

# Kin Selection and Social Insects

*Social insects provide the most surprising predictions and satisfying tests of kin selection*

David C. Queller and Joan E. Strassmann

**S**ocial insects so dominate many terrestrial habitats (Wilson 1990) that they can hardly escape the attention of biologists, but even if they were rare, they would still attract special interest because of the intricate cooperation within their societies. William Morton Wheeler (1911) described the social insect colony as an organism (or as a higher-level organism or superorganism) because of the degree to which individuals appear to operate as a unit that is dedicated to the perpetuation and reproduction of the colony as a whole. The reinvention of the organism at a higher level has occurred at a number of crucial junctures in the history of life (Maynard Smith and Szathmáry 1995). For example, the eukaryotic cell arose from several prokaryotic ancestors (Margulis 1970), and multicellular plants, animals, and fungi arose from single-celled ancestors (Buss 1987). Because insect societies are macroscopic, and because they span the entire range from solitary individuals to essentially superorganismal colonies, they offer an accessible model for how such transitions can happen.

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**Social insect workers  
reproduce indirectly  
by helping kin,  
sometimes within  
societies with an  
almost organismal  
degree of integration**

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Social insects vary in many ways. Some have small colonies with only a few individuals, whereas the colonies of many others include thousands, or even millions, of individuals. Colonies may be started by a single individual or by a large cohort of a parent colony. In some species, colonies are short lived or seasonal; in others, they may persist for many years. Some consist of both sexes, whereas others are entirely female, with males being present only briefly prior to dispersing. Variation in genetic systems is of particular interest. For example, social aphids can reproduce clonally. Termites, by contrast, have typical diploid sexual reproduction. And a large number of social insects, including all the Hymenoptera (ants, bees, and wasps), are haplodiploid, with diploid females produced from fertilized eggs and haploid males from unfertilized eggs. The key feature that these societies have in common is a reproductive division of labor. Colonies, even the largest ones, usually have only

one or a few reproductives, called queens (and, if male, kings). Most individuals are workers, which specialize in foraging, defending the colony, and caring for juveniles, but which may or may not be morphologically distinct from the reproducing caste.

Two key questions must be asked to understand the evolution of insect societies. First, how do the individuals interact to create a greater, more successful whole? And second, how does natural selection favor this kind of cooperation? In particular, how can it be that individuals sacrifice themselves to the whole without the property of sacrifice being eliminated by selection?

Kin selection theory provides the framework for addressing these questions. Versions of this idea have been around since Darwin, but William D. Hamilton (1964) generalized it, quantified it, and was the first to argue that kin selection is widely important. The basic logic of kin selection is that a gene can produce copies of itself either by the familiar route of increasing the fitness of its bearer (direct fitness) or by increasing the fitness of relatives who share copies of the gene (indirect fitness). The sum of these effects, each weighted by relatedness, is called inclusive fitness. Kin selection theory formalizes the obvious point that helping relatives is advantageous, whereas harming them is not. More important, it explains how to analyze situations in which there are tradeoffs between help and harm. When should an individual aid one

relative at the expense of another? Hamilton's rule provides the answer:

$$r_b b > r_c c$$

Altruistic behavior will be favored when the fitness gain to the beneficiary ( $b$ ) times the actor's relatedness to the beneficiary ( $r_b$ ) exceeds the fitness loss to the relative experiencing the cost ( $c$ ) times the actor's relatedness to this individual ( $r_c$ ). If the actor herself suffers the cost, the relevant  $r_c$  is 1, and her aid to a relative is termed altruistic. Hamilton's rule is, of course, a shorthand for a full population genetics model, but it is remarkably robust (Seger 1981, Michod 1982, Grafen 1985, Queller 1992).

The interplay between kin selection theory and social insects has been complex. In this article, we examine this interplay by focusing on three main questions. First, what evidence do social insects provide for kin selection theory? Second, how does kin selection theory account for the evolution of sociality in insects? Third, what kinds of kin-selected conflicts exist, and to what extent do these conflicts constrain the evolution of colonies that are so cooperative as to appear organismal?

Kin selection operates in organisms other than social insects, and an important goal is to include all of these organisms in a common explanatory framework. We nevertheless believe that a focus on social insects is appropriate for three reasons, one for each of the three main questions we treat. First, with respect to the evidence for kin selection, it is among the social insects that the most surprising predictions and the most satisfying tests are found. Second, the selective reasons for insect sociality are distinct from those applying to most social vertebrates. Third, social vertebrates generally show only modest degrees of social integration, and it is the most highly social insects that really raise the question of the evolution of super-organismal societies.

## Support for kin selection

Support for kin selection theory comes from a variety of sources. Mathematical models support the

basic logic of inclusive fitness (Seger 1981, Michod 1982, Grafen 1985, Queller 1992). As Darwin knew, artificial selection on traits of nonreproductive individuals could be accomplished by breeding their relatives, a process that is now regarded as artificial kin selection. However, artificial selection experiments do not address the importance of kin selection in nature, a gap that is filled best by studies of social insects. Kin selection theory predicts that colony members must be related and that sterility must be conditionally expressed, and as we will show, these predictions are strongly supported. But the strongest support for kin selection theory comes from some rather esoteric but beautiful predictions concerning the sex ratio.

**Studies of genetic relatedness.** The most basic prediction of kin selection theory—that reproductive altruism should be directed toward kin—is firmly supported. Numerous studies show that social insect colonies are family groups (Crozier and Pamilo 1996), often headed by a single female. Unrelated individuals can be recognized and excluded (Fletcher and Michener 1987).

