Conflicts of Interest Within Colonies

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The Scope for Conflict in Insect Societies

The societies of ants, bees, wasps, and termites are frequently viewed as one of the pinnacles of social evolution. Indeed, their ► [eusocial](#) organization implies that some individuals specialize in reproduction and others in altruistic helping. In many species, the level of coordination and division of labor within the worker caste reaches such extreme levels that their societies are frequently described as ► [superorganisms](#). Yet, underneath the surface, research has shown that conflicts are rife, especially when it concerns reproduction. The scope for such conflicts can be understood based on ► [inclusive fitness theory](#). While this theory predicted that cooperation and altruism can evolve when aimed at genetic relatives, the flipside of the theory is that individuals may also be selected to harm or compete with less related individuals. The genetic asymmetries that occur in insect societies provide much scope for such conflicts, both among the queen and workers and among the workers themselves (Fig. 1) [10, 25]).

Empirical study of conflicts within insect societies began with Trivers and Hare [39], who used inclusive fitness theory to show that in social Hymenoptera, there is strong potential conflict between the mother queen and her daughter workers over the rearing of young males versus queens [10, 25, 49]. Specifically, they noted that in colonies headed by a single once-mated queen, workers would on average be three times more related to sisters ($r = 0.75$) than to brothers ($r = 0.25$), whereas the queen would always be related equally to sons and daughters ($r = 0.5$) (Fig. 1). Hence, it was predicted that the queen and workers would have conflicting evolutionary optima, with the workers selected to invest three times as much in females as in males, but the queen being favored to invest equally in both [10, 25, 49]. Since then, researchers have documented many other areas where conflict can be expressed, including over male parentage [10, 45, 47], queen rearing [13, 25, 37], and caste fate [3, 48] or in societies lacking morphologically distinct queens and workers, over breeding role, and the choice between helping and breeding independently [25]. We review how some of these conflicts have been documented in different lineages of social insect and how this has led to some of the best tests of inclusive fitness theory to date. We also discuss how in some species these conflicts can be resolved via social coercion or “policing” mechanisms, while in others social conflicts remain unresolved, sometimes leading to large costs to the colony as a whole. We will

Conflicts of Interest Within Colonies, Fig. 1 Genetic relatedness values in colonies of haplodiploid social Hymenoptera under either single or multiple mating. The occurrence of polyandry lowers the average relatedness in a eusocial colony. Red dashed arrows represent the relatedness between the focal worker and her full siblings, sons, and (full or half) nephews. Pie charts represent the share of the genome derived from the different parents (the diploid mother queen and one of the possibly several haploid fathers). The kin structure of the colony affects both queen-worker conflict over sex allocation and conflict

over male parentage. For example, under single mating, workers can capitalize most on the rearing of highly related full-sister queens. Alternatively, under single mating, the workers can also benefit from the rearing of worker-produced males (highly related sons or full nephews), while under multiple mating worker, reproduction is generally not favored at a collective level, as workers are less related to the sons of half-sister workers (half-nephews, $r = 0.125$) than to the sons of the queen (brothers, $r = 0.25$). P = parental generation; r = relatedness

principally focus on the social Hymenoptera, where reproductive conflicts have been studied most extensively, but we will also mention termites when relevant studies are available.

Conflict over Sex Allocation

Sex ratio theory predicts that workers in the social Hymenoptera should be selected to invest in queens versus males in proportion to the

relatedness asymmetry to both sexes, at least if such sex allocation biasing can be achieved at no cost [5, 49]. The relatedness asymmetry to queens versus males becomes smaller in species where queens mate with multiple males, where colonies are headed by multiple related queens, or when the majority of the males in the colony are produced by the workers [5, 49]. Hence, in these situations, the sex ratio favored by the workers becomes closer to the 1:1 investment sex ratio favored by the mother queen(s), resulting in

reduced potential conflict. If worker sex allocation biasing is costly, i.e., in cases where sex ratio biasing causes a drop in colony productivity, workers may be selected to bias the sex ratio less strongly, leading to an investment sex ratio that in species with single monandrous queens would be predicted to be less female-biased than 3:1 [49]. Theory also predicts that intraspecific variation in the kin structure of colonies should favor facultative sex ratio biasing or *split sex ratios*, whereby workers should specialize on rearing of queens in colonies with single-mated queens or low queen numbers, where relatedness asymmetry is high, and on rearing of males in colonies with multiple-mated queens or multiple related queens, where relatedness asymmetry is low [5, 49].

