

The basics of kin selection theory

Kin selection theory has its origins in attempt to unlock the puzzle of why some organisms have evolved to help other organisms of the same species. Such helping behavior is a puzzle because an organism that helps another will likely incur some reproductive cost, such as a loss of resources to allocate to its own offspring, increased mortality risk, or reductions in other components of Darwinian fitness (i.e., reproductive success). This means that any gene that increases the probability of helping behavior will reduce its frequency in future generations and ultimately will be lost unless there is some compensating reproductive benefit, i.e., some additional path by which helping behavior causes a net increase in the underlying gene's frequency.

William D. Hamilton (1964) provided a pivotal insight into the evolution of altruistic helping by pointing out that altruistic acts directed toward relatives produce an important kind of reproductive compensation. By enhancing the reproduction of relatives, a help-inducing gene indirectly propagates copies of itself in those relatives. When the relatives are the helper's own offspring, most authors refer to the helping as 'parental care' and the enhancement of propagation of the helping genes is often referred to as a positive 'direct effect' of those genes. The power of Hamilton's theory was that it showed that help-inducing genes benefit in an essentially identical way when the help is directed toward non-descendant relatives, such as siblings. When the latter 'indirect' effect is sufficiently strong, the helping gene can spread (increase in frequency in the population) despite decreases in its propagation through the offspring of the individual in which it resides (i.e. the positive indirect effects can outweigh negative direct effects). Despite the terminology, there is no sense in which 'indirect' effects are less robust than 'direct' effects (Dawkins 1979).

There are two distinct, mutually consistent, fitness-accounting methods in quantitative kin selection theory: *neighbor-modulated fitness* or *inclusive fitness* (Hamilton 1964; Grafen 1982; Maynard Smith 1982a; Reeve 1998). Neighbor-modulated fitness, which is closely allied to the concept of fitness used in population genetics theory, focuses on the reproductive costs or benefits *received* by an altruist from others (the term "neighbor-modulated" is intended to connote fitness influences from the social environment). In contrast, inclusive fitness focuses on the reproductive benefits and costs dispensed by an altruist to others (the term "inclusive" is used to emphasize that effects of altruism on all kin, not just on oneself, are to be combined).

Hamilton showed that both methods of accounting lead to exactly the same condition for the spread of altruism, this condition usually termed as "Hamilton's rule". This was an important achievement, because inclusive fitness is generally much easier to compute than is neighbor-modulated fitness (but there are pitfalls: Grafen 1982) as the latter but not the former depends on the population frequency of the altruism allele.

Inclusive fitness

In the inclusive fitness accounting approach, the focus is on reproductive effects dispensed by the individual bearing the altruism-producing gene. The idea is to combine all the dispensed reproductive effects of an individual into an "inclusive fitness" for that individual in a way that correctly predicts the evolution of the altruism (Hamilton 1964). Hamilton's verbal prescription for calculating inclusive fitness was essentially the following: *Take the baseline personal reproductive output of the individual, add to the latter the effect of the individual's behavior on itself (this sum is called the personal component of inclusive fitness), and also add the sum of the effects of the individual's behavior on the reproduction of others, weighted by the individual's genetic relatedness to those other individuals (this weighted sum is called the kin component of inclusive fitness).* The behavior associated with the higher average inclusive fitness will spread.

Before computing inclusive fitness, we need a rigorous understanding of the concept of genetic relatedness. Relatedness is a measure not of the absolute genetic similarity between two individuals (a common misconception), but of the degree to which this similarity *exceeds* the "background" similarity between individuals randomly drawn from the population. One way to compute relatedness is to calculate the probability that a given allele in the altruist of altruism is present in the recipient of altruism via common descent (Hamilton 1964; Grafen 1985); this is the genealogical relatedness. (Another way to compute relatedness from genetic data is explained in vignette 1.) Having obtained the value of the genetic relatedness r between an altruist and a recipient, we can now compute the inclusive fitness. Let the average reproductive output of non-altruists be equal to x offspring. This is also the baseline reproductive output for altruists, and thus the total personal reproductive component for altruists is $x-c$ where c is the cost of altruism. The recipient of altruism receives a mean increment b to its reproductive output. It then follows from the definition that the average inclusive fitness for altruists is equal to:

$$x - c + rb \quad (1)$$

Altruism will begin to spread when the inclusive fitness for altruists exceeds the inclusive fitness for non-altruists, i.e., when $x - c + rb > x$, which simplifies to

$$rb > c. \quad (2)$$

The latter condition is the widely used 'Hamilton's rule' for the evolution of altruism. Hamilton's rule is easily generalized to encompass multiple interactions with different kinds of kin:

$$\sum_{i=1}^N r_i b_i > 0 \quad (3)$$

where N is the number of kin plus self, relatedness to self equals one and the b_i 's associated with the i th kin classes can be either positive or negative (i.e., either benefits or costs to the recipients). Importantly, this rule can be applied to the evolution of any phenotype, not just behavioral altruism.

However, the generalized rule has important limitations (review in Grafen, 1985). In particular, its use assumes that (i) costs and appropriately weighted benefits can be added (as opposed to multiplied or otherwise combined) together to determine the overall fitness effect of altruism, (ii) selection is weak enough that the genetic relatedness can be treated as constant and equivalent to the genealogical relatedness, and (iii) altruism is random according to whether recipients of a given relatedness r actually possess the gene promoting altruism (Grafen 1984, 1991). When these assumptions are not met, other methods of for computing the evolutionary outcomes of kin selection must be sought (Queller 1992; Frank 1998). Importantly, Hamilton's rule is more likely to be valid when altruism is so strongly context-dependent that recipients of altruism do not themselves express the same altruism (Parker 1989).

Altruism between relatives

Hamilton's theory of kin selection predicts that an individual will tend to behave differently toward conspecifics of different degrees of relatedness, and there are numerous examples

demonstrating that this is indeed the case. Here we take the example of alarm calls to illustrate how variation in kin structure can influence the expression of altruism within groups.

In many social groups of vertebrates, individuals give alarm calls when predators approach. For example, when groups of Belding's ground squirrels are threatened by a coyote or a weasel, some of the squirrels stand up on their hind legs and produce a high-pitched screech. Callers most likely suffer a cost because calling makes them conspicuous and presumably more likely to be attacked by the predator. Two lines of evidence suggest that individuals are more likely to give alarm calls when surrounded by a higher proportion of relatives. First, there is sex-biased dispersal and females are more likely than males to stay close to their natal area, resulting in a higher relatedness of females than males to neighbors. Accordingly, females were found to sound much more frequently than males. Second, females that had close relatives nearby called more frequently than females without (Sherman 1977), again as predicted by kin selection.

In another species of rodent, the black tailed prairie dog, Hoogland (1983) further investigated whether individuals behaved differently depending on whether kin were offspring or non-descendent relatives. He experimentally studied alarm calling by presenting individuals with a stuffed badger, a natural predator. He found that the proportion of times individuals gave an alarm call significantly increased when they were surrounded by kin but did not significantly vary according to whether these were offspring or non-descendent kin. These results are in line with the prediction that warning offspring (i.e., parental care) or sisters (direct and indirect effects of altruism, respectively) are, in fact, equivalent ways of increasing propagation of genes identical by descent to future generations.

Reproductive altruism in vertebrate societies

In at least 220 bird and 120 mammal species, young are reared not only by their parents, but by other individuals as well. Typically, these helpers are young individuals that help their parents to rear younger siblings. The occurrence of such co-operative breeding raises two interconnected questions. Why do offspring remain with their parents rather than disperse and attempt to breed independently on their own? And why do the offspring that remain at home engage in costly tasks, for example collecting food to feed their parent's offspring?

Numerous studies, mainly in birds, suggest that offspring stay home because the opportunities for successful dispersal and independent breeding are limited relative to the payoff for staying at home. There are several, additive ways by which helping might be beneficial given that offspring stay at home. First, helpers may obtain direct benefits, for example by gaining experience and thus becoming better parents when they will breed on their own later. Second, helpers may gain indirect benefits by increasing the numbers of relatives produced, thereby increasing their inclusive fitness.