Although colony members are nearly always close relatives, it is worth considering three potentially serious challenges to this generalization. Each case involves colonies with many queens, a condition that could lead to such low relatedness among their collective progeny that altruistic behavior might not be favored by kin selection.

First, in some social insects, particularly ants, colonies are founded by numerous unrelated queens. They collaborate, often in the face of brood stealing by other colonies, in rearing a larger initial worker force, which is crucial for the early survival of the colony (Bourke and Franks 1995). After workers emerge, cooperation among the queens usually ends, and all but one are killed, either by their rivals or by workers. If each queen has some probability of being the sole survivor, the early cooperation among queens has direct benefits and is more mutualistic than altruistic (Bourke and Franks 1995). In other words, no altruistic sacrifice requiring kin selection takes place; instead, each queen takes a calculated risk in

trying to become the sole queen of a large, successful colony. As expected, when unrelated queens fight for control of the nest and worker force, the fights are intense and end in the death of all but one queen.

A second, and greater challenge to the central prediction of kin selection is posed by certain ants, called unicolonial ants, which are characterized by huge colonies, many queens, and little aggression within a network of interconnected nests that are probably formed by budding. Relatedness may approach zero (Bourke and Franks 1995, Crozier and Pamilo 1996), so little kin selection is possible (unless individuals can distinguish close kin from random colony members; see below). Altruism might be maintained because workers in these species are too specialized to revert to a reproductive role. However, although this explanation might account for the maintenance of altruism, a problem remains: With zero relatedness, traits of nonreproductive workers lose all heritability, and worker traits can no longer evolve adaptively (unless there is gene flow from non-unicolonial colonies, as in fire ants; Ross and Shoemaker 1993). Perhaps unicolonial forms are temporary and doomed to failure; this possibility is supported by their scattered, twiggy taxonomic distribution (Hölldobler and Wilson 1990).

This explanation cannot apply to a third group with many queens, the wasps of the tribe Epiponini (Figure 1), because this is a monophyletic group that is both speciose and ancient (Carpenter 1993). These wasps are the ecologically dominant social wasps of the Neotropics and are clearly not an evolutionary dead end. Workers are often indistinguishable from queens, suggesting that workers could become reproductives if relatedness is too low (Hamilton 1972). However, reasonable levels of relatedness are in fact maintained. Although queen number is typically high, aggression or attrition occasionally reduces a colony to a single queen, and it is only on these occasions that new cohorts of queens are raised. As a result, relatedness among queens is always very high, and relatedness among their progeny is moderate rather than extremely low (West-Eberhard 1981, Queller et al. 1993).

**The mechanism of sterile caste determination.** Another successful prediction of kin selection theory is less widely appreciated. For kin selection to produce a sterile caste, genes for sterility must either be expressed conditionally or have low penetrance (Charlesworth 1980, Seger 1981). The reason is as follows: A sterility gene that is always expressed never gets reproduced, even indirectly (i.e., through relatives), because any relatives with the gene are also sterile. However, sterility can evolve under kin selection if, for example, a sterility gene expressed only in poorly fed females causes them to help well-fed relatives, which can then transmit their unexpressed sterility genes. In agreement with the prediction, the division into sterile and reproductive castes is almost universally based on differences in the physical, nutritional, or social environment (Wheeler 1986). Two possible exceptions (Kerr 1950, Buschinger 1990) are only partial exceptions; genes may have some effect on caste, but only among the subset of individuals who are well fed. In addition, the genetic determination of queenship in stingless bees is thought to be due to heterozygosity (Kerr 1950), which is a special mechanism that is consistent with altruism. In this case, the problem of sterility alleles extinguishing themselves is avoided in a different way. As a sterility allele becomes rare, it will increasingly be found in heterozygotes, in which it no longer causes sterility.

**Sex ratio studies.** The most striking support for kin selection theory from any organism comes from studies of sex ratios. Fisher (1930) noted that because each sex produces the same total number of offspring, individual members of the rarer sex outreproduce members of the common one. Hence, sex ratio equilibrium occurs when the numbers of males and females are equal (or investment in males and females is equal, when they cost different amounts). This argument is implicitly a kin-selection one, but the effect of kinship is hidden because the mother's relatedness to her sons and daughters is the same, so relatedness cancels out.

However, relatedness does not cancel if the sex ratio is controlled by

Figure 1. The epiponine wasps, such as this *Polybia ignobilis* from Venezuela, maintain high relatedness within colonies despite having many queens. Most wasps are inside the nest, which consists of series of brood combs, like the one currently under construction on the bottom, covered by a paper envelope. Photo: Colin R. Hughes.