These sex ratio predictions have been tested most extensively in ants, where data from many species support the hypothesis that workers selfishly bias sex allocation in their own favor or facultatively bias sex allocation in response to the colony kin structure [5, 49]). Trivers and Hare [39], for example, presented investment sex ratio data from 20 species of monogynous ants and found that population-level sex ratios were indeed female-biased with an average value of about 3:1 [5, 49]. With this evidence, the authors concluded that queen-worker conflict over sex ratio was resolved in the workers' favor. Trivers and Hare also reported less biased sex allocation in polygynous, multiple-queen ants and found sex allocation to be unbiased in ► [slave-making ants](#), termites, and solitary bees and wasps. However, a later reanalysis of the Trivers and Hare dataset that accounted for differences in the caloric content of males and queens showed female bias in ants to be less than 3:1, consistent with mixed queen-worker control of the sex ratio and conforming to the predicted worker optimum if sex allocation biasing incurs a cost [5, 49].

Probably the best evidence for worker biasing of sex allocation, though, comes from studies that have documented facultative sex ratio adjustment in response to the colony-specific relatedness asymmetry. A meta-analysis of data from 22 species of ants, bees, and wasps, for example, provided evidence that sex ratios are frequently split and that workers often facultatively bias sex ratios

in response to variation in relatedness asymmetry (or mate or queen number, which correlates with relatedness asymmetry) [17]. In single-queen colonies of some ► [wood ants](#), such as *Formica truncorum* and *F. exsecta*, for instance, workers predominantly rear new queens in colonies where the mother queen is singly mated and the relatedness asymmetry is high (3:1), while they rear mostly males in colonies with a doubly mated queen, where the relatedness asymmetry is lower (2:1) ([35, 36], Fig. 2a). Likewise, in the myrmicine ants *Myrmica ruginodis* and ► [Leptothorax acervorum](#), as well as in the ► [paper wasp](#) *Polistes fuscatus* and in five species of swarm-founding epiponine wasps, sex ratios were all found to be split and follow variation in queen number, thereby suggesting worker control of sex allocation [17, 49].

Mechanistically, worker sex allocation biasing can be achieved by the workers trading off increased investment in queens against the rearing of either male brood or worker brood [25, 49]. A tradeoff with male production was documented in some ant species where the sex ratio among pupae or adults proved to be more female-biased than the sex ratio among the eggs laid by the queen, thereby implying that some of the male brood was selectively eliminated [25, 49]. In *F. exsecta*, it was further shown that workers facultatively bias the sex ratio and eliminate male brood only in colonies with a singly mated queen, in line with predictions from split sex ratio theory [36]. Queen production being traded off against worker rearing, by contrast, was documented in another ant species, *Leptothorax acervorum*. Here, colonies displayed split sex ratios in function of variation in queen number, but workers achieved this by rearing more female eggs as queens than as workers in colonies headed by a single queen [9].

Although all these studies demonstrate a degree of worker manipulation of the colony sex ratio, the queen also has some power to keep the sex ratio under her control, e.g., by strategically manipulating the sex ratio of the eggs that she lays. For example, in the ants ► [Pheidole desertorum](#) and in monogyne colonies of the ► [fire ant](#) *Solenopsis invicta* and the Alpine silver ant *Formica selysi* [31], the queen is able to gain

Conflicts of Interest Within Colonies, Fig. 2 Examples of sex allocation conflict being resolved largely in favor of the workers or the queen's optimum. **(a)** Workers in colonies of the ► wood ant *Formica truncorum* capitalize on the rearing of highly related full-sister queens ($r = 0.75$) in colonies headed by a single-mated queen (blue bars) and counteract this female-biased sex allocation by rearing predominantly males in colonies headed by a doubly mated queen (red bars). Such split sex ratio patterns are consistent with workers rearing the sex with the highest kin value and support worker-controlled sex allocation. In line with worker control, overall population investment was also ca. 2:1 female-biased (Based on 1989 data given in ref. [35]. Photo by Lotta Sundström). **(b)** In monogyne colonies of the Alpine silver ant *Formica selysi*, nests also

