# Cooperation among Selfish Individuals in Insect Societies

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**I**nsect societies have long been perceived as being perfectly well organized groups of altruistic individuals engaged in peaceful cooperation. Indeed, the essential characteristics of the eusocial insects (which include all termites and ants, as well as many bees and wasps) is the reproductive altruism of workers. Workers are generally sterile and do not reproduce, whereas other individuals—the queens and the males—specialize in reproduction. Hence, workers forego their own direct reproduction to participate in cooperative tasks such as building the nest, collecting food, rearing the young, and defending the colony. The evolution of reproductive division of labor constitutes the epitome of altruism and self-sacrifice, and it seems paradoxical given the emphasis on the "survival of the fittest" in Darwin's theory of natural selection.

In a set of seminal papers, William D. Hamilton (1963, 1964a, 1964b) provided the key theory to resolve this apparent paradox. Hamilton's theory, known as "kin selection," states that individuals can transmit copies of their own genes, not only directly, through their own reproduction, but also indirectly, by favoring the reproduction of kin, such as siblings or cousins (see box page 900). In fact, kin share identical copies of genes inherited from their common ancestors in exactly the same way that a child possesses copies of paternal and maternal genes. By helping their mother to produce numerous fertile offspring (the males and the future queens), sterile workers are able to transmit copies of their own genes to the next generation.

There is currently no doubt that kin selection has been the all-important selective force for the evolution of eusociality and reproductive altruism by workers (Bourke and Franks 1995, Crozier and Pamilo 1996, Bourke 1997, Queller and Strassmann 1998). Numerous genetic studies in insects, other invertebrates, and vertebrates have shown that eusociality evolved in groups of highly related individuals, such as one mother and her offspring. However, kin selection theory also predicts that the colony should be the scene of potential conflicts because, in contrast to the cells of an organism, colony-mates are not genetically identical (Ratnieks and Reeve 1992, Keller and Ross 1998, Keller and Reeve 1999). Individuals have partially divergent genetic interests and may attempt to favor the propagation of their own genes, possibly to the detriment of their nestmates. Indeed, life within the colony is not always as harmonious as it may first appear, and recent studies

> KIN SELECTION IS THE KEY TO UNDERSTANDING THE EVOLUTION OF COOPERATION IN INSECT SOCIETIES. HOWEVER, KIN SELECTION ALSO PREDICTS POTENTIAL KIN CONFLICTS, AND UNDERSTANDING HOW THESE CONFLICTS ARE RESOLVED IS A MAJOR GOAL OF CURRENT RESEARCH ON SOCIAL INSECTS.

demonstrate that individuals use Machiavellian and sometimes subtle strategies to favor their own interests.

Hence, kin selection predicts a dynamic equilibrium between cooperation and conflict. The evolution and maintenance of cooperation at the level of the colony depend largely on the resolution of potential conflicts among selfish individuals. Understanding how conflicts between selfish replicating units are resolved and how cooperation emerges at a higher level of biological organization has become a major area of research in evolutionary biology. Interest in this field has been bolstered by Szathmary and Maynard Smith (1995), who pointed out that the evolution of complex life forms has occurred through a few major transitions whereby groups of relatively independent, cooperating entities cohered into more integral wholes that then became the central "units of selection" (e.g., genes in cells, cells in organisms, and organisms in societies). Social insects provide an ideal system to study the emergence of higher evolutionary units (in this case, colonies) and the means by which conflicts between lower-level units (individuals) are suppressed or minimized.

In insect societies, the resolution (i.e., evolutionarily

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## Hamilton's kin selection theory

William D. Hamilton spelled out kin selection theory by defining the conditions under which altruism is selected. Hamilton's rule involves three terms: the change in the actor's personal fitness, the change in the recipient's personal fitness, and the relatedness between the actor and the recipient. The degree of relatedness is a measure of the genetic similarity between the two individuals; it is equal to the probability that a random gene of the recipient has an identical copy, by descent, in the actor. Hence, a general description of Hamilton's rule is that altruistic acts are more likely to be selected for when individuals are closely related and when the decrease in the actor's personal fitness is relatively small compared to the increase in the recipient's fitness.

An individual helping a relative indirectly promotes the transmission of copies of its own genes to the next generation. How many of its genes will be transmitted depends on the relatedness between both individuals, the benefit that the altruistic act brings to the recipient, and the cost of acting to the altruistic individual. Benefits and costs typically represent differences in the number of descendants produced. If the degree of relatedness between an actor and a recipient is $r$, the cost to the altruistic individual is $c$, and the benefit for the beneficiary is $b$, the altruistic act will be favored when:

$$br - c > 0$$

A simple example serves to illustrate Hamilton's rule. Imagine a gene that causes an individual to die so as to save relatives' lives. One copy of the gene will be lost if the altruist dies, but the gene will increase in frequency in the population if, on average, the altruistic act saves the lives of more than two siblings ($r = 0.5$), more than four nephews or nieces ($r = 0.25$), or more than eight cousins ($r = 0.125$). J. B. S. Haldane fully apprehended kin selection theory and Hamilton's rule when he announced, having done some calculations on an envelope in a pub, that he would be ready to give his life to save two brothers or eight cousins!

selection, considerable research has focused on identifying the factors that allowed the evolution of worker sterility. The most common approach has been to use Hamilton's rule (see box at left) to determine whether a given female might gain greater inclusive fitness by forgoing direct reproduction to help boost that of her kin. Hamilton's rule describes how the behavior of a focal individual affects the overall transmission of copies of its genes to the next generation. Ultimately, Hamilton's rule defines the conditions under which an altruistic behavior is maintained by kin selection.