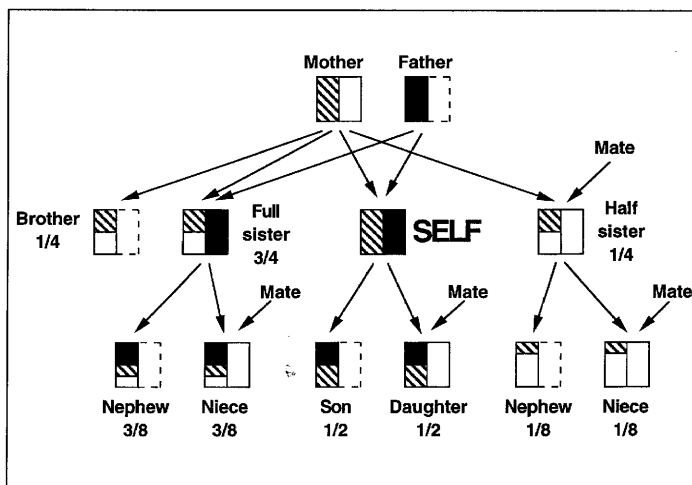
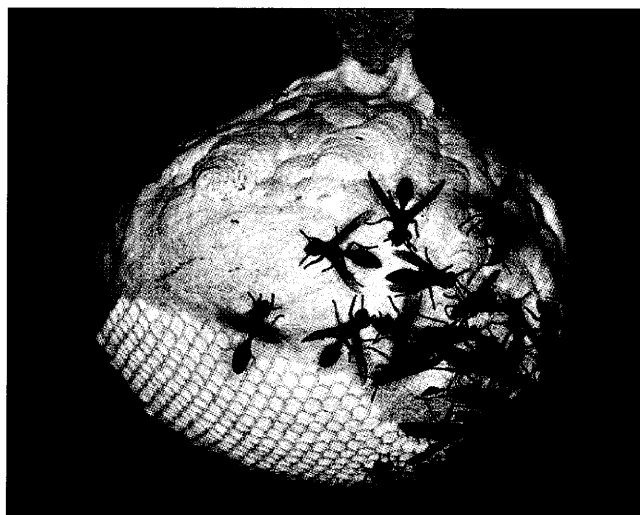


Figure 2. Haplodiploid pedigree showing relatednesses of a particular female, labeled SELF, to individuals she might raise. Her genotype at any given locus consists of a paternally derived allele (solid bar) and a maternally derived allele (cross-hatched bar). The same patterns are used to show the presence of

copies of these two alleles in various relatives, with open bars representing other, unrelated alleles. In haplodiploid organisms, diploid females develop from fertilized eggs, and males develop from unfertilized eggs. Consequently, males are haploid; the space bordered by dashed lines indicates the absence of a paternal gene in males. Relatedness values of SELF to her relatives are given in the form of Hamilton's (1972) life-for-life coefficients, which incorporate a correction for the fact that twice as many genes are usually transmitted through females as through males. A key relationship is that of the female to her full sister. The female has a 50% chance of sharing her maternally derived allele with a full sister, but because her father has only one allele, she must always share the paternal allele with her full sister. Their relatedness is therefore 0.75, the average of 0.5 and 1.0. Under a standard diploid genetic system, the relatedness between diploid full siblings is 0.5 because the paternally inherited gene, like the maternal one, will have a 50% chance of being present in the sibling.

workers in the ants, bees, and wasps, whose haplodiploid genetic system generates peculiar relatedness patterns (Figure 2). In colonies headed by a singly mated queen, workers can allocate their effort between two kinds of reproductives: females, who are full sisters, related by 0.75, and males, who are brothers, related by 0.25 (Figure 2). If reproductive males and females are equally costly to produce, theory predicts a population equilibrium at three reproduc-

tive females for every reproductive male. This ratio is an equilibrium because the average male has a three-fold reproductive advantage over the average female—an advantage that is exactly balanced, from the worker point of view, by the fact that a brother carries only one-third as many of the worker's genes as a sister (Trivers and Hare 1976).

This relatedness asymmetry applies only when workers rear full sisters. Other common relationships

**Table 1.** Studies testing relatedness-based predictions for sex ratio differences among colonies of ants, wasps, and bees.

Species	Taxon	Prediction		Prediction successful?	Reference(s)
		More females in colonies with	More males in colonies with		
<i>Formica truncorum</i>	Ant	Singly mated queen	Multiply mated queen	Yes	Sundström 1994
<i>Formica exsecta</i>	Ant	Singly mated queen	Multiply mated queen	Yes	Sundström et al. 1996
<i>Formica sanguinea</i>	Ant	High worker relatedness	Low worker relatedness	No	Pamilo and Seppa 1994
<i>Formica podzolica</i>	Ant	Single queen	Multiple queens	Yes	Deslippe and Savolainen 1995
<i>Leptothorax longispinosus</i>	Ant	Single queen	Multiple queens	Yes	Herbers 1984
<i>Leptothorax acervorum</i>	Ant	Single queen	Multiple queens	Yes	Chan and Bourke 1994
<i>Myrmica tahoensis</i>	Ant	Single queen	Multiple queens	Yes	Evans 1995
<i>Myrmica detritinodis</i>	Ant	Single queen	Multiple queens	Yes	Evans <sup>a</sup>
<i>Rhytidoponera confusa</i>	Ant	Single queen	Multiple worker egg layers	Yes	Ward 1983
<i>Rhytidoponera chalybaea</i>	Ant	Single queen	Multiple worker egg layers	Yes	Ward 1983
<i>Parachartergus colobopterus</i>	Wasp	Single queen	Multiple queens	Yes	Queller et al. 1993
<i>Polybia occidentalis</i>	Wasp	Single queen	Multiple queens	Yes	Queller et al. 1993
<i>Polybia emaciata</i>	Wasp	Single queen	Multiple queens	Yes	Queller et al. 1993
<i>Protopolybia exigua</i>	Wasp	Single queen	Multiple queens	Yes	Queller et al. 1993
<i>Polistes exclamans</i>	Wasp	Original queen	Replacement queen	— <sup>b</sup>	Strassmann 1996
<i>Halictus rubicundus</i>	Bee	Original queen	Replacement queen	Yes	Yanega 1988, Boomsma 1991
<i>Augochlorella striata</i>	Bee	Original queen	Replacement queen	Yes	Mueller 1991
<i>Apis mellifera</i>	Bee	Singly mated queen	Multiply mated queen	Yes	Fuchs and Schade 1994
<i>Lasioglossum laevisimum</i>	Bee	High relatedness ratio	Low relatedness ratio	Yes	Packer and Owen 1994

<sup>a</sup>Jay D. Evans, University of Arizona, personal communication.

