the types of matings that occur between the forms, as discussed below. Therefore, their study can be valuable for understanding how shifts in social organization affect the routes and magnitude of interform gene flow.

Gene Flow between Alternative Social Forms

A major theme of this review is that shifts from monogyny to polygyny in ants often are accompanied by changes in the breeding biology, such as the site of mating, context in which queens begin reproducing, and mode of colony founding. These correlated changes raise questions as to whether interbreeding between populations differing in colony queen number ever is impeded and, if so, by what route existing interform gene flow occurs. Finally, the related question of whether any such restricted interbreeding can develop into reproductive isolation also must be considered.

The M and P forms of *S. invicta* are conspecific (159). Evidence of their close relationship includes the following: (i) They are more similar genetically than are any two recognized species in their species complex (138, 139); (ii) the P form always is associated geographically with the M form (42, 109, 110, 139); (iii) the forms are not distinguishable by any taxonomically informative morphological characters (JC Trager, unpublished); and (iv) egg-laying queens can be adopted into queenless nests of the alternate form (32, 134). Several studies have sought evidence for interform gene flow and attempted to determine its mode and magnitude, with the following results. Introduced populations typically are more similar genetically to adjacent populations of the alternate form than to distant populations of the same form, based on data from 26 protein markers (139). Adjacent M and P populations in Georgia, United States, possess the identical alleles at similar frequencies at 12 polymorphic protein loci, as well as similar numbers of sex-determining alleles (137). Most significantly, the allele *Pgm-3*$_a$, which occurs at high frequency in M populations, is common also in the P form despite being under intense negative selection in this form (78, 128). Taken together, these results indicate substantial gene flow between the social forms in the United States (128, 135, 137).

Laboratory and field studies using *Pgm-3* as a marker to estimate the magnitude of interform matings suggest that 80–100% of mated P queens are inseminated by M males (128, 135, 137). Such matings may represent the predominant or sole route of interform gene flow in introduced *S. invicta*. Fertile (haploid) males are rare in P nests and thus are not expected to disperse and mate with M queens to any appreciable extent. Moreover, queens of neither form are likely to establish themselves as reproductives in nests of the alternate form. Newly mated M queens attempting to enter P nests likely are destroyed, because P workers are intolerant of the M queen phenotype (see above). Winged P queens may disperse into neighboring M populations, but they also are unlikely to affect interform gene flow. Their meager energy reserves make it doubtful that they can found colonies independently (77, 114), and they are not normally accepted into queenright M colonies (32). Gene flow between the social forms in the United States thus may be largely unidirectional and mediated by males, apparently as a result of the unique suites of reproductive traits distinguishing the two forms.

Patterns of interform gene flow in native populations may differ substantially from those in the United States. Assuming that the rarity of sterile diploid males in native P populations results in less female-biased operational sex ratios than in introduced P populations, gene flow via males is less likely to occur in the direction M→P but more likely to occur in the direction P→M (queens still are unlikely to mediate such gene flow). Although the route of interform gene flow thus may differ between the native and introduced ants, there is no reason to expect differences in the magnitude of gene flow. Nonetheless, significant genetic differentiation has been detected between M and P nests at one location in Argentina (KG Ross, EL Vargo, L Keller, unpublished), suggesting more substantial barriers to interform gene flow at this site than at any sites in the United States (137, 139). Such restricted interbreeding plausibly arises from site-specific assortative mating in native populations, with P sexuals mating primarily at the nest and M sexuals frequenting mating swarms. Mating at the nest in native P populations is strongly suggested by the observed high relatedness of mated nestmate queens.

Gene flow between related social forms seldom has been investigated in other ants. Elmes (30) studied mating swarms of *Myrmica ruginodis* to determine whether assortative mating occurred in the "microgyne" and "macrogyne" forms. No evidence of this was found, but a mating advantage of macrogyne males in swarms, combined with a possible tendency for macrogyne queens to mate in swarms and microgyne queens to mate at the nest, hint that some barriers to interbreeding between the forms may exist. Genetic surveys typically have revealed that monogyne and polygyne forms of single nominal species share identical alleles at similar frequencies (2, 126), as is expected with ongoing gene flow or recent isolation. Conspecific social forms within two separate *Rhytidoponera* species are not differentiated genetically, even though females of the alternate forms probably mate at different sites (174); interform gene flow may be mediated through males in these species, as it is in fire ants. Genetic studies of European *Formica* have failed to reveal significant differentiation between conspecific social forms, despite evidence for occasionally extensive local structure in some polygyne populations (99, 156). Clearly, additional genetic data from diverse taxa are needed to answer the question of whether the derived breeding habits that create local structure in polygyne ants also can restrict interbreeding between sympatric social forms.

ALTERNATIVE SOCIAL ORGANIZATIONS: PATHWAYS TO SPECIATION?

