

Eusociality and Cooperation

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Advanced article

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Online posting date: 19th April 2010

The evolution of eusociality, here defined as the emergence of societies with reproductive division of labour and cooperative brood care, was first seen as a challenge to Darwin's theory of evolution by natural selection. Why should individuals permanently forgo direct reproduction to help other individuals to reproduce? Kin selection, the indirect transmission of genes through relatives, is the key process explaining the evolution of permanently non-reproductive helpers. However, in some taxa helpers delay reproduction until a breeding opportunity becomes available. Overall, eusociality evolved when ecological conditions promote stable associations of related individuals that benefit from jointly exploiting and defending common resources. High levels of cooperation and robust mechanisms of division of labour are found in many animal societies. However, conflicts among individuals are still frequent when group members that are not genetically identical compete over reproduction or resource allocation.

Introduction

Human beings have long been fascinated by the spectacular organisation of social insects. Some ant colonies, for example, contain up to one million workers that are completely sterile and specialise in tasks such as building the nest, collecting food, rearing the young and defending the colony. In these colonies reproduction is restricted to a single or a few individuals, the queens, which can lay up to several thousand eggs per day. The term 'eusociality' refers to such societies, characterised by reproductive division of labour, cooperative brood care and (generally) overlap of generations.

ELS subject area: Ecology

How to cite:

Keller, Laurent; and Chapuisat, Michel (April 2010) Eusociality and Cooperation. In: Encyclopedia of Life Sciences (ELS). John Wiley & Sons, Ltd: Chichester.

DOI: 10.1002/9780470015902.a0003670.pub2

Eusociality was traditionally thought to occur only in insects. All ants and termites as well as some bees and wasps are eusocial. Colonies of termites are headed by one or a few queens and kings, and workers can be either males or females. In contrast, colonies of social Hymenoptera (ants, wasps and bees) are essentially matriarchal colonies. Queens store sperm that they use throughout their lives and all workers are females. Recently, eusociality was discovered in several other invertebrates, including gall-making aphids and thrips, ambrosia beetles and snapping shrimps, as well as in one family of mammals, the mole rats. The discovery of several taxa having social organisations similar to those of some social insects and the realisation that there is a continuum in the extent to which individuals forgo their reproductive rights within animal societies have led to the conclusion that species cannot simply be classified as eusocial or noneusocial. For example, in many cooperatively breeding birds and mammals, some individuals forgo their own reproduction, at least temporarily, and help raise the offspring of others. In this article, we will consider the general issue of the evolution of reproductive 'altruism' in animal societies. **See also:** [Insecta \(Insects\)](#)

The first section deals with the paradox of why, in several taxa of vertebrates and invertebrates, some individuals forgo reproduction to assist other group members. The following section addresses an even more puzzling phenomenon, the evolution of morphological castes. In many social insects, reproductive roles are associated with morphological specialisation, raising the question of why some individuals irreversibly commit themselves to become sterile workers (or have greatly reduced reproductive abilities). In the final sections, we consider two important issues associated with the evolution of large and complex societies. The first is the processes generating an efficient division of labour within the society. The second is the dynamics of conflict and cooperation between members of the society. **See also:** [Altruism – A Philosophical Analysis](#)

Evolution of Reproductive Altruism and Eusociality

Social life provides such advantages that it has led to a tremendous ecological success of social animals, particularly social insects. Social insects are found in almost every

type of terrestrial environment and they make up a considerable proportion of the animal biomass of the Earth, up to 50% in some habitats. Hence, it is not surprising that, in the majority of ecosystems, eusocial insects play crucial roles as predators, soil brewers and pollinators. **See also:** [Population Structure](#)

Paradoxically, this ecological success is based on a system that appears to contradict the very basis of the theory of evolution by natural selection. According to the principle of natural selection, the frequency of genes conferring greater survival and reproduction will increase in a given population, since individuals better adapted to their environment will have more descendants. Yet among many eusocial species, workers are programmed to be sterile, their particular morphology and physiology preventing them from reproducing. How can characteristics that preclude individuals from transmitting copies of their own genes to descendants arise and persist through evolutionary time?