However, conflicts of interest between colony members might also influence the evolution of altruism and the partitioning of reproduction, and these aspects of social interactions are not explicitly taken into account in Hamilton's rule. Moreover, other members of the social group might be able to alter the focal individual's options with respect to helping or reproducing. For example, even if the focal individual would maximize its inclusive fitness by reproducing, other colony members may prevent it from doing so by aggression or egg destruction.

The divergent interests of colony members and their ability to influence one another's reproductive options by coercion or bribing can now be considered with the recent development of reproductive skew models, which are extensions of Hamilton's rule. These new models include ecological, genetic, and social factors in a single explanatory framework and aim to determine how these factors jointly influence the apportionment of reproduction (reproductive skew) among colony members (Emlen 1982, Vehrencamp 1983, Reeve and Ratnieks 1993, Keller and Reeve 1994). In essence, reproductive skew models delineate the possible reproductive strategies available to a focal individual and define the conditions under which the best option for this individual is to cooperate and sacrifice part or all of its direct offspring production. Reproductive skew models achieve this goal by incorporating interactions between social partners and explicitly addressing the question of how conflicts of interest between selfish units are resolved.

Reproductive skew models assume that all colony members have similar reproductive abilities, the likely condition under which reproductive altruism and eusociality evolved. So far, most skew models have been developed for groups of two individuals, one dominant and one subordinate, and they assume that the subordinate has three options: remain in a colony and cooperate peacefully, fight with the dominant to gain exclusive control of the colony's resources, or leave the colony to reproduce independently. Another critical assumption of most skew models is that the dominant has control over the reproduction of the

stable outcome) of potential conflicts among individuals can range from high levels of actual conflict to the complete absence of actual conflict. Overall, the degree of peaceful cohesion of insect societies appears to depend critically on their genetic composition, their size, the benefits and costs of group membership and cooperation, and the benefits and costs of selfish behavior and policing (i.e., the suppression of selfish acts by other group members through aggressive acts and coercion). In the following sections, we outline five major areas of potential conflicts among colony members and discuss recent theoretical and empirical studies of how potential conflicts are resolved.

## Conflicts over partitioning of reproduction

Because the evolution of eusociality was thought to contradict the very principles of Darwin's theory of natural

subordinate (these are the so-called optimal skew models). If the dominant individual benefits from retention of the subordinate, then it may be beneficial for the dominant individual to leave some reproduction to the subordinate as inducement for the subordinate to remain in the colony and not fight to the death for complete reproductive control. Hence, the optimal skew model delineates the ecological, genetic, and social circumstances under which groups are stable, as well as the magnitude of reproduction forfeited by the dominant.

The optimal skew model predicts that four parameters will affect partitioning of reproduction in a colony (Reeve and Ratnieks 1993, Keller and Reeve 1994): the expected success of a subordinate that reproduces alone, the colony's overall productivity if the subordinate cooperates, the genetic relatedness among colony members, and the probability that a subordinate would win a fatal fight with a dominant individual. Reproductive skew will increase when one of the following occurs: ecological constraints on independent breeding increase (because subordinates can expect only small payoffs for leaving and breeding independently); colony productivity increases (because enhanced colony productivity reduces the attractiveness of the leaving and fighting options for the subordinate); the relatedness between a dominant individual and a given subordinate is high (because subordinates that are more closely related to dominants automatically receive larger indirect benefits for cooperating peacefully and therefore require smaller direct reproductive inducements for such cooperation); or fighting ability of the subordinate is low (because subordinates with lower fighting ability will be less tempted to engage in a lethal fight for complete reproductive rights).

