

Kin selection: fact and fiction

Ashleigh S. Griffin and Stuart A. West

Hamilton's inclusive fitness theory represents one of the most important developments in evolutionary biology. In particular, the idea that individuals benefit from the reproduction of relatives (kin selection) has been extraordinarily successful in explaining a wide range of phenomena, especially cases of supposed altruism. However, recent work has emphasized how the importance of kin selection can be overestimated – an estimate of high relatedness between interacting individuals is not in itself sufficient evidence that kin selection is responsible for promoting altruism. In particular, supposedly altruistic traits can have direct fitness benefits, and competition between relatives can reduce the importance of indirect fitness benefits.

KIN SELECTION (see Glossary) theory shows how individuals gain INCLUSIVE FITNESS indirectly through the reproduction of related individuals (INDIRECT FITNESS) as well as directly through their own reproduction (DIRECT FITNESS) [1–3]. By doing so, kin selection theory provides a framework for understanding a wide range of social interactions, including ALTRUISM, cooperation, aggression, selfishness and spite. In its simplest form, Hamilton's rule states that altruism (or reduced aggression and/or selfishness) is favoured when $rb - c > 0$, where c is the fitness cost to the altruist of an action, b is the fitness benefit to the beneficiary and r is their genetic RELATEDNESS.

Kin selection theory has been extremely successful in explaining a variety of phenomena, ranging from sterility in eusocial insects [2] to the avoidance of cannibalism in salamanders [4]. However, the striking successes and generality of this theory have led to it often being taken for granted. In particular, when considering the evolution of a supposedly altruistic behaviour, a high relatedness between interacting individuals is usually taken as evidence for a primary role of indirect fitness even though it is not, in itself, sufficient evidence for the role of kin selection. First, competition between relatives can reduce the kin-selected benefits of altruism [5] (Box 1). Consequently, high estimates of relatedness do not necessarily indicate the potential for strong indirect fitness benefits. Although it is often assumed that this effect of competition between relatives applies only to certain viscous population structures (with limited dispersal), its incorporation into Hamilton's rule shows that it is a general issue that could apply to all areas in which kin selection is invoked (Box 1). Second, supposedly altruistic traits, such as helping relatives to breed, can have a direct fitness benefit that has been overlooked. The relative importance of

direct and indirect fitness benefits for a behaviour needs to be explicitly measured before conclusions can be drawn.

Here, we illustrate the potential importance of these two points, using examples from the fields of cooperative breeding, aggression and PARASITE VIRULENCE, where recent work has shown that previous studies have overestimated the importance of indirect fitness.

Cooperative breeding and helping

A classic example of how Hamilton's ideas of inclusive fitness have been used is in the solution to 'the problem of altruism' [6]. In some species, there are individuals who do appear to join the darwinian struggle to breed; instead, they divert resources into rearing the offspring of other individuals. The extent to which a population is divided into 'reproductives' and 'helpers' varies from eusocial insects with sterile castes (e.g. ants, termites, and some bees and wasps), to cooperatively breeding vertebrate species (most commonly among birds, primates and carnivorous mammals) where all adults can eventually breed at some point in their life cycle. Generally, however, there are 'subordinate' individuals who behave altruistically to help 'dominant' individuals to breed.

Historically, kin selection theory has been a major explanation for helping behaviour, because it suggests that, by helping relatives to breed, an individual can gain indirect fitness [2]. In some cases, the importance of indirect fitness is undisputed, such as favouring sterile castes in eusocial insects [7,8]. Furthermore, the potential power and underlying logic of kin selection theory has been clearly demonstrated with work in areas such as sex-ratio evolution [9–11] and worker policing [12,13], where there can be a striking quantitative fit between the predictions of kin selection theory and the empirical patterns that are observed.

In spite of these successes, support for the role of indirect fitness in explaining helping more generally is less clear. In vertebrates, there is no doubt that cooperative breeding is associated with species that live in groups that are made up of kin [14]. However, limited dispersal can lead to groups being composed of close relatives, irrespective of the opportunities to acquire indirect fitness by helping. Furthermore, it has long been appreciated that cooperative breeding occurs in some species that do not live in family groups, and more recent work has shown examples from species living in family groups where the amount of help given does not correlate with relatedness [15–19]. For example, the large differences observed in the amount of babysitting and feeding of pups carried out by subordinate meerkats *Suricata suricatta* are correlated with the age, sex and weight of the subordinates, rather than with their kinship to the young that they help to rear [18,19] (Fig. 1).