This fundamental problem in evolutionary biology did not escape Darwin's attention. In his book *On the Origin of Species*, published in 1859, he noted that sterile workers of eusocial insects embodied 'one special difficulty, which at first appeared to [him] insuperable, and actually fatal to [his] whole theory'. Although inheritance mechanisms were not known at this time, Darwin drafted a solution to this paradox, namely that selection may operate not only at the level of the individual but also at the level of the family. **See also:** [Darwin](#), [Charles Robert](#)

Kin selection

In two seminal papers, William D Hamilton (1964) expressed Darwin's intuition in genetic terms. Hamilton's theory, known as 'kin selection', states that individuals can transmit copies of their own genes not only through their own reproduction, but also by favouring the reproduction of kin, such as siblings or cousins. In fact, kin share identical copies of genes inherited from their common ancestors, in exactly the same way as 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 have an excellent way of

transmitting copies of their own genes to the next generation. **See also:** [Hamilton](#), [William Donald](#); [Selection: Units and Levels](#)

Kin selection theory gives the conditions under which an altruistic act will be positively selected. It 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 (**Table 1**). 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.

Despite several recent claims to the contrary, there is strong theoretical and empirical evidence that kin selection has been the all important selective force for the evolution of eusociality and reproductive altruism by workers (Foster *et al.*, 2006; Hughes *et al.*, 2008). Numerous genetic studies have revealed that eusociality evolved within groups of highly related individuals, such as one mother and her offspring. Well-marked reproductive division of labour is extremely rare in societies where individuals are distantly related. There are a few ant species in which the relatedness between nestmates is indistinguishable from zero, but this low relatedness stems from an increase in queen number that occurred long after the evolution of morphological castes and reproductive division of labour. Interestingly, workers of these ants generally have only vestigial ovaries and it has been suggested that obligate sterility of workers prevented such societies from collapsing after the drop in relatedness. However, societies with very large numbers of queens are expected to be unstable in the long term because workers will be selected to redevelop their own reproductive abilities.

Although females may maximise their inclusive fitness (their direct fitness plus that of relatives weighted by the relatedness of these relatives) by assisting kin instead of leaving the group and reproducing on their own, non-reproductive individuals almost always have lower inclusive fitness than the reproductive individuals they assist. Thus, although cooperation is favourable to all group members, reproductive individuals usually reap greater benefits than nonbreeders, raising the question of what

Table 1 Hamilton's rule

An individual helping a relative indirectly promotes the transmission of copies of his own genes to the next generation. How many of his genes will be transmitted depends on the relatedness between the two individuals, the benefit that the altruistic act brings to the recipient and the induced cost for the altruistic individual. Benefits and costs typically represent differences in the number of descendants, which is the basic unit used in evolutionary biology. 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 favoured when:

$$br - c > 0$$

Here is a simple example to illustrate Hamilton's rule. Imagine a gene that programmes 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 ($r = 0.125$). JBS 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!

determines reproductive roles and partitioning of reproduction within social groups. **See also:** [Fitness](#); [Haldane](#), [John Burdon Sanderson](#)

Reproductive skew models

Building on kin selection theory, a conceptual framework (known as reproductive skew models) was developed to determine how ecological, genetic and social factors jointly influence group stability and the apportionment of reproduction among group members (reproductive skew: Reeve and Ratnieks, 1993; Johnstone, 2000; Reeve and Keller, 2001). In essence, skew models delineate the possible reproductive strategies available to a focal individual, and define under what conditions the best option for this individual is to cooperate and sacrifice part or all of its direct offspring production rather than leaving the group to breed independently.

Three parameters are important in skew models: (1) the expected success of a subordinate that reproduces solitarily, (2) the group's overall productivity if the subordinate cooperates and (3) the genetic relatedness among group members. The effect of these parameters is expected to vary depending on which group member has control over reproductive skew. If the dominant has full control, skew will increase when: (1) group productivity increases, because enhanced group productivity reduces the attractiveness of independent breeding, (2) ecological constraints on independent breeding increase, because subordinates can expect only small payoffs for leaving and breeding independently and (3) the relatedness between a dominant and a given subordinate is high, because subordinates that are more closely related to dominants automatically receive larger indirect benefits for cooperating peacefully, hence they require smaller direct reproductive inducements for such cooperation. Alternatively, if the subordinate fully controls how reproduction is shared within the group, the same parameters are expected to determine reproductive skew but in ways exactly opposite to the situation where dominants fully control reproductive shares.