<sup>b</sup>Strong trend in the predicted direction was not statistically significant.

are all symmetric (Figure 2). For example, the queen is equally related to her sons and daughters and is therefore predicted to be selected to produce the Fisherian 1:1 ratio. Similarly, workers who rear half-siblings ( $r = 0.25$ ) or nephews and nieces ( $r = 0.375$ ) will also tend toward this 1:1 ratio. When males and females are not equally costly, the same conclusions hold for the ratio of investments; when the queen controls investment, the equilibrium is a 1:1 investment ratio, whereas under worker control the equilibrium investment ratio is 3:1, provided that the females reared are full sisters.

This marriage of sex ratio theory and kin selection theory successfully predicts a variety of interspecific sex ratio patterns (Trivers and Hare 1976, Nonacs 1986). Sex investment ratios are indeed more female biased in single-queen Hymenopteran societies than in those in which the relatedness asymmetry does not apply, including multiple-queen societies, solitary bees and wasps (where control of sex ratios must be maternal), termites (which are diploid), and slave-making ants (where workers are taken from other species and cannot evolve responses to the slave-maker queen's control strategies).

Within-species comparisons of sex ratios provide even more compelling

evidence for kin selection. One reason is that selection is predicted to lead to obvious specialization by different colonies on males and females (Boomsma and Grafen 1991, Pamilo 1991a). For example, consider a species in which some colonies are headed by singly mated queens and others by multiply mated queens. At first, one might think that workers in the single-queen colonies would produce a 3:1 ratio of females to males, whereas workers in the other colonies would produce a ratio closer to 1:1, but this combination is not an equilibrium. The population ratio of females to males will be between 1:1 and 3:1, so the average male will be somewhere between one and three times as successful as the average female. As a result, the threefold relatedness advantage to rearing sisters in singly mated colonies is not completely counteracted by the sisters' reproductive disadvantage, and workers in these colonies will benefit the most by specializing on rearing females. For parallel reasons, workers in the multiple-queen colonies would benefit the most by rearing males.

Colony differences in mate number, queen number, and queen replacement all create relatedness differences among colonies that are predicted to lead to some colonies

specializing on females and others on males. The predicted differences based on all three properties have now been found for at least 17 species of wasps, bees, and ants (Table 1). These outcomes would be extremely hard to explain unless kin selection theory, including the subsidiary theory that offspring (worker) interests differ from those of their parents, is correct. Mechanisms of worker control are likely to include male infanticide (Sundström et al. 1996) and physical distancing from the queen (Herbers 1984).

### The origin of altruism

If social insects have been useful for testing kin selection theory, the reverse relationship has been even more fruitful. Kin selection theory has guided research on social insects in a number of productive directions. For example, how do originally solitary species give rise to social descendants? Kin selection hypotheses for the origin of altruism can be conveniently divided into two categories, based on Hamilton's rule:  $r_b b > r_c c$ . One category, relatedness-centered hypotheses, require that  $r_b > r_c$ : the altruist is more related to the collateral relatives she cares for than to her own offspring. Fitness-centered hypotheses, by contrast, require

that  $b > c$ : the altruist can do more for the collateral relatives than she can for her own offspring. It is important to remember that both relatedness and fitness are required. The two kinds of hypotheses differ only with respect to which factor, relatedness or fitness, tips the balance in favor of altruism.

**The haplodiploid hypothesis.** Hamilton's haplodiploid hypothesis (Hamilton 1964, 1972) is the only serious relatedness-centered hypothesis. The first-born child of the union of kin selection theory and social insects, its beauty brought its parents great renown. It seemed that most of what was important about social insects could be explained by focusing on genetic relatedness. Most social insects are haplodiploid, it was argued, because only in haplodiploids does the special 0.75 relatedness among full sisters make it more profitable to raise siblings than offspring ( $r_b > r_c$ ). This high relatedness applies only among females, explaining why workers are always female in the haplodiploid Hymenoptera, but not in the diploid termites. Finally, because this relatedness advantage applies only when raising sisters, it can explain why workers sometimes still produce sons.

However, many now think that despite its early promise, the haplodiploid hypothesis has not aged particularly well (Evans 1977, Andersson 1984, Strassmann and Queller 1989, Alexander et al. 1991, Seger 1991). The haplodiploid advantage turns out not to be so simple. Because the high relatedness to sisters ( $r = 0.75$ ) is balanced by low relatedness to brothers ( $r = 0.25$ ), workers gain by rearing siblings instead of offspring only if workers lay the male eggs or if workers can concentrate on raising sisters while males are produced by solitary females (Trivers and Hare 1976, Seger 1983, Grafen 1986, Godfray and Grafen 1988). These conditions often do not apply, at least in contemporary species. Moreover, relatedness among females is often well below the full-sister value of 0.75, due to multiple egg layers or multiple mates (Crozier and Pamilo 1996). Haplodiploidy might have provided a temporary relatedness advantage that persisted

**Table 2.** Differences in characteristics of two types of social insects.

Characteristic	Fortress defenders	Life insurers
Taxa	Thrips, aphids, beetle, termites	Ants, bees, wasps
Main advantage of grouping	Valuable, defensible resource	Overlap of adult lifetimes to provide extended care to young
Food	Inside nest or protected site	Outside nest
Juveniles	Active; feed selves and may work	Helpless; need to be fed and do not work
Nonsocial ancestors	Not necessarily parental	Highly parental
First specialized caste to evolve	Soldiers	Foragers
Colony size	Usually small	Often large
Ecological success	Usually limited	Extensive

long enough for the evolution of fitness-related efficiencies that would allow sociality to be maintained (Trivers and Hare 1976), but this hypothesis is difficult to test.