tend to specialize on the rearing of a single sex, but this specialization occurs irrespective of queen mate number and is due to the queen producing either an exclusively male or an exclusively female brood with equal probability. In this way, the queen can gain control over sex allocation, as workers in the male-specialist colonies do not have the power to cause a female-biased sex ratio because of a shortage of female eggs, while in the female-specialist colonies, the queen and workers both agree on producing a female-biased sex ratio. This results in an almost unbiased population investment. Queen control is not complete though, as population investment was still 1.4:1 female-biased due to a limited amount of worker cannibalism of male larvae. (Based on 2001 data given in [31]. Photo by Timothée Brüttsch)

power over sex allocation by producing either an exclusively male or an exclusively female brood with equal probability, thereby resulting in split sex ratios that are independent of the colony kin structure (Fig. 2b). In this case, workers in the male-specialist colonies do not have the power to cause a female-biased sex ratio because of a shortage of female eggs, while in the female-

specialist colonies, the queen and workers both agree on producing a female-biased sex ratio. Likewise, in bumblebees, a temporal segregation in the rearing of males and queens reduces the opportunity for worker sex ratio biasing and results in investment sex ratios that are close to even, in line with the queen's optimum [25]. In some species, such as in *Pheidole* and

► *Pogonomyrmex* ants, the queen can also bias the caste fate of female eggs toward either queens or workers depending on the concentration of certain maternal factors, such as vitellogenin, ecdysone, or juvenile hormone, that she places in the eggs [25]. In that case, the queen can prevent the workers from biasing the sex ratio toward queens by limiting the number of queen-potential eggs [25]. This has been shown to occur in *Pheidole desertorum*, where sex ratios are split but independent of colony kin structure and queens bias the caste fate of female eggs toward workers in male-specialist colonies [25]. Paradoxically, in another *Pheidole* species, *P. pallidula*, sex ratios have also been shown to be split but in the reverse direction than expected if workers would facultatively bias the sex ratio, with multiple-queen and single-queen colonies specializing on queen and male production, respectively [25]. This may be due to the fact that in this species, queens have been shown to be capable of biasing the caste fate of their female offspring and that in multiple-queen colonies, each mother queen benefits if she can have more of her offspring develop as queens, due to her greater relatedness to her own daughters than to the other queen's daughters ([25]; see section below on "Conflict Over Caste Fate"). Finally, lack of worker power over sex allocation is suggested in most slave-making ants, as brood rearing is there carried out by allo-specific slaves and sex allocation ratios are close to 50% female [25, 49].

Conflict over Queen Rearing

Another potential conflict in insect societies arises when there are different degrees of relatedness between individual workers and different queens raised in the colony, e.g., when these queens are derived from different fathers in species with queen polyandry or when they are the offspring of different mother queens in polygynous species. In these cases, one would expect that workers could be selected to nepotistically aid only in the rearing of new queens to which they are most related, i.e., full-sister queens. Such queen-rearing nepotism could incur significant colony-level

costs due to the time and effort required in determining which larvae to feed. In a swathe of species, from ► *honeybees* to ► *stingless bees*, ants, and polistine and ► *vespine wasps*, such nepotism has been looked for, but the consensus is that it is quite rare in social insects overall [8, 13, 37, 42]. In wasps, nepotism and within-colony kin discrimination were, for example, found to be absent in the multiqueen colonies of the ► *swarm-founding wasp* *Parachartergus colobopterus* [32] and in the polyandrous colonies of the yellowjacket *Vespula maculifrons* [8]. It is thought that even though potential conflict over queen rearing exists, recognitional errors often make it too costly at a colony level to be evolutionarily favored [13, 41, 42]. Indeed, cuticular hydrocarbons from polistine and vespine wasps failed to distinguish reliably among patriline in the hornet *Vespa crabro*, even though they could distinguish among nestmate workers of different matriline in the paper wasp *Polistes dominula* [6]. In line with this last finding, Leadbeater et al. [15] reported a limited degree of kin-biased behavior in *P. dominulus*, thereby providing the first evidence for within-nest ► *kin discrimination* in a primitively eusocial wasp.