The parameters that potentially influence reproductive skew are difficult to measure. However, several studies have investigated whether the degree of ecological constraints on independent breeding was associated with the amount of reproductive altruism, and thus the degree of skew. In some birds, the decision of whether or not to become a helper apparently depends on territory availability. For example, in the acorn woodpecker, there is an increasing tendency for yearlings to delay dispersal and remain home with decreasing local availability of breeding vacancies (Emlen, 1984). A positive effect of increased ecological constraints on the tendency of offspring to remain at home and help their parents has also been demonstrated experimentally in the Seychelles warbler (Komdeur, 1992). There is currently only limited data on the role of ecological constraints in social insects. One experimental study in allodapine bee showed that the opportunities for independent breeding did not affect reproductive decisions

(Langer *et al.*, 2004). In contrast, a comparative study in leptothoracine ant provided evidence that reproductive skew among queens is higher in species where ecological constraints on dispersal are more severe (Bourke and Heinze, 1994). This suggests that ecological constraints on dispersal might also play a role in some social insects. However, in some taxa, such as paper wasps, suitable nest sites are not limited and ecological constraints on dispersal are thus unlikely to be key factors leading to cooperation and social life. Rather, it seems that females associate because of the benefits conferred by sociality, particularly lower breeding failure (Reeve, 1991). Nests initiated by several females suffer much fewer failures than nests initiated by a single foundress. Overall, comparative studies suggest that eusocial taxa share some combinations of ecological and life history characteristics predisposing them to grouping and reproductive altruism. For instance, parent-offspring associations and territory inheritance are common features of many cooperative breeders and eusocial species while food-rich shelter and high risks of mortality during brood raising seem to be additional factors promoting eusociality.

Ecological and life history parameters

One important factor that has been suggested to favour the evolution of reproductive altruism is the coincidence of shelter and food. Thus, eusocial thrips, aphids, weevils and shrimps, as well as termites and the naked mole rat, all live in cavities where they obtain their food. This may promote sociality for several reasons. First, the high value of a habitat combining food and shelter may favour altruistic self-sacrifice in defence, leading to the evolution of a soldier caste. Second, this type of valuable habitat may also select for philopatry and helping because of the opportunity for and benefits of habitat inheritance. Third, cavity dwelling helps to keep relatives in close physical proximity and thereby creates opportunities for kin-selected reproductive altruism. Finally, because juveniles in such habitats are frequently self-sufficient with regard to food, they can devote themselves more directly, and at a younger age, to helping to raise younger siblings.

The benefits of remaining with the parent to help raising siblings rather than dispersing and reproducing independently are likely to be particularly important in species where parents are more likely to die before finishing raising their brood. Grouping does not in itself reduce mortality due to predation, but it can decrease the probability of losing all the investment in the brood. Even if a helper dies early, it still gains some indirect fitness benefit if it increased the reproductive output of related individuals. In the same vein, an individual in a group does not lose its investment if it dies before the pupae hatch, because other individuals can continue raising the partly reared brood to adulthood (Queller, 1989; Gadagkar, 1990). By contrast, a solitary breeder that dies before having raised its brood to adulthood loses all its investment as no adults will ever be produced. A direct prediction is that high mortality risk and

delayed maturity of solitary individuals are important prerequisites for selection to favour philopatry and helping behaviour. Those conditions are most likely to occur in insects with extended parental care, such as Hymenoptera, and may thus account for the frequent evolution of eusociality in this taxon (i.e. in ants, wasps and bees).