There are also alternative explanations for the three principal phenomena explained by the haplodiploid hypothesis (Evans 1977, Andersson 1984, Strassmann and Queller 1989, Alexander et al. 1991, Seger 1991). The fact that most cases of altruism are found in the Hymenoptera might be due to the unusually high frequency in this group of parental care, a useful precursor for evolving care of the young of others. Moreover, the providers of this parental care in the Hymenoptera have historically been female, so workers may be female simply because female-specific adaptations for nest building, homing, capturing and transporting of prey, and stinging have been extended to a helping context. Finally, the fact that workers sometimes produce sons, but not daughters, could simply reflect the fact that daughter production requires the extra effort of mating.

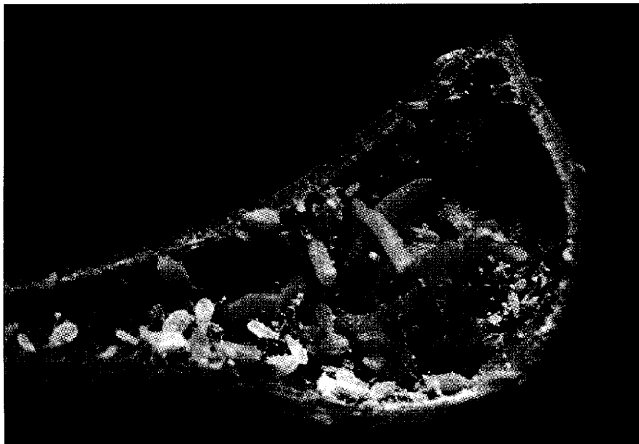
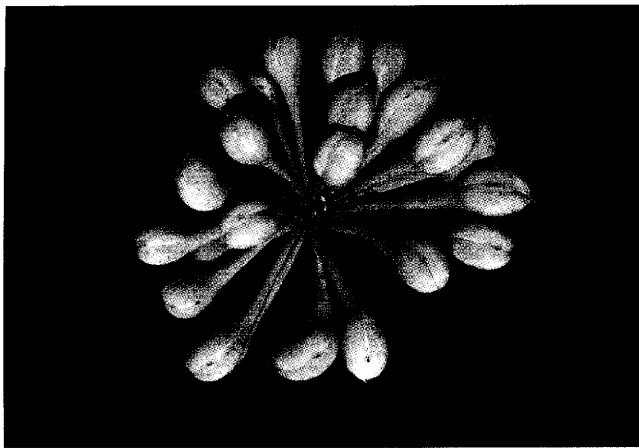
**Fortress defenders and life insurers.** The haplodiploid hypothesis has been so influential that it is sometimes confused with the much more general theory of kin selection itself. Its decline has, therefore, sometimes led to the misimpression that kin selection theory has proven inadequate. Hamilton's rule ( $r_b b > r_c c$ ) can still be satisfied even when the altruists are less related to their beneficiaries than

to their own offspring ( $r_b < 0.5$ ) if the altruist provides enough gain for sufficiently little cost, that is, if  $b > c$  (West-Eberhard 1975). As noted above, many female Hymenoptera have abilities that could make them effective workers. However, the question still needs to be answered: How can an individual provide greater gains to a colony than to her own offspring, even though she carries out the same kinds of tasks in each case?

There are many ways in which groups of individuals can organize their work synergistically (Oster and Wilson 1978, Jeanne 1986, Gordon 1996), but, as a rule, these synergisms must evolve after cooperation has been initiated for other reasons. One exception might arise if females in poor condition are unable to function well as reproductives but are still able to function well as helpers (West-Eberhard 1975, Craig 1983); another exception could arise if grouping provides better defense against predators—two stings might be more than twice as effective as one. Neither advantage of cooperation appears to apply generally in primitively social insects, such as paper wasps (*Polistes annularis*; Strassmann and Queller 1989, Reeve 1991).

However, predation can select for sociality in other ways. We propose that insect sociality evolved under two regimes, one involving escape from predation and the other permitting an escape from one of its effects. These regimes define two distinct advantages of sociality (Table 2),

**Figure 3.** A fortress defender. (top) A gall induced by an aphid foundress of the genus *Astegopteryx* in peninsular Malaysia. The gall provides a defensible feeding site that can accommodate numerous individuals. (bottom) A cross-section of a portion of the gall. Larvae of all stages and adults can be found inside the subgall, but only the soldiers, which are specialized second-instar larvae, will leave the gall to defend it. Soldiers also guard the small entrance to the gall and clean the gall of shed skins and honeydew. Toward the end of the season winged adults will develop and leave the gall through the ostiole to disperse to new host plants. The function of the finger-like projections on the inside of the subgalls is unknown. Photos: David L. Stern.

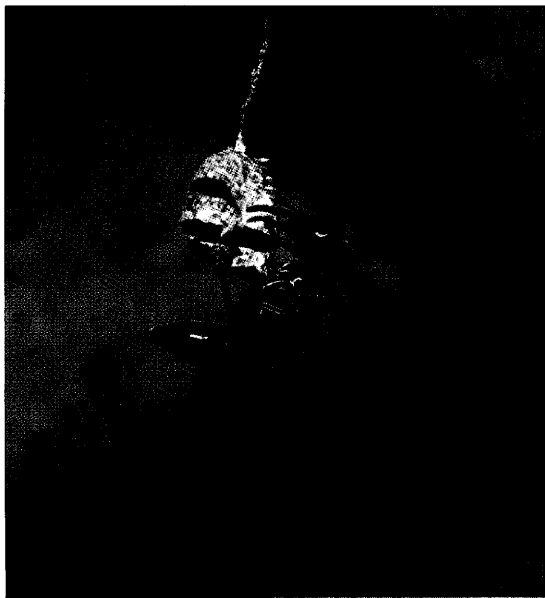


which we call fortress defense and life insurance.