In addition, Reeve and Keller (1995) showed that the asymmetry in relatedness occurring in mother–daughter associations should tend to increase the degree of skew compared to sibling associations. This relative increase reflects the fact that in mother–daughter associations, the mother is predicted to reproduce more than her daughter because she is twice as related to her own offspring than to her daughter's offspring, whereas the daughter is equally related to her mother's offspring and to her own offspring. In contrast, siblings are equally related to one another's offspring; therefore, they are predicted to share reproduction more evenly. The effects of these various parameters
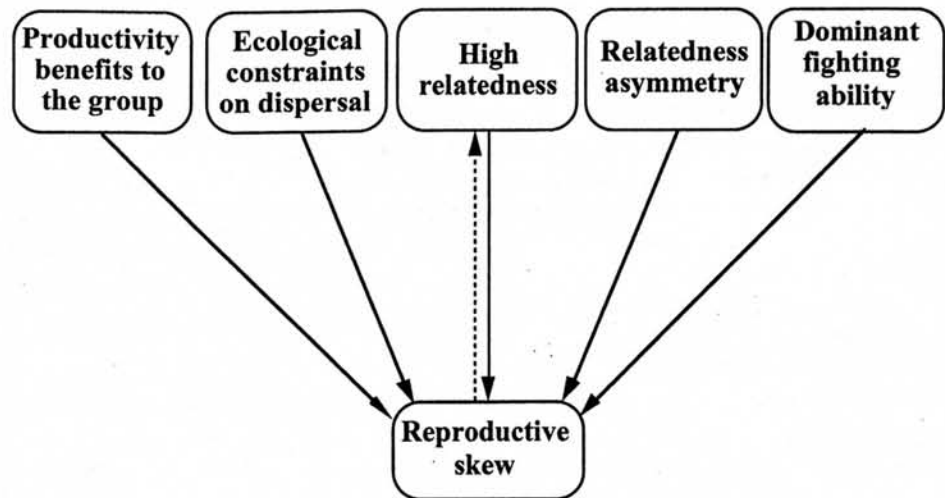


*Figure 1. Factors that, under optimal skew models, increase the stable level of reproductive skew. Summary is based on the models of Vehrencamp (1983), Reeve and Ratnieks (1993), and Reeve and Keller (1995). Increased skew can also result in increased relatedness when individuals are recruited from within the group (dashed arrow) because increased skew decreases the effective number of breeders, thereby increasing the average relatedness of individuals produced (Heinze 1995).*

on reproductive skew are illustrated in Figure 1.

Another prediction of the optimal skew models is that intra-colony aggression should generally be higher in groups of relatives than in groups of less-related individuals (Keller and Reeve 1994) because higher relatedness leads to high skew, and high skew leads to higher payoffs for the aggressive testing of dominants by subordinates and thus advertisement of fighting ability by dominants and subordinates.

The available data are consistent with these predictions. Both intra- and interspecific comparisons in vertebrates and invertebrates indicate that skew tends to be higher in groups consisting of individuals of higher relatedness (Keller and Reeve 1994, Reeve et al. 1998). A good example of the predicted association between high relatedness and high skew comes from the eusocial naked mole-rat, *Heterocephalus glaber*. In this mammal, only one of up to several hundred females monopolizes colony reproduction, and this tremendous skew is associated with extraordinarily high levels of inbreeding, which lead to an intra-colony relatedness (average proportion of shared genes) of greater than 0.80 (Reeve et al. 1990). (It should be noted, however, that because high skew leads to high within-colony relatedness, additional studies will be required to uncover the causal role of relatedness in the evolution of skew.)

Also consistent with predictions from optimal skew models, skew is generally higher in mother–daughter than sibling associations (Reeve and Keller 1996). Moreover, a comparative study of leptothoracine ants suggests that high skew is associated with high relatedness, high ecolog-

ical constraints, and high levels of intra-colony aggression (Bourke and Heinze 1994). However, because almost all of these studies are correlative, it is not possible to rule out the potential effects of confounding variables. Moreover, few attempts have been made to test the assumptions of optimal skew models. Recently, several alternative models based on different assumptions have been developed; the predictions of these new models differ in part from the ones of optimal skew models.

In an effort to devise one alternative model, Reeve et al. (1998) investigated the consequences of the dominant individuals not having full control over breeding of the subordinates. In this case, reproduction by subordinates results from dominants being unable to prevent subordinates from reproducing, rather than dominants yielding some reproduction to subordinates as an inducement to stay and cooperate peacefully. One important prediction of this "incomplete control" model is that reproductive skew should either decrease with or be insensitive to the genetic relatedness between the subordinate and the dominant. This prediction reflects the fact that, as relatedness increases, both the dominant and the subordinate are predicted to reduce their efforts to selfishly enhance their direct reproduction, resulting in little net change in skew, or only the dominant is predicted to decrease its effort, resulting in a reduction in skew. The empirical evidence for a positive relationship between relatedness and skew in vertebrates and invertebrates seems inconsistent with this prediction; however, as mentioned by Reeve et al. (1998), many of the vertebrate and some of the invertebrate cooperative systems involve groups of parents and offspring, with the consequence that dominant and subordinate are asymmetrically related to one another's offspring. In such cases, the incomplete control models, like optimal skew models for groups of two individuals, predict maximum skew in favor of the dominant parent. Studies in which relatedness is experimentally manipulated in groups that are otherwise similar are needed to test which model better describes reality.

In another type of model, Johnstone and Cant (1999) assumed that the dominants have no control over reproduction of subordinates but instead have the power to evict the subordinates, at some cost. To prevent eviction, subordinates may refrain from direct reproduction. This model makes predictions opposite to the optimal skew model. Low skew is expected with high benefits of cooperation, high relatedness, and strong ecological constraints. The available data seem more in line with predictions of the optimal skew models than of the "eviction" model, but again, critical tests of the models will require experimental manipulation of the variables predicted to influence skew.