The ecological and life history parameters described above are unlikely to play a major role in the evolution of reproductive altruism in birds, except for philopatry and territory inheritance. Cooperative breeding birds are not eusocial, and helpers often gain direct fitness after inheriting the territory. Birds do not generally live in a shelter or in proximity to their food. Moreover, a comparative analysis indicates that cooperative breeding evolved more frequently in lineages with low annual mortality. In those lineages, the key ecological factors favouring the evolution of cooperative breeding seems to be sedentariness and living in a warm climate (Arnold and Owens, 1999). High survivorship and climate stability probably lead to low territory turnover and restricted independent breeding opportunities. Under such conditions, helping and reproductive altruism are more likely to be selected for, particularly when associated with the possibility of inheriting the territory and nest. A theoretical analysis indeed suggests that ecological constraints on dispersal should favour helping behaviour mostly or only when helpers have a chance to inherit a breeding territory (Pen and Weissing, 2000). The role of territory inheritance has been acknowledged for a long time by researchers studying cooperative birds, but only recently by those working on social insects. In paper wasps, subordinates have a significant chance of replacing the breeding queen (Queller *et al.*, 2000), and similar findings have been done in other social insects, such as ants and termites (e.g. Heinze and Keller, 2000; Johns *et al.*, 2009). Therefore, it is quite possible that territory and nest inheritance also play a significant role in the evolution of philopatry and reproductive altruism in the social insects. **See also: The Evolution and Ecology of Cooperative Breeding in Vertebrates**

The role of family structure

One factor that probably plays a crucial role in facilitating the evolution of reproductive altruism is the type of family structure. Mother–daughter associations not only provide an opportunity for the offspring to help while they are still juveniles, but they also generate a particular genetic structure favouring the evolution of reproductive altruism.

About 30 years ago, there was considerable discussion about whether eusociality evolved within groups composed of a mother and her offspring, or within groups composed of related individuals of the same generation (e.g. sisters). A theoretical study showed that the asymmetry in relatedness occurring in mother–daughter associations should favour the evolution of eusociality (Reeve and Keller, 1995). In such associations, daughters are on average as related to their mother's offspring (assuming a 1:1 sex ratio in haplodiploid species) as to their own descendants so that they

lose nothing by giving up reproductive rights to their mother. By contrast, mothers are two times more related to their own offspring than to their daughters' offspring and they thus benefit by monopolising reproduction. Thus, high reproductive skew and monopolisation of reproduction by mothers is expected to evolve and be stable in mother–daughter associations (see also Boomsma, 2009). In contrast, siblings are always more related to their own offspring than to those of their sisters and thus should not easily forgo their reproductive rights to help their sisters.

A comparative study of insect species exhibiting both sister–sister and mother–daughter associations indeed demonstrates that reproductive skew is much higher in the latter associations (Reeve and Keller, 1995). Moreover, it appears that groups formed by a mother and her daughters are more stable than sibling associations. For example, sister paper wasps frequently associate to initiate new colonies, but reproductive conflicts almost invariably result in the departure or death of subordinates. By contrast, colonies composed of a mother and her offspring are much more stable in these wasps. The importance of family structure is also confirmed by the fact that large societies with well-marked reproductive division of labour almost invariably occur within families composed of a mother and her offspring.

A recent comparative study of 267 species of eusocial Hymenoptera showed that monandry (i.e. queens mate with a single male) was ancestral on each of the occasions when eusociality evolved and that multiple mating only evolved after workers had lost reproductive totipotency (Hughes *et al.*, 2008). These data confirm that eusociality evolved in simple families where offspring were highly related and thus more likely to forgo reproduction if it increased colony survival and productivity.

In conclusion, there is no doubt that the evolution of philopatry and helping has been favoured by ecological factors that either increase the benefits of remaining and helping in the parental nest or decrease the opportunity of independent breeding. The evolution of reproductive altruism is also greatly facilitated when helpers have a chance to inherit the territory and/or nest of the individuals they assist (Johns *et al.*, 2009). Finally, groups are more likely to be stable and reproductive roles to be differentiated when individuals are more closely related, particularly in groups composed of parents and their offspring. Indeed, a well-marked reproductive division of labour seems to occur almost only in societies with overlap of generations and it is also in such societies that morphological specialisations associated with reproductive roles have evolved.

Evolution of the Queen and Worker Castes

In many social insects (e.g. the honeybee, vespine wasps and most ants and termites), colonies contain distinct morphological castes, the queens being morphologically and physiologically specialised for reproduction and the workers

for other tasks such as foraging and brood care. In species such as the Argentine ant, queens and workers differ strikingly in their morphology, and workers have lost all abilities to reproduce. This raises the question why do some individuals irreversibly commit themselves to becoming workers?