Ashleigh S. Griffin*
Stuart A. West
Institute of Cell, Animal &
Population Biology,
University of Edinburgh,
Edinburgh, UK EH8 9PG.
*e-mail:
a.griffin@ed.ac.uk

Box 1. Kin selection with competition among relatives

Competition between relatives can reduce or remove kin-selected benefits of altruism towards relatives. Theoretical work in this area was spurred by Hamilton's suggestion that a high relatedness (r) could arise through limited dispersal (population viscosity) [a–c]. Several authors pointed out that this can also increase competition between neighbouring relatives, which opposes the evolution of altruistic behaviour [c–h]: altruism towards a related individual is less advantageous if their increased fitness comes at a cost to your other relatives.

This effect of competition between relatives can be incorporated into enhanced versions of Hamilton's rule in several ways [d,i–k].

Demographics: Frank's method

Frank's method [j] emphasizes the demographics of competition. Its advantages are that it provides: (1) a clear demonstration of how competition between relatives reduces kin selection for altruism; and (2) a methodology for incorporating competition among relatives (scale of competition) into a wide range of theoretical situations.

Frank's [j] method allows for competition between relatives, by allowing the scale of competition between individuals to be either more local (increasing competition between relatives) or more global (decreasing competition between relatives). This is done by expressing the marginal benefit of increased altruism, b , as a function of three parameters (Eqn 1):

$$b = B - a(B - c) \quad [1]$$

where B is the benefit that would accrue to the recipients if they did not compete with each other, and c has the standard

meaning of the cost of altruism to the actor. The parameter a is the spatial scale at which competition occurs: an increase in the reproductive success of neighbours by a proportion x increases local competition by a factor ax . a therefore measures the extent to which neighbours (and potentially relatives) compete. If competition is completely global ($a = 0$), any competition between relatives is negligible, and so the classic equation for Hamilton's rule holds. As competition becomes more local (increasing a), any increase in reproduction of a neighbour comes at a greater cost to other neighbours. This increases competition between relatives and reduces the kin selection advantage in being altruistic (reduces b). In the extreme, with competition completely local ($a = 1$), any increase in the reproduction of a neighbour comes at the cost of other related neighbours, and so altruism cannot be favoured.

This model demonstrates extremely clearly that the ability of competition between relatives to reduce the kin-selected benefits of altruism is a robust and general prediction. Clear support for this prediction comes from the studies of extreme aggression during competition for mates described in the main text [l].

Relatedness: Queller's method

Queller [m] showed how the consequences of competition between relatives could be incorporated into the relatedness term. The advantage of this method is that it relates to how relatedness is measured, and so demonstrates extremely clearly how empirical work can overestimate the importance of indirect fitness.

Direct fitness benefits from cooperative breeding are ubiquitous and important

The existence of unrelated helpers in cooperative-breeding species is well documented, and explanations for their behaviour based on direct fitness benefits are well established [14,20]. Our emphasis here is that these direct fitness benefits can also apply when helping relatives, and so it is possible that direct fitness benefits are the main factor influencing the level of help even in species where groups are made up of kin. In other words, there might be a very low correlation between relatedness and the relative importance of indirect fitness in the level of helping. Indeed, the direct fitness benefits of helping could even be greater when living with relatives in family groups, because they will be associated with individuals staying on a familiar territory, and cooperating with individuals where the dominance hierarchy is already established [18]. Possible direct fitness benefits to helping behaviour include:

- **Paying rent.** Helping can evolve as the best strategy for avoiding punishment or eviction from a group [21–23], and might increase survivorship, or the possibility of eventually obtaining

reproductive dominance in that group (e.g. joining a social queue) [15,24–28]. There is strong empirical support for these possibilities. For example: (1) the effect of helping on punishment avoidance has been demonstrated in a study on superb fairy wrens *Malurus cyaneus*. Helpers that were removed from the nest were attacked on their return during the breeding season (when their helping behaviour was removed) but not outside of the breeding season [29]; (2) in groups of white-winged choughs *Corcorax megalorhynchus*, younger helpers try to fool dominant birds by pretending to feed chicks [30]; (3) social queues are well recognized in birds and mammals [27], and have also recently been shown to occur in a social wasp *Polistes dominulus*, where 35% of helpers are unrelated, and benefit from helping by increasing the likelihood of inheriting a nest and worker force [31] (Fig. 1).