Two new studies have modified the skew models to incorporate the possibility that subordinates will inherit colony resources (Kokko and Johnstone 1999, Ragsdale in press). These modified models show that delayed benefits from acquiring dominant status in the future (e.g., if
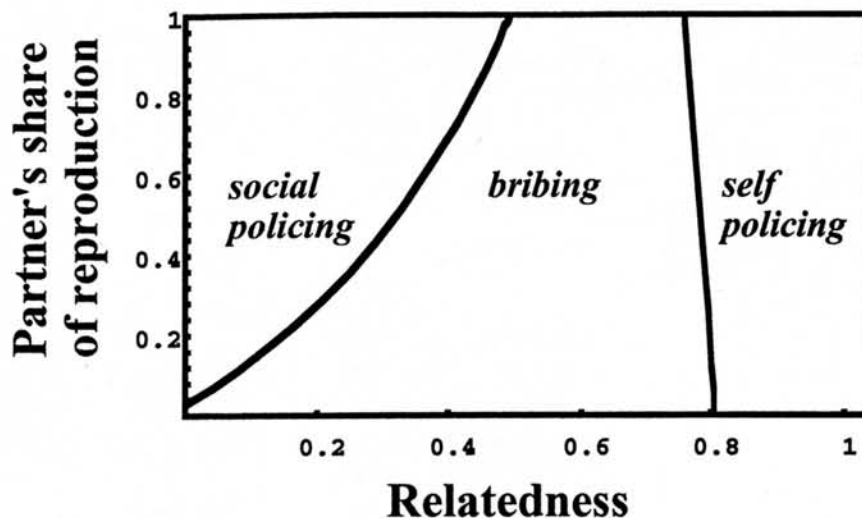
the dominant dies) greatly reduce the need for dominants to offer reproductive concession to retain subordinates peacefully in the group; they also show that stable groups are possible even if social life leads to a decrease in current colony productivity.

These latter two studies are important because they pave the way to incorporating new life-history parameters into reproductive skew models. The role of life-history effects on the evolution of reproductive altruism and eusociality has been discussed by several authors (Queller 1989, 1994, Gadagkar 1990, Nonacs 1991), who suggested that early mortality has a greater impact on solitary breeders than on those living in a group. Even if a subordinate dies early, it still gains some indirect fitness benefit if it contributed to increase the reproductive output of related individuals. In the same vein, the investment of a subordinate in a group is not lost if it dies before the pupae hatch because other individuals in the group can continue raising partly reared brood to adulthood (Gadagkar 1990). By contrast, a solitary breeder that dies before having raised its brood to adulthood loses all of its investment because no adult will ever be produced. The addition of such life-history effects could be added to skew models to generate interesting predictions on skew variation over time. For example, if the death rate of adults increases toward the end of the reproductive season, late-starting individuals should be more inclined to help relatives than to attempt to nest independently because in the latter case they would have a high probability of dying before their offspring have reached adulthood.

Another recent extension of skew theory comes from models showing that dominants and subordinates may forfeit reproduction to each other ("bribe" each other) to suppress selfish acts that reduce overall group output while increasing the reproductive share of the selfish individual (Reeve and Keller 1997). Bribing is important for resolving conflicts because it provides a mechanism by which dominants and subordinates can suppress selfish acts that would otherwise decrease the overall group productivity. Interestingly, the magnitude of bribes is predicted to decrease with increasing relatedness (Reeve and Keller 1997) because the magnitude of reproductive incentive necessary to induce a subordinate to engage in some behavior beneficial to the dominant will always decrease as the relatedness between them increases.

Reeve and Keller (1997) also showed that reproductive bribing is more likely to be favored over social policing when the cost of policing is high, when the benefits of being in a group are not particularly high, when the increment in personal reproduction resulting from a selfish act is moderate, or when relatedness between nestmates is high. The conditions that favor bribing over social policing and "self-policing" (the latter occurring when the individual itself benefits from not acting selfishly because of the harmful effects to kin) are illustrated in Figure 2. The existence of reproductive bribing has not yet been investi-

*Figure 2. Relatedness and the partner's share of reproduction determine the extent to which reproductive bribing will be favored over social policing and self-policing. Other relevant parameters that affect skew (e.g., group-level cost of policing, loss of group productivity that a selfish act would entail, and benefits of group life) are described in Reeve and Keller (1997). Figure slightly modified from Reeve and Keller (1997).*



gated. Its existence could be tested experimentally, for example, by preventing a potentially breeding individual from performing a cooperative act and observing whether, as a result, its share of colony reproduction decreases.