It used to be widely believed that queens were able to chemically manipulate brood development and force female larvae to develop into workers rather than new queens. In several species, it has indeed been demonstrated that queens produce chemical substances (pheromones) preventing the differentiation of female brood into sexuals, 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 evolutionarily unstable, because female larvae becoming resistant to queen pheromones would get 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 (Keller and Nonacs, 1993). Queen pheromones would simply mean 'I am very fertile and if you help me you will get a lot of brothers and sisters'. It should, however, be noted that when queens are larger than workers and require more food during growth, the adult workers can prevent female larvae from developing into queens by controlling their access to food (Wenseleers and Ratnieks, 2004). Such social enforcement probably plays a major role in limiting selfish behaviour in insect societies (Ratnieks and Wenseleers, 2008; discussed in the following text). Finally, in some species, the female developmental fate is largely influenced by genetic polymorphisms and maternal effects (Schwander and Keller, 2008; Schwander *et al.*, 2008).

One important ultimate factor that is likely to favour the evolution of morphological castes is increased colony size. When colony size increases, workers experience a decrease in their chances of becoming replacement reproductives and there is thus decreased selection to retain reproductive ability. Thus, a higher degree of dimorphism between reproductive and worker castes is expected to occur within species forming large colonies (Bourke, 1999). A broad comparison among social insects indeed supports this prediction. Morphological differences between queens and workers are generally absent or small in species forming small colonies (e.g. allopapine bees, hover wasps and sweet bees), whereas the differences are well marked in species forming large colonies (e.g. honeybees, ants and termites). Interestingly, the only vertebrate species where morphological castes have evolved is the naked mole rat. In this species, females increase in size after becoming breeders. The naked mole rat is also the vertebrate species forming the largest societies (up to 300 individuals).

Organisation of Work in Colonies of Eusocial Species

Division of labour is essential to the organisation of eusocial species. By definition, eusociality is associated

with reproductive division of labour. Past the colony founding stage, queens specialise in egg production, while workers care for the brood, build up and maintain the nest, forage for food or other resources and defend the colony. In addition to this basic division of labour between queens and workers, work is further partitioned among workers. In contrast to solitary species, individual workers do not have to perform all tasks needed to produce offspring. They can specialise on particular tasks for various periods (division of labour), and tasks can be divided between many individuals (task partitioning). Hence, work can be performed collectively, with the many concurrent operations and synergistic effects of collective behaviour yielding increased benefits to the whole colony. These benefits certainly facilitated the evolution of altruism and eusociality and contributed to the great ecological success of the social insects. Natural selection, acting at the colony level, selected for societies in which work is organised in a highly efficient, robust and flexible manner.

Efficiency, robustness and flexibility

Division of labour can increase colony performance in several ways. First, the capacity to perform tasks concurrently, rather than sequentially, is a major advantage. In solitary species, a single individual can conduct only one task at a time and must complete a given set of tasks sequentially in order to reproduce successfully. For example, a solitary sphecid wasp has to excavate a nest, find a prey item, sting it, bring it back to the nest and then lay eggs. In contrast, social insects can conduct many tasks at the same time, seizing opportunities as they arise. The efficiency of eusocial species is further increased by the collective performance of tasks that would be out of reach of single individuals. For example, six small ants can immobilise a large insect by seizing one leg each, scouts can recruit foragers to a rich food source or nest temperature can be accurately controlled at all times. Finally, by repeating the same task in one area of the colony territory, for example, collecting food, feeding the brood or guarding the nest entrance, workers can learn and become more efficient. They also minimise costs associated with travelling between tasks and time lost in task switching.

Another feature of concurrent systems is robustness. If one individual fails at one task, this does not compromise the whole enterprise. The redundancy of the system, with many individuals performing the same task and many concurrent production lines, makes it resistant to perturbations or catastrophic events. Finally, it is important to stress that workers do not usually work in a fixed and rigid way. They show behavioural flexibility, so that the number of workers engaged in each task can vary over time to match the needs of the colony and the changes in the environment.

Mechanisms regulating the division of labour

The basic problem faced by a colony is to dynamically allocate the right number of workers to the various tasks. Early researchers on division of labour considered that workers were rigidly programmed to perform only one task over long periods of their life, with task performance being determined by internal factors such as age, size or morphology. Indeed, there is often a correlation between age and task in social insects. Young individuals usually perform tasks within the colony, such as brood care or nest maintenance, whereas older individuals engage in outside, more risky jobs, such as foraging or colony defence. However, a fixed partitioning of tasks according to age or other internal factors gives little flexibility.