- **Group augmentation.** Helping can lead to an increase in group size either by lowering mortality (e.g. increasing vigilance for predators) or by helping to raise offspring [25,32]. This can be advantageous if survival is greater in larger groups and/or if the individual is helped at a later point by the additional group members that they

To understand Queller's method it is necessary to remember that relatedness coefficients measure genetic similarity relative to the population mean [b]. Specifically, relatedness is defined as (Eqn II)

$$r = \frac{\sum (p_y - \bar{p})}{\sum (p_x - \bar{p})} \quad \text{[II]}$$

where \bar{p} is the population frequency of the altruist allele, p_x is the frequency of the allele in all performers of altruism and p_y is the frequency of the allele in the beneficiaries of altruism [n,o]. Queller [m] showed that Hamilton's original rule, $rb - c > 0$ (where b is the fitness benefit to the beneficiary), is correct but as long as relatedness to the beneficiary of altruism (r) is measured with respect to the individuals with which the beneficiary will compete (r_c), rather than the global population (r_g). This makes clear the often underappreciated fact that 'relatedness is not just a statement about the genetic similarity of two individuals, it is also a statement about who their competitors are' [m].

Queller's [m] model demonstrates how standard estimates of r will overestimate the importance of kin selection when there is competition between relatives because r is usually measured globally (r_g), and not at the scale at which competition occurs (r_c) (r_c will lie somewhere between r_g and 0, depending on how much competition there is between relatives). In addition, it emphasizes the importance of when dispersal occurs relative to possible altruism and competition [p]. Altruism is most favoured when it occurs before dispersal (leading to a high relatedness), and competition occurs after dispersal (leading to more global competition and hence low competition between relatives).

have helped to raise (delayed reciprocity) [32]. There is widespread evidence that individuals help raise unrelated young who will later help them either when the helper becomes the dominant breeder in their group [15,18,33] or as part of a coalition to take over breeding in other groups [34,35]. Group augmentation also provides an explanation for extreme cases, such as when white-winged choughs kidnap and raise unrelated young [36], and could even have played a role in the evolution of eusociality – in primitively social termites the workers and/or soldiers retain the ability to become reproductives (either Kings or Queens), and there is a high turnover of reproductives [37].

- Increasing social status [38,39]. Observations that helping can have a significant fitness cost [40,41] suggest that helping can be an honest signal of quality [42]. Advertising quality could increase the probability of obtaining mates whilst still being a subordinate, the quality of those mates obtained, or the probability of obtaining dominance in the group (possibly by moving up a social queue). Although evidence for this idea is limited [43], a related effect does apply to humans, where

individuals are more altruistic to individuals who had been generous to others in earlier interactions [44].

There can be considerable overlap in the mechanisms and predictions of these different direct fitness benefits to helping. In particular: (1) helping can provide a (direct) fitness benefit for more than one reason; and (2) different mechanisms can play different roles in the evolution and maintenance of helping behaviour. For example, although evolutionarily stable, it is hard for delayed reciprocity to favour the initial evolution of helping. If the whole population is in a nonhelping state, then it does not pay an individual to recruit new group members in the hope of obtaining help from them in the future [32]. Consequently, some level of helping might initially evolve by a different direct mechanism or indirect fitness benefits, but when helping becomes common, reciprocal altruism can be paramount in maintaining high levels of helping [32] (it has even been argued that reciprocal altruism might be most common among relatives [45]). At the very least, cooperation between relatives does not imply that indirect fitness is the main factor driving the level of cooperation that is observed, even if it was required for the initial