Fortress defenders nest and usually feed inside a protected site (Figure 3). Staying at home and helping may be favored if the home site is defensible and can accommodate numerous individuals, and if procuring a new site is difficult (Andersson

1984, Alexander et al. 1991, Crespi 1994). Termites nesting in deadwood provide the most familiar example. Several groups of newly discovered social insects have similar fortress-food resources: galleries through living wood for a beetle species (Kent and Simpson 1992), and galls for a number of species of aphids (Aoki 1987, Stern and Foster 1996) and thrips (Crespi 1992).

**Figure 4.** A life insurer. This wasp in the genus *Mischocyttarus* has started a new nest, which hangs by a long, slender pedicel. Her chances of success are similarly slender, for she must undertake perilous foraging trips to feed her young. If she dies, her effort is wasted because all her dependent young will also die. If she does succeed in producing adults, they can gain a life-insurance advantage by staying as workers. Foraging is just as dangerous to the individual worker, but if she dies, her previous work is not wasted because other workers carry on her investments.



By contrast, the life-insuring ants, bees, and wasps must generally forage outside their nest, risking frequent exposure to predators (Figure 4). Grouping does not itself reduce predation mortality, but it can act as a kind of life insurance against one of the consequences of mortality—the loss of all dependent brood. When a solitary adult dies young, it will lose all of its partially reared, dependent young. Therefore, when adult lifetimes are typically short, extended care to young can be reliably provided only through the overlap of adult lifetimes. Individuals in groups can carry on the work of their predecessors and have their own investments completed by their successors, and the advantage accruing from this life insurance can be large (Queller 1989, 1994, 1995, Strassmann and Queller 1989, Gadagkar 1990, Reeve 1991).

Some of the differences between life insurers and fortress defenders are summarized in Table 2. Life insurers evolved from ancestors that provided parental care to their helpless young, just as many extant solitary bees and wasps do. The key role of the first workers was foraging. Fortress defenders differ in each of these attributes (Table 2). In addition, the specialized site requirements of fortress defenders often limit both colony size and ecological success; it is probably no accident that aphids, thrips, and beetles were only recently discovered to be social. The termites are a glaring exception to this rule, for a clear reason: They have been highly successful because their resource, cellulose, is particularly abundant and free of competitors. The life insurers' advantage—overlap of adult lifetimes—continues to apply at large colony sizes, which may explain why ants, bees, and wasps all have representatives with large colonies. The externally foraging life insurers also have greater potential than fortress defenders to expand their ecological domains by exploiting a variety of food sources.

If we are correct that social insects are divided into these two categories, the hope for a universal ecological explanation of cooperative breeding may be doomed. At least two distinct advantages of sociality apply in insects, and neither appears to apply to most social vertebrates. Al-

though two species of mole rats can be classified as fortress defenders (e.g., Sherman et al. 1991; as can a social shrimp, Duffy 1996), social vertebrates as a whole do not seem to fit either pattern. Kin selection may still explain the evolution of vertebrate sociality, but with ecological pressures, such as territory saturation and group hunting (Emlen 1991), that differ from those in social insects.

## Conflicts in the colony

Kin selection theory has solved the general question of how altruism can evolve in the social insects. As important as this accomplishment was, it did not in itself fundamentally alter how social insect colonies are viewed—that is, they could still be regarded essentially as superorganisms. However, this view was deeply shaken by another part of kin selection theory because, in posing the question of when social insects should be altruistic, Hamilton (1964, 1972) also had to ask when they should be selfish.

The sting of the honeybee (*Apis mellifera*) elegantly illustrates the contrast between altruism and selfishness (Hamilton 1964). The workers' sting is a perfect example of an altruistic adaptation. Its barbs anchor in the victim, eviscerating and killing the worker, whose only compensation is the rescue of her kin from danger. The queen's sting is specialized for a diametrically opposite end. It is nearly unbarbed (Erickson et al. 1986) and is curved like the stings of Hymenopteran social parasites, which are specialized for stinging other Hymenoptera (Hamilton 1972). A queen uses her sting solely for the ultra-selfish purpose of killing her own sisters, her potential rivals for the queenship. This behavior makes sense because when there are not enough workers to serve two queens, each queen should prefer that her own offspring be raised instead of her sister's (Figure 1). Kin selection theory predicts both altruism and selfishness, and Hamilton's rule specifies the conditions for each.

Thus, the altruistic side of kin selection turned out to have an evil twin. This more sinister offspring of kin selection has been slower to de-

velop, but it has had surprising and potentially far-reaching effects. The theory showed that social insect colonies might not be as cooperative as they seem on the surface. Instead, each individual might pursue an independent agenda for furthering her own genetic success. The fact that queens might sometimes compete for egg-laying rights is, perhaps, not too surprising. Less expected, however, was that workers would compete for rights to lay haploid male eggs (Cole 1981). Most surprising of all were the varieties of strategies that even nonlaying workers might employ to ensure genetic success.

