

Review

The evolution of extreme altruism and inequality in insect societies

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In eusocial organisms, some individuals specialize in reproduction and others in altruistic helping. The evolution of eusociality is, therefore, also the evolution of remarkable inequality. For example, a colony of honeybees (*Apis mellifera*) may contain 50 000 females all of whom can lay eggs. But 100 per cent of the females and 99.9 per cent of the males are offspring of the queen. How did such extremes evolve? Phylogenetic analyses show that high relatedness was almost certainly necessary for the origin of eusociality. However, even the highest family levels of kinship are insufficient to cause the extreme inequality seen in e.g. honeybees via ‘voluntary altruism’. ‘Enforced altruism’ is needed, i.e. social pressures that deter individuals from attempting to reproduce. Coercion acts at two stages in an individual’s life cycle. Queens are typically larger so larvae can be coerced into developing into workers by being given less food. Workers are coerced into working by ‘policing’, in which workers or the queen eat worker-laid eggs or aggress fertile workers. In some cases, individuals rebel, such as when stingless bee larvae develop into dwarf queens. The incentive to rebel is strong as an individual is the most closely related to its own offspring. However, because individuals gain inclusive fitness by rearing relatives, there is also a strong incentive to ‘acquiesce’ to social coercion. In a queenright honeybee colony, the policing of worker-laid eggs is very effective, which results in most workers working instead of attempting to reproduce. Thus, extreme altruism is due to both kinship and coercion. Altruism is frequently seen as a Darwinian puzzle but was not a puzzle that troubled Darwin. Darwin saw his difficulty in explaining how individuals that did not reproduce could evolve, given that natural selection was based on the accumulation of small heritable changes. The recognition that altruism is an evolutionary puzzle, and the solution was to wait another 100 years for William Hamilton.

Keywords: eusociality; worker policing; inclusive fitness theory; voluntary altruism; enforced altruism; acquiescence

1. INTRODUCTION

The year 2009 is a double anniversary in the life of Charles Darwin, marking 200 years since his birth and 150 years since the publication of *On the origin of species by means of natural selection* (Darwin 1859). With hindsight, it is clear that this book was a turning point in biology, which revolutionized both our understanding of the living world and our place within it. The *Origin* also represents one of the greatest advances in scientific theory ever made by a single individual in a single publication.

This article begins by briefly putting the social insects in the context of the *Origin*. Although social insects were discussed at length and presented great difficulties to Darwin’s theory of natural selection, Darwin was not primarily troubled by what we would now refer to as the evolution of eusociality or altruism.

Darwin’s difficulty was in a sense greater than this, as he had to explain how natural selection could act on individuals—worker insects—that did not have offspring. Although altruism is frequently referred to as a Darwinian puzzle, the puzzle was not brought squarely to attention until over 100 years later by William Hamilton, who also provided the solution with his theory of inclusive fitness (Hamilton 1964).

Hamilton’s theory of inclusive fitness is a major extension of Darwinian theory (Grafen 2006, 2009). Using theoretical ideas from inclusive fitness theory combined with empirical evidence and tests, this article provides an overview of how social evolution in insects has proceeded to the point that some modern-day insect societies, such as the honeybee *Apis mellifera*, are both supremely unequal and harmonious. From a human perspective, extreme inequality and harmony would seem to be incompatible. This illustrates that social evolution can reach diverse outcomes, which in large part arise from the fact that human society is based on cooperation among unrelated individuals while insect societies are based on

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altruism among family members (Ratnieks 2006; Ratnieks & Wenseleers 2008).

2. THE EVOLUTION OF EUSOCIALITY

(a) *Darwin (1859): social insect difficulties and the evolution of altruism in insect workers*

Darwin (1859) makes frequent reference to social insects. In chapter 6 (Instinct), two of the three examples of ‘how instincts in a state of nature have become modified by selection’ that he chooses are from social insects—slave making in ants and comb building in honeybees.

Social insects also provided difficulties to his theory and may even have delayed publication (Prete 1990). In chapter 7 (Difficulties of the theory), he writes ‘so wonderful an instinct as that of the hive-bee making its cells will probably have occurred to many readers, as a difficulty sufficient to overthrow my whole theory’. By drawing on evidence from bumblebees and stingless bees, Darwin presents possible intermediate stages to building combs of hexagonal cells.

Chapter 7 (pp. 236–237) discusses ‘... one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities: for these neuters often differ widely in instinct and in structure from both the males and fertile females, and yet, from being sterile, they cannot propagate their kind’. Although this is often (Starr 1979; Thorne 1997), but not always (Hunt 2007; Herbers 2009), taken by social insect researchers to refer to what we would now call the evolution of altruism or eusociality, this seems not to have been Darwin’s main concern given that he also writes ‘... How the workers have been rendered sterile is a difficulty; but not much greater than that of any other striking modification of structure’.

In terms of the workings of natural selection, Darwin (1859) typically explains traits via their benefit to the individual. Without attempting to justify the change of beneficiary, he variously explains worker traits as being due to benefits to colony or parents. Thus, in reference to the sting of the worker honeybee, which becomes detached during stinging and so results in the worker’s death, Darwin writes ‘if on the whole the power of stinging be useful to the community, it will fulfil all the requirements of natural selection, though it may cause the death of some few members’ (ch. 7). And in reference to worker ants he writes ‘... natural selection, by acting on the fertile parents, could form a species which should regularly produce neuters, either all of large size with one form of jaw, or all of small size with jaws having a widely different structure’ (ch. 7, pp. 236–237).