The potential for restricted interbreeding between conspecific social forms raises the question of whether reproductive isolation ever develops between them and, thus, whether evolution of social organization can be important in promoting speciation in ants (10, 13, 22, 139, 176). Possible steps in this process are:

(i) Some queens in an ancestral monogyne population forgo independent founding to be adopted in their natal colonies, inducing polygyny.
(ii) Polygyne colonies produce small queens with low reserves that specialize on the dependent strategy, leading to the coexistence of two queen reproductive strategies and phenotypes.
(iii) A shift in queen mating site to the area of the natal nest occurs in the novel type, increasing the probability that queens are adopted into their

own colony and further diminishing the need for reserves to support flight and independent founding.

(iv) Sexual selection acts on males to track the novel mating behavior of polygyne queens.

(v) Positive assortative mating by site and continued disruptive selection on queen (and perhaps male) phenotypes leads to decreased interbreeding and increased differentiation between the ancestral monogyne and derived polygyne forms, culminating in reproductive isolation.

Evidence for such a mode of speciation, such as it exists, is highly inferential. Polygyny seems often to arise secondarily within essentially monogyne taxa (5, 13, 22, 37, 60, 124), resulting both in clusters of closely related species that differ in colony queen number and in frequent intraspecific variation in this trait (4, 5, 8, 13, 60, 142). In some cases the species status of the social variants is difficult to decide (50, 105, 142), possibly because these socially polymorphic clusters are actively radiating. Two predictions concerning the phylogenetic distribution of queen number across species in such clusters have been generated to test this hypothesis of speciation (176): Sister species should differ frequently in social organization, and species-rich clades should display more variation in social organization than do their species-poor sister clades. Unfortunately, the phylogeny and social biology of the relevant taxa seldom are sufficiently well understood to search for either pattern (but see 176). Furthermore, frequent shifts in social organization relative to the pace of cladogenesis (36a) as well as extinction may obscure the predicted pattern of fixed alternative social organizations in sister species.

Divergence in breeding behaviors observed between conspecific social forms constitutes the best available evidence for this proposed route of speciation. Restrictions on gene flow may be caused by differences in mating sites between the forms (13, 30, 99, 174), as well as by an inability of queens to establish themselves in populations of the alternate type due to worker intolerance (13, 137) or phenotypes ill-suited to the alternate breeding system (5, 12, 48, 65, 77, 79, 114). Pronounced queen morphological differentiation may accompany continued divergence in breeding strategies, an extreme result of which is a stable queen dimorphism featuring a winged morph specialized for independent founding and a miniaturized wingless morph specialized for adoption (see above). Disruptive sexual selection on males to track queens of both types may lead to the evolution of alternative male mating habits and morphologies as well (52). Both queen morphs may be maintained in some cases, presumably due to balancing selection associated with environmental heterogeneity and consequent variation in the success of independent founding (12, 50, 53, 124; also 174). In other cases, the queen morph specialized for adoption may replace the independent-founding morph (5, 13, 53). This latter pattern generally has been attributed to anagenesis but could result from a polygyne daughter species replacing its monogyne parent after reproductive isolation has been achieved.

Virtually no comprehensive genetic studies have been undertaken in the relevant species clusters to quantify the magnitude of differentiation that can develop between social variants. The studies cited above suggest that interform gene flow is not restricted sufficiently to permit substantial differentiation in sympatry in *Formica* and *Rhytidoponera,* although the significant genetic divergence found between the M and P forms of *S. invicta* in one native habitat hints at such a process. A frequently cited example of divergence between the "microgyne" and "macrogyne" forms of *Myrmica rubra* (105) is, unfortunately, based on only a single genetic marker.

Additional evidence that incipient barriers to gene flow between conspecific social forms can progress to complete reproductive isolation may come from combining population genetic and phylogenetic studies. Genetic analyses can resolve the species status of populations, quantify the extent and route of gene flow between socially divergent populations, and provide data for phylogeny reconstruction. With well-supported phylogenies, social organization in ancestral groups can be inferred (85) to determine whether speciation events typically coincide phylogenetically with shifts in social organization, and species richness of sister groups can be compared to learn whether significant radiations are associated with pronounced variation in social organization (14, 176).

Although questions remain about whether the inception of polygyny can drive speciation in the manner described above, there is growing consensus that polygyny plays an important role in ant speciation through its link to social parasitism (10, 13, 16, 17, 28, 176, 178). True social parasites in ants establish new colonies dependently by means of queens infiltrating nests of closely related polygyne host species, suggesting that they arose from populations in which unrelated foreign queens sometimes were adopted. Such "preparasitic" queens likely experienced selection to specialize in production of sexuals, to the detriment of the colony and their unrelated nestmates (reduced importance of workers is characteristic of social parasitism). Changes in parasite queen phenotypes facilitating more effective colony entry likely contributed to disruptive selection for alternative reproductive strategies in parasite and host subpopulations, analogous to the selection driving divergence between conspecific monogyne and polygyne social forms. Temporal or spatial isolation arising from changes in the incipient parasites' mating behaviors (perhaps associated with their diminutive size) and subsequent sexual selection on males may have further restricted interbreeding between parasites and hosts (10). The evolution of polygyny thus may set the stage for a subsequent dramatic innovation in social organization, social parasitism, that appears to be prominently involved in cladogenesis in ants.

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