The relationship between the benefits of group living and social attributes such as policing are well illustrated in a recent study by Reeve and Nonacs (1997), who presented a general model of how the optimal level of aggression should vary in different social contexts. They investigated the effect of the degree to which group members are reproductively valuable to one another, assuming that aggression both increases the aggressor's share of the group's expected total reproductive output and decreases the magnitude of the overall reproductive output. Their analysis showed that the optimal level of aggression toward a recipient decreases as the recipient's value in terms of effect on overall group productivity increases (i.e., an aggressor is more likely to self-police when there is a larger benefit of being in a group). In a series of field experiments, Reeve and Nonacs (1997) provided strong support for this prediction by manipulating the value of nestmates (i.e., by reducing the size of the future worker force) in colonies of paper wasps. They found that aggression decreased when the value of the cofoundress was increased, whereas aggression increased when the value of the cofoundress was decreased.

Current skew models aim to determine the stable partitioning of reproduction among totipotent and morphologically similar individuals under given social, genetic, and ecological conditions. Interestingly, these models might shed light on the conditions that have promoted the evolution of more complex societies in which the specialization of individuals in reproductive and nonreproductive roles is associated with morphological castes. When genetic, ecological, and social conditions are such that they promote unequal partitioning of reproduction among group members, some individuals continue to transmit genes directly by their personal reproduction, whereas others rely increasingly on indirect transmission of genes through the reproduction of related individuals. This partitioning of reproductive roles may result in some individ-

uals evolving morphological specializations for reproduction, such as enlarged ovaries, whereas other individuals may evolve morphological specializations for better foraging, brood tending, nest building, and colony defense (Gadagkar 1997). However, as we discuss below, several potential conflicts can arise in societies with such morphological castes.

## Conflicts over caste determination

In many social Hymenoptera (e.g., the honeybee, bumblebees, vespine wasps, and most ant species), partitioning of reproduction is associated with differences in morphology between reproductive and nonreproductive individuals. The queens are morphologically and physiologically specialized for reproduction, and the workers are specialized for other tasks, such as foraging and brood care (Wilson 1971, Wheeler 1991, Keller and Vargo 1993, Peeters 1993, Bourke 1997). In these species, the question about partitioning of reproduction thus becomes, Why do some individuals irreversibly commit themselves to become workers?

Until recently, it was believed that queens are able to chemically manipulate brood development and force female larvae to develop into workers rather than new queens. Indeed, queens of several species have been shown to produce chemical substances (pheromones) that prevent the differentiation of female brood into sexual individuals (Wilson 1971, Fletcher and Ross 1985, Vargo and Passera 1991), and this inhibition was taken as evidence of queen manipulation of the brood against the genetic interests of the latter. However, chemical manipulation is bound to be evolutionary unstable because those female larvae that become resistant to queen pheromones would have higher fitness. Hence, it seems more likely that queen pheromones act as an honest signal to which colony members respond in ways to increase their inclusive fitness (Seeley 1985, Keller and Nonacs 1993). Queen pheromones would simply mean, "I am in good health and fertile, and if you help me you will get a lot of brothers and sisters." Then, on the basis of this pheromonal signal, each

immature individual could decide whether to develop into a queen or a worker, with the choice depending solely on the relative benefits of becoming a queen or a worker. For example, there is a lower incentive to becoming a worker in older colonies because the larger the colony, the lower the benefit of each new additional worker in terms of increasing colony survival and productivity (Keller and Nonacs 1993, Shellman-Reeve 1997). Alternatively, adult workers may respond to the queen's signal by manipulating brood to develop into workers—for example, by differential feeding—and thereby control caste determination (Keller and Reeve 1994).

The question of who is in control of the developmental pathway followed by the larva (i.e., the larva itself, the queen, or the workers) is important, yet it has received little theoretical attention until recently. Pamilo (1991) suggested that there is a conflict between queens and workers over caste determination in eusocial Hymenoptera, with workers preferring a greater investment into new sexuals (queens and males) than into new workers. By contrast, Bourke and Chan (in press) suggested that there should be no conflict and that both queens and workers should favor an investment in workers that will ultimately maximize the lifetime colony production of reproductive individuals. New models (Max Reuter and Laurent Keller, unpublished data) show that Bourke and Chan are correct when the decision of whether a larva develops into a queen or a worker does not affect the sex ratio of the adult sexuals produced. For example, when there is unlimited egg number in the colony, increased production of workers does not occur at the expense of female sexuals. By contrast, when increased production of female sexuals occurs at the cost of worker production (e.g., if the number of female eggs in the colony is limited), there is a queen–worker conflict over the optimal investment in worker function (Max Reuter and Laurent Keller, unpublished data). Reuter and Keller also found that Pamilo's (1991) model is implicitly similar to a model with "egg limitation," accounting for the discrepancy between Pamilo's (1991) and Bourke and Chan's (in press) results.

The conflict between the developing larvae and other colony members has also been analyzed recently (Bourke and Ratnieks in press). This analysis suggests that developing females are more closely related to their own offspring than to the offspring of other females. Therefore, they may prefer becoming adult queens, rather than workers, a preference that runs contrary to the interests of the other developing females, adult queens, and workers. The same preference for becoming queens was found by explicit kin selection models (Max Reuter and Laurent Keller, unpublished data). Moreover, Bourke and Ratnieks (in press) suggest that the potential conflict between the developing larvae and other colony members is more likely to translate into actual conflict when queen–worker size dimorphism is low, because developing larvae have greater power over their own development. For example, they

suggest that stingless bees and ants with multiple queens per nest provide examples of actual conflicts because excess larvae with queen potential are either forced to develop as workers or are culled as adults.