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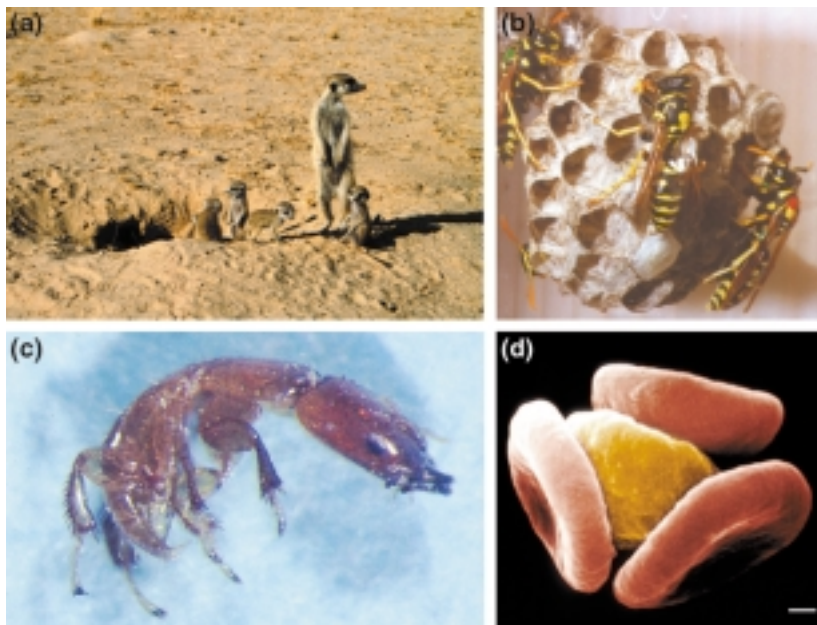


Fig. 1. Examples of species in which kin selection might not be as important as it was previously thought to be. (a) Helping behaviour in meerkats *Suricata suricatta* is not correlated to relatedness [18]. This babysitting subordinate meerkat might not be gaining any fitness through kin selection, but rather increasing its chances of successfully breeding in the future. (b) In the social wasp *Polistes dominulus*, 35% of helpers are unrelated, and benefit from helping by increasing the likelihood of inheriting a nest and worker force [31]. (c) The severity of fighting between male fig wasps is not correlated to relatedness [46]. This is a male *Sycoscaptor australis* wasp, a species in which there is severe fighting, and in which decapitation is common. (d) Scanning electron micrograph of a *Plasmodium falciparum*-infected erythrocyte forming a rosette, a process associated with virulence in human malaria; scale bar = 1 μm . Virulence in malaria parasites does not consistently correlate with relatedness [57]. Photographs, reproduced with permission, from Ashleigh Griffin (a); Joan Strassman (b); James Cook (c); and David Ferguson (d).

evolution of some helping. All of these possibilities, and their interactions, can be considered using inclusive fitness theory (Box 2). It is clear that a major outstanding task is to estimate the relative importance of direct and indirect fitness benefits in favouring observed levels of helping.

Competition between relatives reduces the kin-selected benefits of cooperative breeding

Competition between relatives reduces, and can even completely overcome, any kin-selected benefits of altruism towards relatives (Box 1). There is considerable scope for this to be important in cooperatively breeding vertebrates, where the same limited dispersal (population viscosity) that leads to high relatedness within groups also leads to competition between relatives. In particular, related individuals compete for dominance and breeding opportunities within the group (the extent of this will differ between the sexes as well as across species). Although conflicts of interest between relatives within a group are well appreciated, the more subtle point of how this reduces the importance of indirect fitness (Box 1) is generally ignored, and there have been few attempts to estimate its importance [46].