Recent research showed that in spite of physiological or age-related predispositions for certain tasks, workers are usually able to switch tasks when needed. For example, if one behavioural caste is experimentally removed, a forager can become a guard or a nurse can become a forager. However, task switching is likely to be costly and should occur only when necessary. A new approach considers that the colony is a self-organising system where a flexible division of labour arises from the independent actions and decisions of workers, without any central or hierarchical control (Bonabeau *et al.*, 2000; Beshers and Fewell, 2001). Several models in which division of labour emerges by self-organisation have been proposed. These models are based on spatial location, task-encounter or physiological threshold. One important example is the response threshold model, which postulates that a worker performs a task when a specific stimulus for this task exceeds its individual threshold. In the response threshold model, the task and stimulus are linked in a negative feedback loop that regulates the system: when an individual performs a task, it decreases the stimulus for this particular task. Importantly, variation in response thresholds among individuals results in worker specialisation but also incorporates flexibility. For example, workers will start feeding larvae if these larvae signal hunger above a given threshold. Workers with the lowest response threshold will perform the task first. By doing so they decrease the stimulus, which may not reach the threshold of other workers under normal conditions. However, if the stimulus increases, other workers with higher response thresholds will automatically start performing the task. Hence, a subset of workers becomes task specialists because of small differences in threshold response, but all workers are able to perform the task if needed. Variation in response threshold can come from many sources, including genotypic differences (Smith *et al.*, 2008), and within-group genetic diversity can thus improve division of labour, for example when honeybees ventilate in order to thermoregulate their hive (Jones *et al.*, 2004). Interestingly, a division of labour may emerge spontaneously when individuals with different response thresholds group together. Natural selection, acting at the group level, can then select for an optimal response threshold distribution among individuals, ensuring

efficient allocation of workers to tasks. **See also:** [Selection: Units and Levels](#)

Evolution of morphological castes among workers

In some ants and termites, division of labour is associated with morphological differences between workers. Morphological castes have evolved in about 20% of the ant genera and in most of the higher termites. The evolution of morphological specialists among adult workers seems to require two major conditions. The first is strong partitioning of reproduction and morphological differentiation between workers and queens. If partitioning of reproduction is not complete, workers are selected to retain reproductive ability and to stay close to the egg pile. They will not be selected to evolve morphological specialisations for colony defence or foraging, as such specialisations are likely to decrease their reproductive ability. In contrast, in societies where workers never reproduce, they are free to evolve into morphological specialists if this increases colony survival and productivity. The second condition favouring the evolution of morphological castes among workers is strong selective pressure from ecological factors, primarily from the size and distribution of food particles or from the level of competition and predation. For example, major workers with enlarged heads and mandibles are usually involved in colony defence or grain milling. In some species of ants and termites, some workers have thickened and enlarged heads which they use as an armoured door to block the nest entrance. However, as aforementioned, a fixed association between morphology and task lacks flexibility. It will only evolve in species with large colonies where a minority of morphologically specialised workers provide strong benefits under fairly predictable environmental conditions. One example is the ant *Pheidole pallidula*, where colonies react to the threat from foreign colonies by producing more soldiers (Passera *et al.*, 1996). **See also:** [Selection: Units and Levels](#)

Conflicts Within and Between Castes

In spite of high levels of cooperation and apparent harmony, potential conflicts persist in colonies of eusocial species. Potential conflicts arise because, in contrast to cells of an organism, colony mates are not genetically identical. Hence, kin selection predicts that individuals with partially divergent genetic interests may attempt to favour the propagation of their own genes, possibly to the detriment of their nestmates. Colony members can compete over direct reproduction or over how to allocate colony resources to various relatives, and the potential conflict may translate into actual conflict or may remain unexpressed. **See also:** [Evolutionary Conflicts](#); [Parent–Offspring and Sibling Conflict](#)

Conflict over who reproduces is common in many eusocial species. For example, dominance behaviour and

linear hierarchies are frequent in small colonies of wasps, bees and ants. Another potential conflict exists in societies containing multiple queens, or where the queen mates with multiple males. 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 favouring the individuals most related to them. Interestingly, most studies in ant, bee and wasp species have failed to detect nepotism within colonies (Keller, 1997; but see Hannonen and Sundström, 2003; Holzer *et al.*, 2006). A uniform treatment of colony members might have been selected because differential treatment of kin classes decreases colony productivity, and by so doing reduces the inclusive fitness of all colony members. Alternatively, kin-biased behaviours may be disfavoured because of the cost of recognition errors.