Conflict over Caste Fate

The presence of morphologically distinct queen and worker castes is the key characteristic that sets advanced eusocial Hymenoptera apart from other primitively social counterparts where all individuals in principle remain reproductively totipotent. Caste inequality in highly eusocial insects leads to potential conflict because each individual would gain inclusive fitness benefits if it could bias its development toward the queen (or in termites king) pathway [3, 10, 27, 48]. This is linked to the fact that each individual is more related to her own offspring than it is to her sisters' offspring [3, 10, 27, 48]. If many individuals in the colony would decide to selfishly develop as reproductives, a great excess would form though, and the consequent shortage of workers could lead to large colony-level costs. Such problems where individual exploitation of the group causes a cost

to all are known as “tragedies of the commons.” Whether or not queens are produced in excess of colony needs is in social Hymenoptera most easily verified in swarm-founding species, as the collective colony-level optimum there is to produce only very few queens – just enough to be able to swarm effectively or replace a failing mother queen [27, 48].

In most social Hymenoptera that reproduce by swarming, caste fate conflict is efficiently resolved in favor of the collective colony-level optimum, and colonies consequently produce only few new queens [27, 48]. This is because most species have large queen-worker dimorphism, which enables the workers to coerce immature females to become workers simply by providing them with insufficient food to be able to develop into queens. In line with this prediction, swarm-founding species with large queen-worker caste dimorphism such as honeybees and trigonine stingless bees rear queens from larger royal cells and produce new queens sparingly [25]. Likewise, army ants rear only small numbers of new queens [25]. In honeybee, for example, only ca. 0.02% of the female brood are reared as queens [25] (Fig. 3a, b). This is despite the fact that inclusive fitness models have shown that if honeybee larvae were free to choose their own caste fate, approximately half should develop as queens, assuming a linear cost of queen overproduction [27, 48].

In trigonine stingless bees, queens are typically reared from larger royal cells. However, in some species, such as *Schwarziana quadripunctata* (Fig. 3c, d), females reared in small cells can evade their worker fate and become dwarf queens [30, 43] (Fig. 3d). Even though dwarf queens can successfully head colonies, they may have lower fecundity than normal queens and are sometimes eliminated by the workers [43] (Fig. 3f). In other species, such as *Plebeia remota*, regular queens, but not dwarf queens, are kept by the workers in special wax “reserve chambers,” where they are kept by the workers until a new queen is needed [30, 43]. Strategies such as these reduce the benefit for females to develop as dwarf queens [43]. This likely explains why in *Schwarziana* bees only ca. 0.6% of the females reared in worker

cells develop into dwarf queens [30, 43]. Small microgyne or wingless intermorphic queens are also occasionally produced in some ants [3, 25]. Queen miniaturization also allows socially parasitic ants to develop as queens even when reared on an amount of food that is normally sufficient to produce only workers in the parasitized host colony [25].

In one genus of stingless bees, *Melipona*, cheating of caste fate has secondarily become the norm, with ca. 5–20% of all females continually developing as queens and colonies no longer produce regular queen cells (Fig. 3g). The consequence is a massive queen overproduction, with most of this excess being culled by the workers soon after the queens emerge from their cell (Fig. 3h). Due to *Melipona* queens and workers being morphologically distinct but of similar size, caste fate in this case is individually determined. Hence, caste fate conflict is resolved in favor of the individual interests of the developing females, but this occurs at a cost to the colony as a whole. Cheating and queen overproduction in *Melipona* are kept within limits by genetic relatedness. In particular, inclusive fitness models have shown that under a linear cost function, female larvae would be selected to develop as queens with a probability of 14–20%, depending on the amount of male production by workers [27, 48]. Nonlinearity of the colony-level cost function could explain why in some *Melipona* species queen overproduction is actually lower than these values [48].

In termites, similar evidence for overt caste fate conflicts occurs in the lower termite families Kalotermitidae and Termopsidae, where nymphs can control their own caste development because they feed directly from the wood in which they live [19, 25, 27]. In particular, upon loss of the royal pair, a great excess of workers (which are immature instars) can be observed to molt into replacement reproductives in some species [19]. For example, in *Cryptotermes brevis*, *C. domesticus*, and *Kaloterms flavicollis*, ca. half of all nymphs quickly molt into replacement reproductives, even though only a single pair (male and female) is needed [19, 25]. This is then followed by same-sex fighting among the reproductives until only a single member of each