The degree of potential conflict between developing larvae and other colony members also depends on the genetic structure of the colony, which is affected by the number of reproductive queens per colony and the number of males that mated with the queens (Max Reuter and Laurent Keller, unpublished data). Several predictions may allow us to test who is in the control of caste determination in the colony. For example, if the workers or larvae control caste determination, then increased mating frequency of queens should lead to increased investment in queen production rather than worker production. By contrast, if queens control caste determination, the prediction would be that mating frequency is not correlated with relative investment in queen versus worker production. These theoretical studies open new perspectives on the outcome of the conflicts among queens, workers, and larvae over caste determination and will, we hope, lead to evolutionarily oriented experiments in a field of study that has focused mainly on the proximate mechanisms underlying the developmental pathway of larvae.

## Conflicts over male parentage

Interestingly, potential conflicts over partitioning of reproduction are still present in many eusocial insect societies with morphological castes. Although workers always have reduced reproductive abilities, in many bee, wasp, and ant species they have retained the ability to produce males from unfertilized eggs (Bourke 1988). The male = haploid, female = diploid sex-determination system of social Hymenoptera results in asymmetrical relatedness among colony members, with workers being more related to their full sisters than to their mother (Table 1). Hence, there is a conflict of interest between adult females (i.e., between queens and workers) with respect to the parentage of males. In colonies with one singly mated queen, workers are more closely related to their own sons ($r = 0.5$) and to their sisters' sons ($r = 0.375$) than they are to their brothers ($r = 0.25$; Table 1). Hence, each worker would benefit from monopolizing male production. However, even if a given worker cannot monopolize male production, this worker should still favor male parentage by other workers (full sisters) rather than by the queen. A queen, however, should prefer to produce sons ($r = 0.5$) rather than let her daughters produce males to which she is less related ($r = 0.25$). The result is a conflict between queens and workers.

The potential conflict over male parentage is influenced by the number of times a queen mates because an increased number of matings decreases the average relatedness among workers and, thus, the relatedness between workers and worker-produced males. If the queen mates with more than two males and uses the sperm equally,

*Table 1. Kin structure (i.e., degree of relatedness) in male = haploid, female = diploid species.[a]*

| Sex of actor | Recipient | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | Mother | Father | Sister | Brother | Son | Daughter | Niece or nephew (via sister) |
| Female | 0.5 | 0.5 | 0.75 | 0.25 | 0.5 | 0.5 | 0.375 |
| Male | 1 | 0 | 0.5 | 0.5 | 0 | 1 | 0.25 |

[a]The sex determination system of Hymenoptera leads to asymmetrical relatedness between family members. Males develop from unfertilized eggs and possess only one set of chromosomes, whereas females develop from fertilized eggs and thus have two copies of each chromosome. This haplodiploid mechanism of sex determination means that full sisters always receive the same genetic material from their father. Hence, three-quarters of their genes are identical by descent, compared to one-half of the genes in species in which both sexes are diploid. Degrees of relatedness between males, females, and various kinds of close relatives in haplodiploid species take into account the fact that females usually have twice the value of males in terms of gene transmission because females pass genes to both daughters and sons, whereas males pass genes to daughters only.

then workers are on average more related to queen-produced eggs than to worker-produced eggs and thus benefit from preventing one another's reproduction (Starr 1984, Woyciechowski and Lomnicki 1987, Ratnieks 1988). The honeybee provides a good example of such worker policing. Queens mate up to 20 times (Estoup 1994), and, as predicted, only 0.1% of the adult males produced derive from workers (Visscher 1989). The very low contribution of workers to male production is enforced in two ways: workers physically attack workers with developed ovaries (Visscher and Dukas 1995), and workers selectively destroy eggs laid by other workers (Ratnieks and Visscher 1989). In the honeybee, worker policing effectively regulates male parentage and provides a mechanism that ensures relative harmony within the colony, despite the potential for kin conflicts (Ratnieks and Reeve 1992).

## Conflicts over colony sex ratio

Another type of conflict that has received considerable attention after Trivers and Hare's seminal study (1976) is queen–worker conflict over the optimal investment of colony resources into females and males. Kin selection theory predicts that the value of new queens and males is influenced by their relatedness to other colony members. Again, asymmetry in relatedness generates potential conflicts among colony members. In male = haploid, female = diploid species, workers in colonies headed by one singly mated queen are related by 0.75 to their full sisters, but only by 0.25 to their brothers (Table 1). Trivers and Hare first pointed out that workers should favor a 3:1 biased population sex investment ratio (among the sexual forms) in favor of females as a result of their three times higher relatedness to females than males (i.e., relatedness asymmetry). In contrast, because queens are equally related to their sons and daughters, they should invest equally in both sexes. Therefore, kin selection predicts a conflict between queens and workers over population sex ratio, with workers, but not queens, preferring to invest more resources in producing females than males. The outcome of the conflict will depend on the relative power of queens and workers in controlling the sex-investment ratio.