The crucial point is that the potential importance of indirect fitness is often estimated by measuring within-group relatedness. For example, consider the

naked mole-rat *Heterocephalus glaber*, a species that is frequently invoked as support for the kin selection model for the evolution of cooperative breeding. This is a highly social species (in fact, it is the only vertebrate that has ever been described as eusocial) and the importance of kin selection (indirect fitness) is often argued on the basis of an extremely high intracolony relatedness (estimates using DNA 'fingerprinting' range from 0.81 to 0.99) [47,48]. However, these estimates of relatedness were made with respect to the population (r_g ; Box 1), and not at the relevant level with respect to competitors (r_c ; Box 1) [49]. Consequently, if competition between relatives occurs (which will depend upon the demographics of the species [50]), the importance of indirect fitness will have been overestimated [46,49]. In the extreme, if all competition was between members of the same colony, then the average effective intracolony relatedness (r_c) would be zero. Clearly, empirical work is required that estimates the extent to which competition between relatives reduces indirect fitness [although the effect of competition between relatives can be incorporated into measurements of the r [49] or b [50] terms in Hamilton's rule (Box 1), we have focused here on r because it is estimated more frequently].

Furthermore, the same situations that provide direct fitness advantages to helping can also increase competition between relatives. For example, when the direct fitness advantages of helping in a group, such as eventually inheriting dominance (rather than starting a new group), are maximized, competition between relatives within that group might also be maximized. The possible importance of this could be calculated by extending existing theoretical models [32] to allow for estimates of relatedness (calculated with respect to competitors; Box 2) to flow from the population dynamics of the model [28], rather than be kept as an independent variable as is currently the case. Nonetheless, this emphasizes how, even when groups are composed of close relatives, the relative importance of indirect fitness might be negligible.

Fighting and extreme aggression

Hamilton pointed out that kin selection theory could also be applied to aggression and levels of fighting [2]. Specifically, he suggested that individuals would be expected to be less competitive with, and less likely to fight, closer kin. Hamilton used this idea to explain variation in fighting levels between males during competition for mates, across a range of insect and mite species [51], especially fig wasps (Fig. 1), and this has become a classic example of the importance of kin selection [52]. However, this prediction has not been supported by more recent work, which showed that fighting levels did not correlate with relatedness across fig wasp species [46]. In addition, there are several cases in which close relatives show extreme

Box 2. Inclusive fitness and Hamilton's rule explain altruism between nonrelatives

It is generally assumed that inclusive fitness is merely kin selection. However, as Hamilton pointed out, inclusive fitness theory is much more general than kin selection [a]. Specifically, when considering the evolution of altruism, inclusive fitness theory states that what is necessary is a statistical association of (altruistic) genotypes (or partners) [a,b]. Kinship is only one way in which this can occur (albeit the most obvious). Alternatives include altruists recognizing fellow altruists as such and repeatedly interacting with them (e.g. through tit-for-tat type strategies in prisoner's dilemma games or green beard genes), patterns of dispersal leading to altruists settling together, and selection creating positive correlations between altruistic individuals [a,c-h].

Inclusive fitness theory and Hamilton's rule can be used to understand a range of social phenomena, such as the evolution of reciprocal altruism [f,g] and MUTUALISM (see Box Glossary) [c,h]. An advantage of this approach is that Hamilton's rule provides an extremely clear and useful way of summarizing selection on social characteristics [h]. In particular: (1) it shows how the same underlying logic applies to these different problems (the spread of altruism through reciprocity is analogous to the spread of altruism through relatedness); and (2) it allows different mechanisms to be combined and compared using a single framework such as kin and reciprocal selected altruism (and their interactions) [g,h].

Furthermore, it makes clear how the main points of this paper also relate to interactions between nonrelatives. For example, limited dispersal has been suggested as a factor that would favour reciprocal altruism or mutualism [i], but this would clearly depend upon the scale of competition [j].

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Box Glossary

Mutualism: mutually beneficial relationships between members of different species.

aggression [51]. For example, fights to the death occur between brothers of parasitic wasps in the genus *Melitobia* when competing for mates [51], and between honeybee *Apis mellifera* sisters as they compete to head the original colony after it divides and swarms [53].