Conflicts of Interest Within Colonies, Fig. 3 Caste fate conflict in insect societies can be resolved in favor of either the individual optimum or the collective colony-level

optimum. (a and b) In ▶honeybees (*Apis mellifera*), developing larvae are reared in open cells and progressively fed by the workers. This allows the workers to

sex remains [19]. In contrast to the situation in *Melipona*, the probability for different individuals in these lower termites to successfully develop as reproductives is highly unequal, due to termites being hemimetabolous and some of the younger instars being much less likely to successfully develop as replacement reproductives. This inequality may explain why in some species, where replacement reproductives form much more slowly, such as *Cryptotermes primus* and *C. queenslandis*, no excess reproductives are formed [19]. It is likely that in this case, only the nymphs that are closest to molting into male and female replacement reproductives succeed and that the rest simply give up their chance to compete in the lottery to become a new queen or king. In higher termites (Termitidae), the immature forms are fed by workers, and workers differentiate irreversibly early on in their development. As predicted, they never overproduce reproductives, and caste fate conflict is there resolved in favor of the collective colony-level optimum [19].

Conflict over Breeding Role

In many social Hymenoptera, including polistine and ► *stenogastrine wasps*, ► *sweat bees* and ► *allopapine bees*, and the crabronid genus ► *Microstigmus*, queen-worker dimorphism is either weak or absent, and females are in principle reproductively totipotent, i.e., being able to mate

and produce both male and female offspring [25]. Reproductive totipotency also occurs in about a hundred species of ponerine ants that have secondarily lost the queen caste and that have colonies headed by one or more mated workers [25]. Totipotency provides significant scope for conflict over breeding role, as it allows any individual in the colony to replace the existing queen, to become an additional queen, or, except in ponerine ants and swarm-founding wasps, to find a nest independently [25]. The relatedness benefits for females to mate and breed are similar to those that underlie caste fate conflict in species with morphologically specialized queens [3, 48]. That is, in the face of reproductive competition with other females, a female benefits if she can become the dominant breeder and produce own offspring (sons and daughters, $r = 0.5$) rather than a worker rearing the less-related offspring of other females ($r \ll 0.5$). The cost of helping can be significantly reduced or can disappear altogether though if there are potential direct fitness benefits associated with delayed nest inheritance or if there are insurance-based advantages of helping [14, 22]. In most species, helping is associated with direct fitness costs though, and conflict over breeding role can then express itself in various ways. For example, in annual societies, females can leave the colony early in order to enter diapause to find a colony the next year, an excess of females can attempt to mate and breed, or females

Conflicts of Interest Within Colonies, Fig. 3 (continued) tightly control the caste fate of female larvae, with most being reared as workers (a) and only some, ca. 1 in 5000, being reared as queens, in line with the colony-level optimum (b). Queen-destined larvae are fed a special type of food, royal jelly, and are reared in larger queen cells (b). (c and d) In stingless bees, by contrast, larvae are reared in closed, mass provisioned cells (c). In most trigonine ► *stingless bees*, queens are also reared in larger queen cells (Q), while workers (and males) are reared in smaller cells. In some species though, such as in this Brazilian species, *Schwarziana quadripunctata* (d), female larvae reared in small cells can cheat on their intended worker fate and develop as dwarf queens (indicated in this comb with opened cells with a q; Q = regular large queen) [30,

43]. (e and f) However, as a countermeasure, newly enclosed regular queens can be kept in wax reserve chambers where they are kept until the colony requires a new queen (here in *Plebeia remota*) [30] (e), while dwarf queens are often selectively killed (here in *S. quadripunctata*) [30, 43] (f). (g and h) In one genus of stingless bees, *Melipona*, such cheating of caste fate has become the norm, with up to 20% of all females continually developing as queens (indicated with a q in an opened up *M. subnitida* comb, g) and colonies no longer producing regular large queens [3, 48]. The consequence is a massive queen overproduction, with most of the excess being killed off by the workers soon after the queens emerge from their cell (here in *M. subnitida*, h). All photos by Tom Wenseleers, except (b) Wikimedia Commons

can attempt to overthrow the existing queen (reviewed in [22, 25]).