Because workers rear the brood, they may have the final word and achieve their preferred optimum.

Interestingly, the magnitude of the potential conflict is predicted to decrease when changes in the social structure result in a decrease in relatedness between workers and female sexuals compared to that between workers and males. Such a decrease in relatedness asymmetry occurs when the queen mates with more than one male (because workers are less related to half-sisters than to full sisters), when multiple related queens live in the colony, and when workers produce some males. In ants, empirical data across species and populations indicate that workers often win the conflict, at least partially. Population sex-investment ratios are generally biased toward females in species with one queen per nest but not in species with multiple queens per nest, which suggests that workers manipulate colony sex ratios in their favor (Nonacs 1986, Pamilo 1991, Bourke and Franks 1995, Crozier and Pamilo 1996, Bourke 1997).

Kin selection and sex-ratio theories also predict that the strength of the conflict between queens and workers should vary among colonies if colonies located within the same population differ in their relative relatedness asymmetry. At the colony level, workers benefit by producing the sex to which they are relatively more related, as compared to workers in other colonies of the same population (Nonacs 1986, Boomsma 1990, Boomsma and Grafen 1991). Hence, workers should rear mainly or only females in colonies with relatedness asymmetry above the population average, and mainly or only males in colonies with relatedness asymmetry below the population average (Boomsma and Grafen 1990, 1991). Under worker control, sex ratio should be split among colonies with high and low relatedness asymmetry.

Overall, relatedness-induced split sex ratios have been documented in 17 species of social Hymenoptera (Queller and Strassmann 1998). As expected under worker control, colonies with higher relatedness asymmetry produce more females than colonies with lower relatedness asymmetry. The most complete demonstration of this queen–worker conflict over colony sex ratio comes from a recent study of

the ant *Formica exsecta* (Sundström et al. 1996). The study population consists of colonies headed by single queens mated with either a single or multiple males. When the queen has mated with one male, workers are three times more related to their sisters than to their brothers, creating an important conflict because females have a much greater value to workers than males. By contrast, if the queen has been fertilized by multiple males, the colony contains sisters and half-sisters, decreasing the average degree of relatedness among females. The relatedness between workers and their brothers, however, remains constant. Consequently, the conflict between the queen and workers is, at least in theory, weaker, if not absent, in nests headed by a multiply mated queen because females have a lower relative value in these nests compared to other nests in the population (Boomsma and Grafen 1990).

The actual conflict was monitored by comparing the sex ratio among eggs and among pupae in colonies headed by singly mated and multiply mated queens, in which levels of conflict would be predicted to be high and low, respectively (Sundström et al. 1996). The queen controls the primary proportion of males and females by regulating the proportion of haploid and diploid eggs that she lays. However, workers may subsequently modify the sex-investment ratio by selective rearing of the brood. In *F. exsecta*, workers altered the proportion of males and females produced in their colony as a function of the number of times their mother mated. Workers eliminated a high proportion of males between the egg and adult stage in colonies headed by singly mated queens, leading such colonies to produce mostly females. By contrast, males were not killed in colonies headed by a multiply mated queen (Sundström et al. 1996). Hence, in this species, the potential conflict degenerates into a dreadful war over sex ratio between queens and workers, with workers killing their brothers to favor their more related sisters and bias colony investment toward their own interest.

Overall, studies of sex allocation in social Hymenoptera demonstrate that the nature and expression of many intracolony conflicts depend on the genetic structure of the colony, as predicted by kin selection. Paradoxically, the outcomes of within-colony conflicts strongly support kin selection theory—a theory that was first proposed to explain the evolution of cooperation! More generally, these conflicts also reflect the most basic principle of Darwinian evolution, namely, that organisms are selected based on their ability to maximize the number of copies of their own genes transmitted to the next generation. Ultimately, gene-centered natural selection generates intra-colony conflicts among genetically heterogenous individuals.

## Nepotism and selfish behavior

Colonies of social insects frequently contain multiple reproductive queens or queens that have mated with more than one male (Keller 1993, Bourke and Franks 1995, Crozier and Pamilo 1996, Chapuisat et al. 1997). In such colonies, workers belong to several genetically distinct lineages, which are groups of more-related individuals, such as full sisters. Hence, workers might benefit from behaving nepotistically, that is, favoring the individuals most related to them. Earlier studies on honeybees suggested that workers favor full sisters over half-sisters (e.g., Getz and Smith 1983, Page et al. 1989). However, these studies have been justifiably criticized on a number of grounds (Oldroyd et al. 1990, Frumhoff 1991, Breed et al. 1994), and new empirical studies using molecular markers have demonstrated no differential family composition during swarming (Kryger and Moritz 1997). Moreover, studies in a number of ant and wasp species also did not detect nepotism within colonies (Keller 1997).