Darwin’s (1859) theory was about evolution, not social evolution. Darwin’s theory of evolution by natural selection was built on a foundation of small heritable changes, and his ‘special difficulty’ was in explaining how individuals that had no offspring could evolve body shapes that were radically different from their fertile parents. He did not specifically try to explain how natural selection could cause the origin of altruistic workers in the first place, which he basically dismissed as a problem. But he did not

need to. Only much later was this seen as an important evolutionary puzzle in its own right.

(b) *Altruism: an evolutionary puzzle*

The altruism of worker insects is often referred to as a Darwinian puzzle or paradox. How can natural selection, which normally favours the evolution of traits that increase an organism’s reproduction, favour the reverse—foregoing reproduction. But it seems to have been an inconsistency that for a century worried few evolutionary biologists. The evolution of altruism makes brief appearances in the work of both Haldane and Fisher, two of the founders of the ‘modern synthesis’ in evolutionary biology (Dugatkin 2006). But it was evidently not considered a major problem as both only made brief reference to it, even though both were on what proved to be the right track and certainly had the necessary mathematical abilities to make a formal theory (Dugatkin 2006). Altruism was recognized as an important evolutionary puzzle by Hamilton (1964) and solved by him in a general way. Natural selection can favour altruistic acts provided that the interacting individuals are related. Specifically, Hamilton’s rule $c < rb$, states that, for a social act to be favoured by natural selection, the cost to the actor should be lower than the benefit to the recipient times their relatedness.

(c) *Altruism: the basis of eusocial insect societies*

Eusocial insects, the bees, wasps, ants and termites that live in colonies with a queen and workers, are one of the pinnacles of social evolution (Wilson 1975). The key characteristic of eusociality is reproductive division of labour, in which some society members specialize in reproduction (queens, and also kings in termites) while others (workers) carry out the other tasks such as foraging, building and defending the nest and caring for the brood. Workers have reduced or even zero direct reproduction. The evolution of eusociality is, therefore, both the evolution of altruism and the evolution of inequality.

In some modern-day social insects, reproductive inequality has reached remarkable levels with a single female (and her mate or mates) exclusively or almost exclusively monopolizing reproduction. For example, a colony of honeybees, *A. mellifera*, may contain 50 000 females all of whom have developed ovaries and can lay eggs. But 100 per cent of the females and 99.9 per cent of the males are offspring of just one female, the queen, who is the mother of the other females—the workers (Visscher 1989; Ratnieks & Wenseleers 2008).

(d) *Kinship and the origin of eusociality*

Hamilton (1964) proposed an attractive explanation for the fact that eusociality is especially frequent in the Hymenoptera (bees, wasps, ants), which comprise the majority of eusocial species and which represent approximately nine independent origins of eusociality. Because Hymenoptera are haplodiploid, this leads to a female being more related to full-sisters (0.75) than to daughters (0.5). Although this explanation was convincing at the time, because it seemed to show that

hymenopteran females would have higher inclusive fitness if they worked to rear their mother's offspring rather than their own, it overlooked the fact that haplodiploidy also leads to a female being less related to brothers (0.25) than to sons (0.5). On average, therefore, hymenopteran females are not more related to siblings than to offspring (Trivers & Hare 1976).

Nevertheless, recent evidence shows that high levels of relatedness almost certainly played a critical role in the evolution of eusociality in the Hymenoptera. A phylogenetic analysis of the mating systems of 267 species of ants, bees and wasps in eight eusocial lineages shows that the mating of queens to multiple males is a derived trait (Hughes *et al.* 2008). When eusociality evolved in the Hymenoptera, it was in the context of the highest family levels of kinship possible: a colony headed by a single queen mated to a single male (Hughes *et al.* 2008). Under these circumstances, a daughter helper is as related to siblings as to offspring. Hamilton (1964) pointed out that multiple mating by queens would reduce relatedness and that this would lower the incentive to helping and suggested, therefore, that multiple mating evolved after eusociality. The contention that high kinship may have evolved after eusociality (Wilson & Holldobler 2005; Wilson 2008) is rejected.

Although single mating by females does not provide any special kinship incentive towards working versus breeding alone from the perspective of an incipient worker, it also provides no disincentive provided that a helper's efforts are as productive in rearing siblings as in rearing offspring when nesting independently. High relatedness is certainly not a sufficient condition for the evolution of eusociality but it appears to be necessary. When relatedness is high, even small asymmetries in costs versus benefits that favour rearing siblings instead of offspring can select for helping. In addition, offspring are not selected to resist manipulation and coercion from parents or siblings that increase the probability of helping instead of nesting independently (Charnov 1978; Stubblefield & Charnov 1986; Linksvayer & Wade 2005). A favourable benefit-to-cost ratio may arise in a simple way via a reproductive head start (Queller 1989), extended parental care (Queller 1994) or ecological factors that make it hard for offspring to nest independently. There must also be a way of providing aiding and directing the aid to kin, such as by defending the natal nest and feeding the young there. Thus, in addition to high relatedness, factors such as nest building and the need for brood care or defence are necessary for eusociality to evolve (Queller 1989, 1994; Strassmann & Queller 1989; Gadagkar 1990).