The explanation for high levels of aggression between close relatives in all of these cases is that competition between relatives is sufficiently high that it overcomes the kin-selected advantage of altruism towards relatives [46]. This occurs because competition is always extremely local – within a single fruit for fig wasps, over a single brood for *Melitobia* wasps, or within a colony of honeybees. In terms of Frank's [50] and Queller's [49] enhanced version of Hamilton's rule described in Box 1, competition is completely local ($a=1$, where a is the spatial scale at which competition occurs; Box 1) or the actor is equally related to the potential benefactor and their competitors, and so the effective relatedness (r_c ; Box 1) will be zero. Put simply, there is no point being altruistic towards a brother if his increased fitness comes at the cost of a different brother. Instead, levels of violence correlate positively with the importance of winning any individual fight (e.g. fig wasp males fight more

aggressively when there are fewer females to mate with within the fruit [46], and honeybees fight so aggressively because only one or a few are needed). Similar logic can also explain cases in which cannibalism occurs between close relatives [46].

Parasite virulence

Considerable attention has been paid to how kin selection might shape the evolution of parasite virulence. Kin selection models of parasite virulence suggest that increased parasite genetic variability within a host (i.e. lower r ; increased numbers of unrelated parasite strains infecting the host) favours higher virulence [54,55]. This occurs because it leads to greater competition for host resources, which favours rapid growth to achieve greater relative success within the host, and that higher parasite growth rates lead to higher virulence. Although there has been some support for these models in parasites of invertebrates [56], it is unknown to what extent the theory can explain variation in levels of virulence more generally, especially in parasites of vertebrates with complex immune systems [57].

One system in which kin selection explanations of virulence have been investigated empirically is

Glossary

Altruism: acting to increase another individual's fitness at a cost to one's own.

Direct fitness: the component of fitness gained through reproduction (i.e. the production of offspring).

Indirect fitness: the component of fitness gained from aiding the reproduction of nondescendant relatives.

Inclusive fitness: 'the effect of one individual's actions on everybody's numbers of offspring ... weighted by the relatedness' [a].

Kin selection: the process by which traits are favoured because of their beneficial effects on the survival of relatives, including offspring (direct fitness) and nondescendant offspring (indirect fitness).

Parasite virulence: the damage caused to a host by a parasite infection.

Relatedness: a measure of genetic similarity.

Reference

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malaria, a disease caused by protozoan parasites of the genus *Plasmodium* (Fig. 1). Kin selection models have gained some support from studies of human, lizard and rodent malaria. Specifically, observational field data [57,58] and experimental laboratory work [59] show higher virulence when relatedness between parasites within a host is lower. However, contradictory to the assumptions and predictions of kin selection models of virulence: (1) more mixed infections (lower r) have higher densities of transmission stages (gametocytes) and are more infectious to mosquitoes than are less mixed infections; (2) competitively suppressed clones are able to transmit as well or even better from mixed infections than are unsuppressed clones; (3) some field studies show higher virulence when relatedness between relatives is lower; and (4) experimental studies show that competition between nonrelatives can reduce virulence [57,60]. These results suggest that variation in virulence correlated with the relatedness of parasites might be caused by other factors, such as a reduced ability of the immune system to control a more genetically variable

infection [57]. Another complication is that the scale of competition (Box 1) needs to be incorporated into parasite virulence theory [50,55,61,62].

Conclusions

There is no doubt that kin selection theory has been very successful in explaining a wide range of phenomena. Our aim here has been to emphasize caution in its application. In particular:

- There can be considerable direct fitness benefits to supposedly altruistic traits. These can be more important than indirect fitness benefits even when interactants are close relatives. Empirical work is required to quantify the relative importance of indirect and direct fitness benefits of behaviours.
- Multiple mechanisms and their interactions working simultaneously might be crucial in many cases. For example, a subordinate meerkat that helps raise the offspring of another individual's offspring might be increasing: (a) its own survival; (b) its chance of attaining dominance in a group; and (c) the number of helpers it will have if it obtains dominance in that group (let alone any indirect fitness benefits) [18,19,63]. Importantly, the relative importance of different mechanisms might vary with sex and status (e.g. natal versus immigrant), as well as between species. Empirical work is required to determine the relative importance of different mechanisms, how they interact and how they vary both within and across species.
- Competition between relatives reduces kin selection for altruism. Extreme cases, such as fighting in fig wasps, show how this can even totally negate kin selection for altruism towards relatives. The next crucial step is to estimate the importance of competition between relatives in other systems where it is likely to have more intermediate effects, ranging from cooperatively breeding vertebrates to facultatively social insects to malaria parasites to bacteria.

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