Two general explanations may account for the lack of nepotism within insect societies (Reeve 1998). One is that selection has favored uniform treatment of colony members because differential treatment of kin classes incurs costs in colonies in which all individuals are related (albeit to a variable degree). For example, preferential treatment of full sisters over half-sisters in a colony whose queen is mated with several males is likely to affect colony performance and lead to decreased fitness of half-sisters. Hence, nepotism will be selected against if the cost incurred by less-related individuals outweighs the benefits provided to more-related individuals.

Alternatively, kin-biased behaviors may be disfavored because of the cost of recognition errors. No recognition system is perfect, and the decision of an individual to behave nepotistically depends on the ability to correctly identify desirable and undesirable recipients. Interestingly, recognition mediated by genetic cues might be unstable and error prone. Theoretical studies indicate that allelic diversity of recognition systems should decrease under a wide range of ecological circumstances because more frequent alleles are favored until they become fixed (Crozier 1988, Ratnieks 1991). Finally, Reeve (1998) has suggested that colony members may also benefit from reducing or eliminating information about kinship within the group when nepotism entails a cost for colony productivity. This phenomenon illustrates that mechanisms may evolve at the colony level to prevent the outbreak of conflicts (Ratnieks and Visscher 1989, Reeve 1998, Keller and Reeve 1999).

## Resolution of conflicts and social cohesion

The recognition that insect colonies are far from simply being arenas of self-sacrificing altruism has led to a drastic change in the focus of research efforts on social insects during the past decade. The advent of "selfish-gene" thinking has led to the development of theoretical studies predicting the nature of potential conflicts among colonymates. In some cases, empirical studies have supported the view that these potential conflicts translate into actual conflicts, as illustrated by the queen–worker conflict over sex ratio. By contrast, in other cases potential conflicts do

not seem to translate into actual conflicts. For instance, although workers might benefit from behaving nepotistically toward the most related individuals in colonies consisting of several genetically distinct lineages, they apparently do not treat kin classes differently (Keller 1997).

Understanding how potential conflicts among selfish individuals are resolved is of primary importance to fully apprehend the emergence of cooperation at the colony level as well as the subsequent evolution of more complex societies. More generally, studying the dynamics of within-colony conflicts is important to gain a better understanding of the process of natural selection in a hierarchical framework (genes in individuals, individuals in colonies, colonies in populations) and may also shed light on other major evolutionary transitions characterized by the integration of replicating units into a higher level of biological organization.

Four major types of factors contribute to aligning the divergent interests of colony members, resulting in peaceful cooperation in cohesive social groups. The first factor is genetic homogeneity, which results in high and symmetrical degrees of relatedness among group members. High and symmetrical relatedness reduces the arena for potential conflicts.

A second important factor changing the nature of intracolony conflicts may be colony size. More precisely, an increase in the number of colony members may, to some extent, facilitate social cohesion (Alexander et al. 1991, Bourke 1999). When the number of individuals present in a colony is low, each individual has a high probability of becoming a replacement reproductive individual. Therefore, individuals are selected to maintain their reproductive abilities, and a high level of conflict over partitioning of reproduction is predicted. In contrast, when colony size increases, each individual is less likely to become a replacement reproductive. Hence, morphological castes are more likely to evolve in large societies, and a reduced level of conflict over partitioning of reproduction is predicted. To date, the effect of colony size on the nature and resolution of conflicts has not been fully appreciated, and this theme deserves further investigation (Bourke 1999).

A third major group of factors relies on the benefits of group living as compared to solitary breeding. This balance is determined largely by ecological conditions. In addition, nonadditive, synergetic fitness benefits associated with cooperation play a major role in promoting social cohesion. When several individuals cooperate, the benefits often combine in a nonlinear way. For example, two individuals working together can rear more offspring than the same two individuals rearing offspring on their own. Eusociality and division of labor may allow greater individual efficiency through specialization of individuals to perform particular tasks (Oster and Wilson 1978). Cooperation also allows species to accomplish tasks that isolated individuals would not manage alone, be it construction of the nest or efficient location of food.

The fourth group of factors encompasses socially mediated mechanisms restraining within-group selfishness. Such factors include some pacific "social contracts," such as leaving each individual reproducing enough to stay peacefully in the group. In other cases, the best collective optimum can be enforced by direct actions against selfish behavior, such as worker policing. Sometimes, social cohesion is ensured by less peaceful means, such as aggression, dominance, coercion, or punishment. Further mechanisms limiting selfish actions might act at the level of information transfer, such as scrambling of recognition cues to limit nepotism. The study of these factors is still in its infancy, but it is clearly a promising avenue for future research.

Kin selection theory has been central to the understanding of the evolution of insect societies. Recent developments in social evolution theory may be just as useful in the elaboration of a general and unified framework to study the dynamics of conflicts among entities with partially divergent interests, be these entities genes, cells, individuals, or any other replicating device.

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