Boomsma (2007, 2009) also addresses the importance of kinship in the evolution of eusociality versus cooperative breeding, which he views as two alternative social outcomes, rather than as a continuum. High levels of kinship over the life of the parents arise from lifetime pairing in termites and the absence or remating in ants, bees and wasps. In contrast, changing partners is frequent in vertebrate societies and leads to a reduction in kinship among offspring (Boomsma 2007). As a result, where helping

occurs in vertebrates, it is usually on a temporary basis and has never led to a morphologically specialized worker caste (Clutton-Brock 2009).

(e) *Kinship and the origin of distinct queen and worker castes*

The most familiar and abundant eusocial insects do not merely have working and reproducing colony members. They have morphologically distinct castes in which the workers have reduced reproductive abilities and the queens have increased reproductive abilities. The evolution of distinct castes has not occurred in all lineages, but is characteristic of termites and three groups of eusocial Hymenoptera: ants, Vespinae wasps (hornets and yellowjackets) and Apidae bees (honeybees, stingless bees and bumble bees) and also occurs in allodapine bees (Schwarz *et al.* 2007) and Epiponini wasps. Queens in some of these species can have amazing egg-laying abilities, and in the Hymenoptera, the ability to store, keep alive and eke out the millions of sperm needed to fertilize up to millions of female eggs over up to 20 years of egg laying following the nuptial flight (Hölldobler & Wilson 2008). Workers in these groups of Hymenoptera have typically lost the ability to mate and so can only lay unfertilized, haploid, male eggs. (In a few genera of ants and stingless bees, the workers are completely sterile.) Workers of these species have lost the ability to nest independently—they cannot 'opt out' of social life.

Interestingly, it is only in groups with non-totipotent workers that we see high levels of multiple mating by queens (Hughes *et al.* 2008). It may be restricted to these species because multiple mating in species with totipotent workers may lead to workers opting out. Opting out could select against multiple mating in one of two ways. First, queens that mated multiply would be disadvantaged relative to queens that mated singly if their daughters facultatively adjusted their probability of helping versus nesting independently based on queen-mating frequency. Nesting independently would be a relatively better option for daughters in a colony headed by a multiple-mated versus a single-mated queen. (Social insect workers are capable of detecting the mating frequency of their queen, probably through assessing the diversity of her offspring, and adjusting their helping behaviour (Sundstrom 1994; Sundström *et al.* 1996; Ratnieks *et al.* 2007).) Second, even if workers do not facultatively respond to the mating frequency of their mother queen, species with multiple mating by queens might revert back to non-eusociality as an evolved response by offspring over many generations to reduced average relatedness. Reversions to non-eusociality have occurred in Halictidae bees (Danforth *et al.* 2003; Schwarz *et al.* 2007), but probably not for this reason.

3. THE EVOLUTION OF EXTREME ALTRUISM AND INEQUALITY IN MODERN-DAY SPECIES

(a) *To reproduce or to help others reproduce?*

A female bee, ant or wasp in a species with morphologically distinct queens and workers, makes two life-history decisions that determine whether she will