Evidence that females may leave the colony early to mate and reproduce on their own exists in both *Polistes* wasps ([22, 29], Fig. 4a) and halictid bees [25] and illustrates overt conflict over the decision to either help or reproduce. In polygynous swarm-founding epiponine wasps, an excess of females mate and are readopted in the natal nest when colonies have few mother queens left [33]. This excess is then reduced as a result of queen-queen competition or active elimination by workers [33]. Similar evidence for an excess of individuals attempting to mate and breed exists in some ► [queenless ponerine ants](#) [25]. In the Brazilian queenless ponerine ► *Dinoponera quadricaps*, high-ranking workers may attempt to overthrow the existing breeder [18].

Different mechanisms may help to resolve conflict over breeder role. In *D. quadricaps*, for example, social coercion limits the incidence of attempted overthrows of the alpha breeder. When challenged by a beta female, the alpha breeder marks the beta with a pheromone, causing other female nestmates to punish the contender ([18], Fig. 4b). In some *Polistes* paper wasps, conflicts over breeding role have been suggested to be resolved via patterns on the foundresses' clypeus which act as "badges of status," i.e., signals of dominance and fighting ability [38]. In this way, conventional settlements can resolve conflict and prevent overt aggression. Some models have also suggested that social contracts could help to reduce conflict among cofounding females [21, 28]. Dominants, it was argued, should offer a sufficiently large reproductive share to the subordinate, lest the subordinate would leave to find her own nest [28]. The evidence for social contracts being used in social insects, however, is somewhat contentious [21].

Conflict over Male Parentage

A final area in which significant scope for conflict is expected in eusocial Hymenoptera is in the context of male parentage (reviewed in [10, 22, 47]). Conflict over male parentage in social

Hymenoptera originates from the fact that the workers, though typically unable to mate, retain functional ovaries and can therefore lay haploid eggs (Fig. 5a). This can lead to potential conflict over male parentage between the queen and workers, since workers are more related to their own sons ($r = 0.50$) and their full sisters' sons (full nephews, $r = 0.375$) than to the queen's sons (brothers, $r = 0.25$), whereas the queen is more related to her own sons ($r = 0.50$) than to the workers' sons (grandsons, $r = 0.25$) (Fig. 1) [47]. Indeed, worker reproduction has been documented in a large number of ants, bees, and wasps and in an analysis of 90 species, the proportion of adult males that were workers' sons averaged at 12% and ranged from 0% to 100% [47]. In only seven genera of ants (► *Atta*, ► *Carebara*, ► *Linepithema*, ► *Monomorium*, *Pheidole*, *Tetramorium*, and *Solenopsis*) and three genera of stingless bees (*Duckeola*, *Frieseomelitta*, and *Tetragonula*), workers are fully sterile on account of lacking functional ovaries, thereby resolving male parentage conflict in the queen's favor. If worker reproduction is common, it can reduce colony productivity and cause a "tragedy of the commons" due to the fact that reproductive workers usually work less than the other workers [45]. Potential conflict over male parentage can also be caused by intraspecific worker parasitism, whereby workers try to deposit male eggs in other colonies to have them reared by nonrelatives. Such "egg dumping" or intraspecific worker parasitism is known in bees [1] and is also suspected in some wasps (e.g., [34]).

In polyandrous species like the honeybees, where the queen mates with multiple males, the workforce comprises a mix of full sisters ($r = 0.75$) and half-sisters ($r = 0.25$). In this case, conflict over male parentage also occurs among the individual workers. That is, while a single worker would still be most related to her own sons, the rearing of brothers would be preferred by the workers as a collective, since workers are on average less related to nephews (a mix of full nephews, $r = 0.375$, and half nephews, $r = 0.125$) than to brothers ($r = 0.25$) [24]. These specific relatedness patterns were proposed to favor a situation in which

Conflicts of Interest Within Colonies, Fig. 4 Instances of conflicts over breeding role in insect societies. (a) In some ► *paper wasps*, such as in this North American *Polistes fuscatus*, some of the first-generation workers (three individuals at the bottom) may abandon their nest and go in hibernation to become a foundress the next year [29]. This causes a

cost to the colony due to the resulting depletion of the workforce. Photo by Ansel Oommen. (b) In the Brazilian dinosaur ant ► *Dinoponera quadriceps*, a worker that attempted to overthrow the alpha breeder (center) is punished by nestmates [18]. Photo by Thibaud Monnin