In the most extreme scenario, each worker might assess her relatedness to each colony mate encountered and always favor closer over more distant kin, for example, feeding only full sisters and rejecting half-sisters. This possibility has proven difficult to test, with some early positive results in honeybees being challenged on the basis of statistical bias and artificial conditions (Carlin and Frumhoff 1990, Breed et al. 1994). The bulk of the evidence suggests that social insects do not perform this kind of discrimination (Keller 1997), although it would be premature to assert that they never do.

Although this most extreme case of conflict may not apply, other conflicts clearly exist, and workers sometimes win. This conclusion is supported most clearly by the sex ratio studies discussed earlier (Table 1); workers successfully modify sex ratios away from the queen's optimum and toward their own. Kin selection theory also predicts other conflicts that have not been thoroughly tested. Workers could choose among potential queens (Forsyth 1980, Bourke and Franks 1995) or even kill their only queen if doing so gives them a high enough return through rearing their own males (Bourke and Franks 1995). They might also choose nonrisky tasks or no tasks at all to increase their chances of eventually laying eggs (West-Eberhard 1981).

The discovery of these real and potential conflicts within social insect colonies wounded the superorganism paradigm. The blithe assumption that workers must be acting for the good of the colony has been shown to be suspect. If sterile work-

ers retain their own distinct reproductive interests and strive to enforce them, how much harmony can there really be?

## Reprise of the superorganism

The blow to the superorganism was serious but not fatal; there have lately been signs of recovery (Seeley 1989, Wilson and Sober 1989, Moritz and Southwick 1992, Ratnieks and Reeve 1992). There are two reasons for the reprise of this paradigm. First, in spite of potential conflicts, social insect colonies are undoubtedly highly cooperative and integrated. Second, the bar has been lowered by parallel studies of conventional individual organisms, which have shown that even individual organisms have internal conflicts involving meiotic drive, organellar genomes, B chromosomes, transposable elements, and genomic imprinting (Hurst et al. 1996). Social insect colonies may fail to meet the standard of perfect harmony, but some might still be as harmonious as organisms.

The reality of both conflict and cooperation suggests a twofold challenge for the future. The first challenge is to determine how widespread conflict really is, particularly in the more advanced societies. How superorganismal are these societies? A strict classification into superorganismal and non-superorganismal societies seems unlikely because the gradation may be nearly continuous and multidimensional (Ratnieks and Reeve 1992); however, this fact does not make the effort less worthwhile. Indeed, comparative study of various stages of social organization should aid in addressing the second challenge, which is to explain how extensive cooperation can evolve in the face of conflicting interests.

A key issue is who gets to reproduce. Even if biologists understand why colonial life is better than nesting alone, we still need to explain why one or a few individuals in each colony get to reap all the direct benefits of colonial life (Ross and Fletcher 1985). Although helping may be advantageous, being helped is often even more advantageous. So what prevents societies from breaking down due to the efforts of each individual to be a favored reproductive?

Part of the problem is to explain how worker reproduction is limited, but the general question is larger. Daughter queens should also be tempted to reproduce in the natal nest, particularly in species with large colonies. For example, if the average successful nest produces 100 female reproductives, then in a stable population only 1 in 100 of these reproductives can expect to initiate a new successful colony. A daughter's expected direct reproduction would be as high if she could obtain only a one-hundredth share of an established colony. Although both worker egg-laying and multiple queens indeed occur, both are limited despite their clear direct reproductive advantages. There are two possible explanations for the limits: self-restraint due to indirect inclusive fitness costs, and restraint imposed by others.

Workers that are morphologically specialized as helpers might exercise reproductive self-restraint to focus on the job that they do best, but as a general explanation of queen reproductive monopoly, this hypothesis fails on several counts. First, the effectiveness of helping should only increase the attractiveness of usurping a portion of that help. Workers may be less effective reproducers than queens, but what is to keep them from laying as many eggs as they are able? Indeed, they sometimes do reproduce by producing sons (Bourke and Franks 1995). Second, the explanation assumes what it seeks to explain: How did these worker specializations evolve, given the attractiveness of direct reproduction? Third, this explanation does not explain reproductive restraint in the many species lacking specialized worker castes. Finally, even if it explained worker restraint, it cannot explain why daughter reproductives refrain from usurping part or all of the output of their natal colony.

Self-restraint can, however, evolve for two reasons other than prior worker specialization. First, selection can favor peaceful settlement—even an arbitrary settlement—if the settlement reduces high costs to the colony (Maynard Smith and Parker 1976, Ratnieks and Reeve 1992, Pollock 1996). Arbitrary cues appear to be used in some paper wasps because, although size determines

fighting ability, older individuals take precedence in queen succession even if they are smaller (Hughes and Strassmann 1988).

Second, for haplodiploid species, there may be a relatedness cost to reproducing, even if total colony production stays the same. If a female stays in her natal colony and replaces the queen's eggs with her own, she may be replacing sisters ( $r = 0.75$ ) with daughters ( $r = 0.5$ ), a poor tradeoff (Figure 2). However, this explanation does not work for male production: It is better to rear sons ( $r = 0.5$ ) than brothers ( $r = 0.25$ ). Moreover, relatedness to the replaced females often falls below the 0.75 maximum and sometimes below the 0.5 relatedness to daughters (Crozier and Pamilo 1996). This lower relatedness is always true when the reproductive rivals come from the same generation, as often occurs when the original queen dies or when new colonies are begun by cooperating foundresses (compare offspring with nephews and nieces in Figure 2).