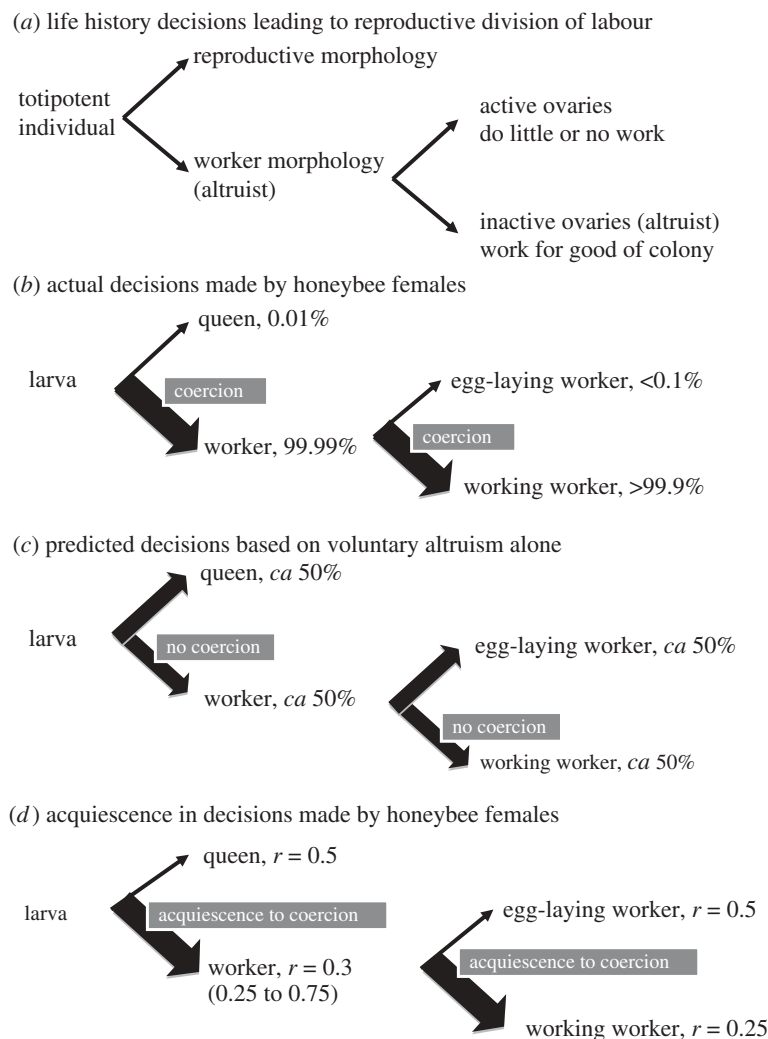


Figure 1. Working versus reproducing. (a) In insect societies with morphologically distinct queens and workers, a female makes two life history decisions that determine whether it will reproduce or work. (b) In the honeybee, *A. mellifera*, owing to social coercion, most females become altruists at both these decision points. (c) In the honeybee, a species with low relatedness ($r = 0.3$) among female offspring owing to multiple mating by the mother queen, the proportions becoming altruists are much higher than expected based on 'voluntary' altruism alone, as would occur in the absence of coercion. (d) Individuals acquiesce to coercion by becoming altruists because they rear kin and so gain inclusive fitness. Worker honeybees are related to the queen's female and male offspring ($r = 0.3, 0.25$) even though this is not as high as the relatedness of a queen or an egg-laying worker to its own offspring ($r = 0.5$).

reproduce or help (figure 1a). Early in life, females in most species are totipotent and can develop into either a queen or a worker depending on environmental factors, and in particular on how they are treated as larvae (Wilson 1971). In the larval stage, the individual commits to developing either as a queen or as a worker. In the adult stage, an individual that has developed into a worker can activate its ovaries and lay eggs or not. At both decision points, almost all honeybee females take the non-reproductive option (figure 1b).

From an inclusive fitness perspective this is puzzling because we expect a large proportion to try to reproduce (Bourke & Ratnieks 1999; Ratnieks 2001; Wenseleers *et al.* 2004a). If individual honeybee females were free to choose their own caste fate, approximately 50 per cent should develop into queens, given that honeybee queens mate with approximately 10–20 males, which reduces relatedness among the female offspring to 0.3–0.275 (figure 1c). Even in species with high relatedness, in

which the mother queen is mated to a single male, a large proportion, up to 20 per cent, are expected to develop into queens. Similar results are obtained when analysing the proportion of workers that lay eggs (Wenseleers *et al.* 2004b).

These proportions are calculated by determining the critical proportion at which the inclusive fitness benefit from helping is equal to that of attempting to reproduce (by a larva developing into a queen or a worker activating its ovaries and laying eggs) under the assumption that reproducing individuals do not do any work and that the productivity of the colony is in direct proportion to the proportion of working individuals. If these assumptions are relaxed (Wenseleers *et al.* 2004a,b), the general result that a substantial proportion of individuals should attempt to reproduce instead of work remains, but the proportions change. Family levels of relatedness are simply not high enough to eliminate potential conflict over reproduction. Relatedness of 1, as occurs in a

clonal group, would be needed (Ratnieks & Reeve 1992; Gardner & Grafen 2009).

(b) Social coercion: the cause of extreme altruism and inequality

There is a bad fit between the theoretical prediction (figure 1c) and the empirical data (figure 1b) because the model leaves out social coercion. The model's prediction is based on 'voluntary' altruism alone (Ratnieks & Wenseleers 2008). That is, on the assumption that an individual's options are not affected by social interactions. In fact, both reproductive decisions are greatly affected by coercion imposed by adult workers and sometimes the mother queen.

In most social insects, queens are considerably larger than workers. Although nests may contain abundant food stores, larvae lack mobility and can normally eat only what they are given by the adult workers. In the honeybee, for example, queens are reared in special royal cells that are larger than the small hexagonal cells used to rear workers and receive special food known as royal jelly. As a result, female larvae are normally powerless to determine their own caste fate because they cannot obtain the additional food needed to develop into a queen if the adult workers do not provide it. *Melipona* stingless bees are a telling exception. In stingless bees, each larva is reared in a sealed cell on a food mass placed there by the workers before the queen lays an egg. Each cell is sealed by a worker immediately after egg laying. *Melipona* queens are not larger than workers, although they are morphologically distinct. Queens and workers are reared side by side in identical sealed cells. Far more queens are reared than required by the colony, which would normally need just a few 'spare' queens in the event that the mother queen dies or the colony is swarming (Ratnieks 2001). Excess queens are executed shortly after emerging as adults from their cells (Wenseleers & Ratnieks 2004). The *Melipona* situation is a clear example of individual colony members being able to make decisions about whether or not to be altruists in the absence of coercion. Self-interest causes more to develop as queens than is needed for the colony to function effectively.

In the case of male production by workers, in many species worker-laid eggs are eaten by other workers (worker policing) or by the queen (queen policing) (Ratnieks 1988; Wenseleers & Ratnieks 2006a). As a result, a worker that lays eggs does not necessarily have offspring. In the honeybee, worker policing is approximately 98 per cent effective in killing worker-laid eggs. Egg-laying workers can also be subject to physical aggression (Visscher & Dukas 1995; Monnin & Ratnieks 2001), and in some ants, this is known to cause the victim's ovaries to regress (Monnin & Ratnieks 2001). In the honeybee, worker policing is normally (Miller & Ratnieks 2001) but not always (Châline *et al.* 2004) switched off in queenless colonies and a batch of males is reared before the colony dies out through dwindling of the work force. In a honeybee colony with a queen, egg laying by workers is not needed for the colony to function effectively. The queen has sufficient fecundity to lay all the

eggs, both male and female, that the colony can rear into adults. In queenless colonies, far more workers activate their ovaries than are needed to allow a batch of males to be reared. Each male cell can only be used to rear one larva at a time, but typically has many eggs laid in it.