nonreproductive workers would be selected to inhibit the reproduction of other workers by selectively cannibalizing the eggs they lay or by aggressing egg-laying workers – a behavior known as ► *worker policing* [24, 26]. Worker policing was first shown to occur in the multiple-mated honeybee [26] but has since been discovered to occur in a range of eusocial species, including many wasps and ants, and as expected occurs most frequently in species where workers are collectively most related to the queen’s sons. In the Saxon wasp, *Dolichovespula saxonica*, worker policing has also been suggested to be facultatively expressed, with workers only policing worker-laid eggs in colonies headed by a multiple-mated queen (Fig. 5c). In some species, including in bumblebees [50] and small-colony polistine and vespine wasps [2, 16], reproductive workers have been shown to partake in policing. In this case, policing is aimed at obtaining direct fitness benefits and has been referred to as “selfish policing” [2, 50]. Finally, in many species, e.g., in bumblebees [50] (Fig. 5b), halictid bees, and small-colony polistine and vespine wasps, the queen herself is implicated in policing worker reproduction. In bumblebees and vespine wasps, workers may counter such queen policing by killing the mother queen near the end of the season,

so that they can then reproduce a last batch of their own males without interference (Fig. 5d). This provides an extreme example of unresolved queen-worker conflict over male parentage.

Irrespective of whether worker reproduction is policed by the queen, nonreproductive workers, or reproductive workers, it is expected to disincentivize workers to even try to reproduce, as they would have little to gain from laying eggs if most of the workers’ eggs would be eaten by nestmates anyway [43, 45]. Hence, policing is expected to act as a social control mechanism and favor a system of “enforced altruism,” in which workers would refrain from reproducing because of the low chances they have to successfully rear their male offspring into adulthood [27]. A comparative study of nine species of wasps and two species of honeybees has provided support for this prediction, as the percentage of workers that try to reproduce inside the colony in these species was shown to be negatively correlated with the effectiveness with which worker-laid eggs were policed. Furthermore, given that worker policing is selected for most strongly under queen polyandry and low worker-worker relatedness, attempted worker reproduction in the presence of the queen was found to be the lowest in species with low relatedness ([46], Fig.

Conflicts of Interest Within Colonies, Fig. 5 Conflict over male parentage in insect societies and queen and worker policing of worker reproduction. (a) An anarchistic honeybee (*Apis mellifera*) worker lays a male egg in the presence of the queen [1]. Photo by Ben Oldroyd. (b) A worker of the buff-tailed bumblebee, *Bombus terrestris*, lays an egg, which is later cannibalized or “policed” by the queen (inset). Photo by BBC Natural History Unit (Life in

the Undergrowth series). (c) A worker of the Saxon wasp *Dolichovespula saxonica* lays an egg (left) that is later policed by another worker (right) [7]. Photos by Kevin Foster. (d) A *B. terrestris* worker kills her mother queen (worker matricide) in order to reproduce without interference [4]. Photo by BBC Natural History Unit (Life in the Undergrowth series)

6a, red symbols). This pattern flips in queenless colonies, as species with high worker-worker relatedness there have the lowest levels of attempted worker reproduction ([46], Fig. 6a, blue symbols). This is in line with Hamilton’s rule, which specifies that higher relatedness should favor greater altruism and less selfishness. In other species, variation in male parentage proved to be unrelated to variation in relatedness or policing but was instead caused by variation in the cost of worker reproduction. For example, a comparative analysis of male parentage in eight species of *Melipona* stingless bees showed a

significant fraction of the males were workers’ sons only in those species where the queen mostly lays female eggs (Fig. 6b). This was because only in those species the workers could afford to replace some female, worker-destined individuals by their own male offspring without compromising the long-term survival of the colony [44]. It is worth noting that in many species, queen pheromone signaling systems evolved that effectively regulate levels of worker reproduction and cause workers to reproduce in the presence of the queen to the extent that it serves their own inclusive fitness interests [11, 23, 40].