Two potential conflicts between queens and workers are specific to eusocial Hymenoptera, which are haplodiploids. First, workers and queens may compete over the production of males (Ratnieks and Visscher, 1989), and second, they may conflict over how to allocate colony resources into males and females (Chapuisat and Keller, 1999). These potential conflicts sometimes degenerate into open conflicts. For example, in some species there is a war over the relative investment in males versus females. Workers kill brothers to favour their more related sisters (Sundström *et al.*, 1996), but queens can influence colony sex allocation by biasing the sex ratio of their eggs (Passera *et al.*, 2001; Rosset and Chapuisat, 2006). **See also:** [Natural Selection: Sex Ratio](#)

The evolution of morphological differences between queens and workers generates a new type of potential conflict. Queens, workers and developing larvae may conflict over the caste determination of the larvae (Bourke and Ratnieks, 1999). This potential conflict has been little studied empirically, and the question of who is in control of the developmental pathway followed by the larvae (i.e. the larva itself, the queen or the workers) is still open.

Resolution of conflicts

In animal societies, the resolution (i.e. evolutionarily stable outcome) of potential conflicts among individuals can range from high levels of actual conflict to the complete absence of actual conflict (Ratnieks *et al.*, 2006). Understanding how potential conflicts among selfish individuals are resolved is of primary importance to fully comprehend the emergence of cooperation at the colony level, as well as the subsequent evolution into more complex societies.

Four major types of factors contribute to align the divergent interests of colony members, thereby favouring peaceful cooperation in cohesive social groups. The first factor is genetic homogeneity, which results in high and symmetrical degrees of relatedness among group members and reduces the area for potential conflicts. The second factor is colony size (Bourke, 1999). When the number of individuals in a colony increases, each individual is less

likely to become a replacement reproductive, which reduces conflicts over partitioning of reproduction. The third major group of factors relies on the benefit of group living compared to solitary breeding and the cost of selfish behaviour. Solitary or selfish behaviours are most likely to be selected against when cooperation and division of labour provide large synergistic fitness benefits. Finally, the fourth group of factors encompasses socially mediated mechanisms restraining within-group selfishness (Ratnieks and Wenseleers, 2008). These factors include some pacific 'social contracts', such as leaving each individual enough reproduction to stay peacefully in the group. In other cases, social cohesion can be enforced individually or collectively by direct actions against selfish behaviour, including aggression, coercion or punishment. One primary example is worker policing of male-destined eggs laid by other workers (Ratnieks and Visscher, 1989; Wenseleers and Ratnieks, 2006). Power asymmetries, or unequal information, may tip the balance in favour of one party. Collective manipulation of information may also serve to restrain selfish actions. For example, the expression of nepotism depends on individual labels revealing kinship, such as genetically based odours. There is empirical evidence that odours are actively scrambled among colony members in several ant colonies, which may prevent nepotism. The study of socially mediated factors limiting selfishness is still in its infancy, but is a promising avenue for future research.

Conclusion

Eusociality is one of the major evolutionary transitions of life on earth (Szathmary and Maynard Smith, 1995). The transition to eusociality has been primarily driven by kin selection. Indeed, permanent reproductive division of labour evolved in family associations exposed to ecological conditions limiting independent breeding and favouring cooperation. Subsequently, the development and maintenance of large eusocial groups is associated with second-order processes. For example, division of labour has to be finely regulated by feedback loops typical to self-organising systems. In addition, social processes such as coercion and policing have a great potential to restrain within-group conflicts and stabilise eusociality. Overall, our understanding of eusociality remains rooted in evolutionary genetics and ecology, but greatly benefits from novel insights from the fields of self-organisation and social dynamics. Further progresses will also come from recent advances in genomics and behaviour genetics that will permit to better understand the origin and development of castes.

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