(c) Beating the system by evading coercion

Why do not individuals rebel against social coercion? In some cases, they do. Evasion is predicted by inclusive fitness theory because an individual is generally more related to its own offspring. In the case of male production, a worker is more related to sons (0.5) than to nephews (other workers' sons, maximum of 0.375) or brothers (0.25). Thus, there is a strong relatedness incentive to rebel. Similarly, in caste fate conflict, a female larva will be more related to its own offspring (0.5) than to a sister queen's offspring (maximum of 0.375). So even if actual conflict over whether or not to reproduce is reduced through coercion, potential conflict still exists.

A good example of evasion is provided by dwarf queens in trigonine stingless bees. Unlike *Melipona* stingless bees, trigonine queens are larger than workers and are normally reared in larger sealed cells. But in some species, a female larva being reared in a worker cell develops into a small-sized queen. These dwarf queens can mate and head colonies (Ribeiro *et al.* 2006). In some trigonine bees, a larva may be able to break into a neighbouring cell to obtain additional food, and thereby develop into a queen (Faustino *et al.* 2002; Ribeiro *et al.* 2006). In the honeybee, *A. mellifera*, some workers are able to lay eggs that evade egg policing (Barron *et al.* 2001; Martin *et al.* 2002). In some Asian species of honeybees, workers can adopt a parasitic strategy of joining queenless colonies and laying eggs (Nanork *et al.* 2005, 2007). As workers in queenless honeybee colonies stop policing worker-laid eggs (Miller & Ratnieks 2001), the chance that eggs laid by a joining worker will be reared is greater in a queenless colony.

(d) Comparative tests of the effects of kinship and coercion

The above examples make sense from an inclusive fitness perspective. *Melipona* bees are a particularly compelling case showing how the absence of coercion can allow individuals to attempt to reproduce even when this is against the best interest of their colony as a whole. But a good theory should ideally provide quantitative tests and predictions. Because levels of kinship and coercion vary across species, a comparative approach provides a powerful way of testing theory.

In terms of voluntary altruism, inclusive fitness theory predictions are supported by a comparison of queenless colonies in nine species of wasps and the honeybee (Wenseleers & Ratnieks 2006b). Among these 10 species, there is great variation in relatedness among the female offspring, from 0.75 to 0.3 owing to variation in queen mating frequency, and in the proportion of egg-laying workers, from *ca* 8 per cent to 37 per cent. As predicted, there is a strong positive

relationship between the proportion of altruists (non-laying workers) and relatedness. For example, the species with the lowest relatedness, the honeybee, has the highest proportion of egg-laying workers.

When colonies with a queen are studied, the relationship in the same 10 species is reversed (Wenseleers & Ratnieks 2006b). The honeybee is now the species with the lowest proportion of egg-laying workers (less than 0.1%). Here the prediction based on voluntary altruism is not relevant because kinship is not the only factor influencing levels of altruism in queenright colonies. A second factor is coercion in the form of egg policing. In the 10 species, the proportion of worker-laid eggs that are killed, either by the queen or by the workers or by both, varies from approximately 40 to 100 per cent. The proportion of egg-laying workers declines significantly as the effectiveness of policing increases. Policing has long been known to kill worker-laid eggs and to be highly effective in doing so (Ratnieks & Visscher 1989; Ratnieks 1993; Visscher 1996; Foster & Ratnieks 2001a). The comparative study shows that it also deters workers from attempting to lay eggs in the first place (Wenseleers & Ratnieks 2006b). Although egg policing does not directly punish egg-laying workers, when most of their eggs are killed it is better in terms of inclusive fitness to work to rear relatives than to lay eggs few of which will be reared into offspring. However, policing by aggression against workers who are activating their ovaries is punishment (Monnin & Ratnieks 2001).

(e) *Application of inclusive fitness theory*

The above examples show that making predictions from inclusive fitness theory is relatively complex. In particular, it is necessary to consider how the theory influences both attempted reproduction and coercion (figure 2, table 1). In some circumstances, the effects of kinship work in opposite directions (table 1). Thus, a colony headed by a single mother queen mated to a single male gives high relatedness among the female offspring and, in the absence of coercion, causes a higher level of altruism (i.e. a lower proportion of individuals attempting to reproduce instead of working). Multiple mating by queens leads to lower relatedness among the workers and reduces the expected level of voluntary altruism. But it also increases the incentive for workers to police the reproduction (production of males) of other workers (Ratnieks 1988; Wenseleers & Ratnieks 2006a). Counter-intuitively, therefore, low relatedness can lead to greater levels of altruism than high relatedness (Ratnieks 1988). This is because family levels of relatedness cannot reach the value (1) necessary to eliminate all potential conflicts over reproduction versus working based on voluntary altruism alone. But social coercion, via the policing of worker-laid eggs, can be sufficiently effective to reduce the benefits of attempted reproduction to a level at which very few or even zero workers should attempt to lay eggs (Wenseleers *et al.* 2004b). The resolution of conflict due to coercion does not depend on removing the source of the conflict—potential conflict still exists.