Conflicts of Interest Within Colonies, Fig. 6 Relatedness, policing, and colony-level costs can all limit worker reproduction in insect societies. **(a)** Relatedness limits the occurrence of workers that selfishly reproduce in queenless colonies (blue symbols) of bees and wasps (triangles and dots resp.). By contrast, in queenright colonies (red symbols), lower relatedness among workers caused by polyandry ensues in less reproductive workers. This contradictory result is explained by the fact that lower worker relatedness selects for stronger worker policing, which in turn disincentivizes workers to attempt reproducing [45]. Data from [12, 20, 46] for ► *Apis cerana*. **(b)** A comparative study of eight *Melipona* bee species (dots) showed that in species in which the queen lays many female, worker-destined eggs, the workers end up producing most of the male offspring. However, if the proportion of queen-laid eggs that are female drops below ca. 85%, most of the

males are produced by the queen instead. Models have shown that this is due to the colony-level cost of worker reproduction then becoming too large, as there would be too high a chance that a worker son would end up replacing a female worker-destined individual, which would then cause a shortage of workers [44]. The dashed line shows the theoretical evolutionary optimal level of worker reproduction from the workers' perspective and how it depends on the percentage of female eggs laid by the queen. Species abbreviations: **(a)** *Ac*, *Apis cerana*; *Am*, *A. mellifera*; *Dm*, *Dolichovespula media*; *Dn*, *D. norvegica*; *Dsax*, *D. saxonica*; *Ds*, *D. sylvestris*; *Pc*, *Polistes chinensis*; *Vc*, *Vespa crabro*; *Vg*, *Vespula germanica*; *Vr*, *V. rufa*; *Vv*, *V. vulgaris*. **(b)** *Ma*, *Melipona asilvai*; *Mbe*, *M. beecheii*; *Mbi*, *M. bicolor*; *Mf*, *M. favosa*; *Mm*, *M. marginata*; *Mq*, *M. quadrifasciata*; *Msc*, *M. scutellaris*; *Msu*, *M. subnitida*

Conflict Resolution Mechanisms

As discussed above, both kinship and social coercion mechanisms can influence the expression of intracolony conflict in insect societies, whether it be over sex allocation, caste fate, breeding role, or male parentage. The comparable role that social coercion and policing mechanisms play in resolving caste fate conflict and male parentage conflict is particularly striking and implies that the social insects' altruism is frequently socially enforced [27, 43, 46]. At the same time, if social insects are frequently coerced into acting altruistically, one would also expect strong selection for individuals to evade coercion. Indeed, there is extensive evidence for such evasion, and a couple of examples were already mentioned. In the context of policing of caste fate via differential feeding,

developing as a dwarf queen was one mechanism for females to evade their intended worker fate [3, 30]. Another mechanism is found in the trigonine stingless bee *Frieseomelitta varia*, where female larvae can cheat on their caste fate and develop as queens by biting through their cell wall and consuming the provision mass of a neighboring cell in addition to their own (Fig. 7a). In the context of conflict of male parentage, we mentioned that bumblebee workers sometimes go to the extreme measure of killing their mother queen to evade queen policing [4]. There is also evidence that workers actively try to evade egg policing. In anarchistic and parasitic ► *Cape honeybees* (Fig. 7b), workers can lay eggs that evade policing, possibly by chemically mimicking queen-laid eggs [27]. Workers of the Asian honeybees ► *Apis florea* (Fig. 7c) and ► *A. cerana* evade

Conflicts of Interest Within Colonies, Fig. 7 Evasion of policing in insect societies. (a) In the trigonine stingless bee *Frieseomelitta varia*, female larvae can cheat on their intended worker fate and proceed to develop as queens by biting through their cell wall and consuming the provision mass of a neighboring cell in addition to their own (inset) [30]. Photos by Tong X. Chinh and Claudia D. Faustino (inset). (b) Parasitic ► [Cape honeybee](#) (*Apis mellifera*

capensis) workers lay eggs in colonies of their host, *Apis mellifera scutellata*, which are not policed, resulting in the accumulation of multiple eggs per cell [1]. Photo by S.J. Martin. (c) Workers of the ► [dwarf honeybee](#) *Apis florea* join and lay eggs in unrelated queenless colonies in which worker policing is switched off [1]. Photo from Wikimedia Commons

policing by a form of parasitism, laying eggs in unrelated queenless colonies in which worker policing has been switched off so that the colony can rear a last batch of males [1]. In most cases, though, evasion of policing only occurs at low levels, so that the social cohesion of the colony never really completely breaks down. In any case, it appears that insect societies in which most individuals are altruists and intracolony conflict is almost completely resolved, such as in honeybee colonies, generally appear to be the result of effective social coercion [27].

Cross-References

- [Atta](#)
- [Carebara](#)
- [Linepithema](#)
- [Monomorium](#)

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