When self-restraint fails, restraint may still be imposed by other members of the colony. The queen will be selected to prevent replacement of her eggs by less related ones (West-Eberhard 1975) or, possibly, to allow subordinates just enough direct reproduction to induce them to stay and help (Reeve 1991, Ratnieks and Reeve 1993). However, this solution seems inadequate for larger, more advanced societies because one queen is unlikely to physically dominate thousands of other individuals. Queen pheromones sometimes inhibit reproduction of others, but this fact does not necessarily imply queen control, because the response to the pheromone evolves via the responders' inclusive fitness (Keller and Nonacs 1993).

A particularly attractive alternative explanation for reproductive restraint is collective worker control, or worker policing. Workers control sex ratios, so they may also control reproductive rights. Even if a worker prefers to reproduce (at least via sons), she may be held in check by other workers (Starr 1984, Woyciechowski and Lømnicki 1987, Ratnieks 1988). Suppose a worker can choose between raising the son of a queen or of another worker. If

workers are full sisters, they ought to prefer raising each other's sons ( $r = 0.375$ ) over brothers ( $r = 0.25$ ; Figure 1). But if workers are usually half-sisters, as in honeybees, then they should be selected to suppress each other's male production ( $r = 0.125$ ), allowing their mother to produce the males. As yet, there is little evidence for this theory of worker policing, although there is some support from intraspecific comparisons (Ratnieks 1990), and it does successfully predict that honeybee workers should eat eggs laid by other workers (Ratnieks and Visscher 1989).

Although worker policing theory has focused on male production, it offers a potential solution to the larger problem of how queens can maintain a reproductive monopoly when self-restraint and queen dominance fail. Who should lay the fertilized female eggs? A worker should prefer to rear sisters rather than sisters' daughters (Figure 2). Paper wasp workers display this preference, joining a new nest headed by their mother but not one headed by their sister (Strassmann 1981). By the same logic, workers are expected to prevent inseminated sisters from reproducing in the natal colony (unless the current queen cannot supply enough eggs; Ratnieks 1988, Pamilo 1991b). In this respect, the interests of the workers and the current queen often converge, but instead of a lone queen facing down many possible usurpers, she has the assistance of the entire worker force. Such worker control seems likely in stingless bees. Daughter queens are often present as a reserve, but they are harried by workers and sometimes imprisoned in wax cells. A few are allowed to reproduce when they are needed for a reproductive swarm or to replace a presumably failing queen, but most are eventually executed by workers (Engels and Imperatriz-Fonseca 1990).

Thus, there may be two kinds of external control over who reproduces. In smaller societies, one queen may dominate by force or by threat of force. However, in larger societies, despotism may give way to something more like a constitutional monarchy: The queen serves with the collective consent of her subjects, and the subjects may retain certain



rights (i.e., producing males, adjusting sex ratios). Each subject might aspire to be queen but is kept in place by her peers.

### Prospects for the future: molecular genetic markers

We have suggested that important tasks for the future are to understand both the extent of conflicts of interest and how they are resolved. The prospects for success look particularly good because of the advent of new types of hypervariable molecular genetic markers (Evans 1993, 1995, Fondrk et al. 1993, Mueller et al. 1994, Oldroyd et al. 1994, Estoup et al. 1995, Strassmann et al. 1996). These markers serve two purposes. First, to understand conflicting kin-selected interests within colonies, one must estimate genetic relatedness, which can be inferred from the degree of marker sharing above random levels (Queller and Goodnight 1989). Second, to determine whose interests are in fact being served, it is necessary to know who reproduces and how much they reproduce. When parentage is not obvious, it can be determined by comparing markers in offspring and putative parents.

Recent studies of the rules for queen succession in a paper wasp illustrate both of these uses for molecular markers (Peters et al. 1995, Queller et al. 1997). In the paper wasp *P. annularis*, colonies are started in the spring by several related females, called foundresses, who compete for egg-laying rights. The high relatedness of foundresses makes it difficult to determine parentage of their progeny with genetic markers, but it proved possible with a set of seven variable microsatellite loci, together with a trick. The trick takes advantage of the ability to score microsatellite genotypes from tiny amounts of tissue using DNA that has been amplified by the polymerase chain reaction. When the sperm stored in each foundress's spermatheca is amplified, one obtains the genotypes of her mate, even though the mates had not been observed or collected. With both maternal and paternal genotypes known, unambiguous assignments of offspring were achieved (Peters et al. 1995). Many foundresses reproduced, but,

as a rule, one gradually emerged as the dominant queen in each colony.

The first brood of offspring reared by the foundresses consists mainly of females who are called workers because that is the role they usually play. However, they can mate and become queens. In most colonies, the original queen dies before the end of the season, and a successor takes over. To ask if collective worker preferences determine who succeeds the queen, the same microsatellite markers were used to estimate average worker relatedness to the progeny that would be produced by different classes of queen successor. On the basis of relatedness to potential brood, workers should prefer a random worker successor over a subordinate foundress, and a young worker over an old one. However, the actual succession rules are the opposite: a subordinate foundress takes over first, and if only workers remain, an older worker becomes queen. Obviously, the collective worker control hypothesis cannot explain these results. However, it does not necessarily follow that the outcome results from individual dominance of the winner, because older workers win in spite of the fact that they are often smaller than younger workers. Perhaps the costs of conflict to win the queenship are high, and age is used as the cue for a conventional settlement.

The answers to the question of how conflicts of interest are resolved may, of course, differ for different species and in different contexts, but the general approach is widely applicable. The new molecular markers, combined with traditional observation and experiment, promise to reveal much more about who reproduces and whose interests are served. The next challenge for kin selection theory will be to use these tools to explain the evolution of the superorganisms it once seemed to deny.

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