kinship and relatedness in social group

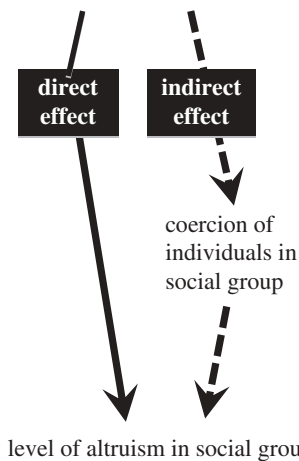


Figure 2. Direct and indirect effects on the level of altruism in a social group, as affected by kinship and relatedness. Kinship has a direct effect (voluntary altruism) but also a wide range of indirect effects via its effect on coercion (enforced altruism). In applying inclusive fitness theory, it is necessary to integrate these multiple effects. See table 1 and the text for examples of indirect effects.

Rather, effective policing reduces actual conflict by making working relatively more worthwhile than attempting to reproduce, given that few of the eggs laid by a worker will be reared and egg-laying workers do less work. In terms of Hamilton's rule, policing reduces the cost of altruism.

Many inclusive fitness factors influence coercion (figure 2, table 1). Thus, worker policing of worker-laid male eggs can be favoured on relatedness grounds (Ratnieks 1988), sex allocation grounds (Foster & Ratnieks 2001b) and colony efficiency grounds (Ratnieks 1988). In addition, queen policing and selfish worker policing (the situation in which egg-laying workers also kill eggs laid by other workers (Wenseleers *et al.* 2005)) are both based on the inclusive fitness benefit that arises from the fact that a female is more related to her sons (0.5) than her grandsons (0.25) (queen policing) and to her sons than her nephews (full nephews 0.375).

In addition, theory is only part of the picture. In a situation where coercers have one optimum and individuals that have the potential to reproduce have another optimum, what is the outcome? Is there an outright winner or is there some intermediate stalemate or balance? The outcome cannot be predicted by theory because it depends on a wide range of biological factors, which are often highly idiosyncratic and vary among groups at all taxonomic levels from subspecies to order (Beekman & Ratnieks 2003; Ratnieks *et al.* 2006). One obvious difference in the biology of honeybees and stingless bees is that honeybees rear brood progressively in open cells while stingless bees rear brood in sealed cells. This difference has profound effects on the outcome of reproductive conflicts. In particular, it has given individual female larvae more power over their caste fate because it limits the power of the adult workers to check the development of larvae. In *Melipona* stingless bees, mass provisioning combined with the fact that

Table 1. Challenges in applying inclusive fitness theory to the alternative individual strategies of reproduction versus altruism in insect societies.

challenge in applying inclusive fitness theory	empirical example in relation to reproduction versus altruism	selected references
must consider both direct and indirect effects of kinship	in queenless colonies, only the direct effect applies in relation to worker egg laying (production of males). In queenright colonies, indirect effects, via coercion (e.g. killing of worker-laid eggs, aggression of egg laying workers), also occur but vary in importance among species	Wenseleers & Ratnieks (2006b)
must consider both reproducing and coercing individuals	worker policing (coercion) is more strongly selected for when relatedness among female offspring is low due to multiple mating by the queen. Self-restraint/acquiescence is more strongly selected when relatedness is high or when coercion is effective	Ratnieks (1988), Wenseleers <i>et al.</i> (2004b)
must take into account all relevant parties	egg policing, for example, can be carried out by the queen or by workers. Worker policing of eggs may be carried out either by egg-laying workers (selfish policing) or by non-reproducing workers	Wenseleers & Ratnieks (2006a)
must consider idiosyncracies that affect power relations among colony members	brood-rearing method of stingless bees versus honeybees. When each larva is reared in a sealed cell (mass provisioning) individual larvae have more power over their own caste fate than in the honeybee, in which each larva is reared progressively in an open cell	Bourke & Ratnieks (1999), Wenseleers & Ratnieks (2004)
must consider information	egg policing requires policing individuals to be able to discriminate between queen-laid and worker-laid eggs	Beekman & Ratnieks (2003)
evasion	individuals have an incentive to evade social coercion. Dwarf queens in trigonine stingless bees develop in a worker cell. Honeybee workers may lay eggs that evade worker policing, or enter a nearby queenless colony in which worker policing has been switched off	Beekman & Oldroyd (2008), Ribeiro <i>et al.</i> (2006)
must consider interactions with other conflicts	worker policing of worker-laid eggs can be selected for on sex allocation grounds. This may account for the occurrence of worker policing in species with queens mated to a single male	Foster & Ratnieks (2001b)
must consider also benefits and costs	policing on colony efficiency grounds. Insurance and head start benefits in the origin of eusociality. Ecological factors that affect the ease or difficulty of founding a nest independently	Ratnieks (1988), Queller (1989)

queens are not larger than workers has resulted in almost complete power being in the hands of individual larvae. Brood rearing in sealed cells may also give stingless bee queens more power over colony sex ratio, as this will make it difficult for workers to manipulate the sex ratio during brood rearing as occurs in ants (Sundström *et al.* 1996).

4. CONSEQUENCES AND WHY DOES IT MATTER?

(a) *Enforced altruism and acquiescence*

An important consequence of the fact that eusocial insect societies are families is acquiescence (Wenseleers *et al.* 2004a,b) by coerced individuals. As noted above, there is a strong incentive for evasion given that individuals are more related to their own sons than to the queen's sons (incentive to evade control over worker production of males) and to their own offspring versus their sister's offspring (incentive to evade caste-fate control and incentive to evade control over worker

production of males). But living in a family also means that individuals who are coerced into a non-reproductive role do not have zero inclusive fitness. In the honeybee, for example, workers are approximately half as related to the female and male offspring being reared in the colony as the queen (figure 1d).

The relative significance of coercion and relatedness vary considerably at different stages in the origin and elaboration of eusociality and inequality (figure 3) (Bourke 1999). Coercion probably played a minor role compared to high relatedness at the origin of eusociality (Ratnieks & Wenseleers 2008). Once eusociality has evolved, coercion (especially by the mother queen) may then evolve, with high relatedness helping to select for acquiescence in the offspring for working at the parental nest versus nesting independently. When workers and queens are morphologically different, such that workers have lost the ability to nest independently, high relatedness is not necessary to prevent offspring from opting out to nest independently. In the majority of species, the evolution of distinct worker

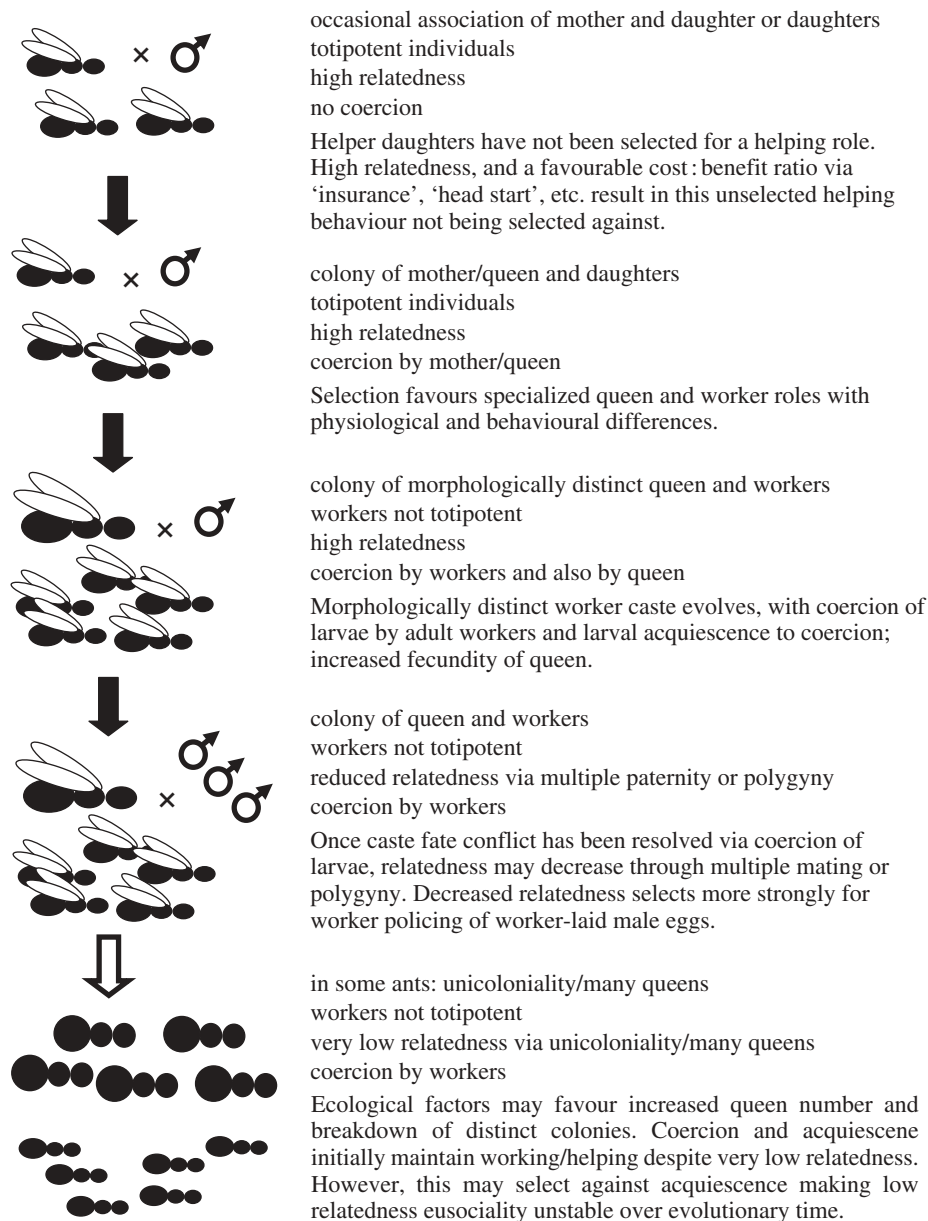


Figure 3. How relatedness and coercion interact in the evolution of insect societies. At the origin of eusociality, relatedness is high but coercion is low or non-existent. As eusociality evolves further, the role of coercion and acquiescence increases and workers become morphologically distinct from queens. This allows relatedness to decrease via multiple mating by queens and/or polygyny. Extreme polygyny, as in some ants which are shown without wings, can cause relatedness to drop almost to zero. This may be an evolutionary dead end.

and queen castes will also result in female larvae being subject to effective coercion via food control so that excess offspring queens are not reared. At this stage, a large diversity of social structures with a wide range of relatedness values (Bourke & Franks 1995) may evolve. But even in highly derived eusocial species where conflicts seem extremely well resolved through enforced altruism, relatedness still plays a major role in determining potential conflicts (Ratnieks & Reeve 1992) and, through its effect on coercion, on actual conflict. The lower the relatedness in a colony, the stronger the incentive for evasion. This may explain why species where colony relatedness approaches zero, such as unicolonial ants, seem to be evolutionary dead ends (Helanterä *et al.* 2009). Very low-relatedness societies may be successful in the short term, such as for invasive

unicolonial ants, but not in the long term if selection favouring selfishness predominates over selection favouring working for the colony via acquiescence.

One analogy sometimes used to describe an insect society is that of a factory (Oster & Wilson 1978). To extend the analogy, it is a factory in which the working individuals are not as well paid as the boss or owner (the queen). But neither are they badly paid. There are few human businesses or organizations in which the highest salary is only twice the lowest, as occurring in the honeybee.

(b) *Creating a better society: building an organism made of many individuals*

Why does it matter that many insect societies, including the honeybee, seem to have almost entirely

resolved their internal conflicts over reproduction via coercion? On the one hand, it matters because the understanding of this issue shows the explanatory power of Hamilton's (1964) theory and is important in the study of social evolution. But it also matters in that it shows how natural selection can cause societies to become more organism like, so that the actions of all or most individuals serve colony rather than individual interests (Ratnieks & Reeve 1992; Seeley 1995; Ratnieks *et al.* 2006; Gardner & Grafen 2009; Queller & Strassmann 2009; see also Wilson & Hölldobler 2005; Hölldobler & Wilson 2008; Wilson 2008 for alternative viewpoints).

Many insect societies have high levels of actual conflict. *Melipona* bees are a good example. They have the highest possible levels of family relatedness (a single queen mated to a single male), and their colonies show remarkable levels of internal organization. But they also show one of the most glaring examples of an unresolved conflict that can be seen in social insects. Colonies rear and execute many excess queens, and this clearly comes at a cost to the colony as every queen executed takes up exactly the same resources as needed to produce a worker—a cell provisioned with food. Complete or almost complete resolution of these conflicts requires coercion to play an additional role. In contrast to *Melipona*, honeybee societies have almost zero actual conflict due to effective coercion of individuals at the two critical decision points in an individual's life (figure 1).

5. DISCUSSION

The examples, theory and evidence presented above make it clear that many modern-day insect societies, as exemplified by the honeybee, are harmonious because of effective social coercion. Coercion has evolved after eusociality and acts to prevent individuals attempting to reproduce instead of working. Without coercion, more insect societies would be like colonies of *Melipona* or queenless honeybees, in which a large proportion of colony resources and individual lives are directed into intra-colony competition over reproduction rather than into working to increase the colony's total reproduction.

Insect societies are not the only type of social group in which the interests of different individuals vary and in which social coercion plays a role in reducing conflict (West *et al.* submitted; Ratnieks & Wenseleers 2008). In insect societies, this has led to extreme inequality. But in other social groups, the outcome may be greater equality or fairness. In interspecies mutualisms, for example, the partners are completely unrelated and coercion often serves to prevent one partner overexploiting the other (Kiers *et al.* 2003; Foster & Wenseleers 2006).

Human society at the family level involves interaction among kin and the possibility of extreme altruism (Foster & Ratnieks 2005). But at the wider level, relatedness is low. Human society is based mainly on the benefits of mutual cooperation (Ratnieks 2006). As in insect societies, coercion is prevalent in human society (West *et al.* submitted). We are all constantly subject to subtle and sometimes

not so subtle forms of coercion from the people we interact with. Coercion of this type exists even in primitive societies (Henrich *et al.* 2006) and is probably a very long-established part of human life and that of the ancestors of *Homo sapiens*. Advanced societies, such as the modern-day nation states, typically have elaborate ways of coercing group members including institutionalized police forces, taxation, punishment and surveillance. Opting out (except by migrating to another nation, which probably has similar restrictions) is not permitted. Coercion is well known for enforcing inequality, such as when it serves to promote the advantage of an elite. One encouraging trend in human political development in the use of coercion is that it is increasingly used to promote greater equality and cooperation. In a modern nation state, no one is supposed to be above the law and extremes of wealth and poverty are reduced via redistribution through the tax system and the provision of education, healthcare, pensions, social safety nets, etc. Although such attempts at creating greater equality are inevitably contentious, and in the extreme have proved to be unworkable, the elimination of extreme inequality is surely a worthwhile objective.

In regard to equality, therefore, the current endpoints in human and insect social evolution are almost exactly opposite, with human society moving towards greater equality and insect societies to greater inequality. But in some other respects, such as in achieving greater social complexity, size and ecological importance, the current endpoints have much in common.

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