Several lines of evidence demonstrate that kin selection is an important force favouring the evolution of co-operative breeding. Both in birds and mammals co-operative breeding seems to be largely restricted to family structures composed of close kin. Moreover, in most of the co-operative breeding species where it has been investigated it turns out that individuals preferentially assist their closest relatives (Emlen 1997). For example, in white-fronted bee-eaters, kinship is a strong predictor of both whether a given individual becomes a helper and to whom it provides help (Emlen and Wrege 1988). Non-breeders are more likely to become helpers when the breeding pairs in their family are close genetic relatives, and when faced with a choice of potential recipient nests, they preferentially help the pair to whom they are most closely related.

Interestingly, kinship does not only determine whether or not an individual will help, but also the amount of help provided. In pied kingfishers, for instance, helpers may be related or unrelated to the breeding pair. Related helpers work as hard as the breeding pair, but unrelated ones work less (Reyer 1984). Similarly, co-operative breeding Seychelles warblers exhibit significantly higher helping efforts (food provisioning and period of helping) when rearing full sibs than when rearing half-sibs (Komdeur 1994). Overall, these results demonstrate that, as predicted by kin selection, individuals are more likely to help kin than non-kin and that the level of altruism increases with relatedness.

Eusociality in insects

Of all the cases of altruism to be found in the animal kingdom, surely the most extreme is the behaviour of the workers in social insects. Some ants, for example, form colonies comprising up to one million sterile workers specialising in tasks such as building the nest, collecting food, rearing the young and defending the colony. In these colonies reproduction is restricted to one or a few individuals, the queens. The term "eusociality" refers to such societies, which are characterised by reproductive division of labour, co-operative brood care and (generally) overlap of generations.

There is currently no doubt that kin selection has been the *all important* selective force responsible for the evolution of eusociality and reproductive altruism by workers (Bourke and Franks 1995; Crozier and Pamilo 1996). Numerous genetic studies have revealed that eusociality evolved within groups of highly related individuals, such as one mother and her offspring. There are a few ant species in which the relatedness between nestmates is close to 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. It is still unclear whether such societies are of recent origin and evolutionarily unstable, or whether the benefits of worker

helping in such societies is large enough so that Hamilton's rule is still satisfied despite the low relatedness of workers to the helped brood (Bourke and Franks, 1995; Keller 1995).

Eusociality has evolved independently many times among the insects and most frequently in the Hymenoptera (wasps, bees and ants). Interestingly, Hymenoptera have a haplodiploid mechanism of sex determination which generates peculiar patterns of relatedness. Because unfertilised eggs give rise to males and fertilised eggs to females, sisters always receive the same set of paternal genes and therefore share 75% of their genes identical by descent. As a consequence, Hymenopteran females are more related to their full sisters than to their own offspring and it has been suggested that this may explain the prevalence of eusocial origins in the Hymenoptera (Hamilton 1964). The haplodiploidy hypothesis would also explain another interesting feature, that workers are exclusively females in social Hymenoptera but not in the termites (which are always diploid).

Although the haplodiploid hypothesis is appealing, it turns out that it is not so simple because the high relatedness between sisters is balanced by the low relatedness of females to brothers ($r=0.25$). Hence, workers gain by rearing siblings rather than offspring only if workers lay the male eggs or if workers can concentrate on raising sisters while males are produced by solitary females (Seger 1983). Clearly, these conditions do not apply in contemporary species and it thus seems unlikely that haplodiploidy has been a very important factor responsible for the maintenance and possibly even origin of eusociality. The fact that most cases of extreme reproductive altruism are found in Hymenoptera might be due to other features of this group, for example the unusually high frequency of parental care, a useful precursor of evolving care of the young of others (Alexander 1974), or the enhanced protection from chance loss that rare alleles for worker altruism receive in haplodiploid compared to diploid systems (Reeve 1993).

Conflicts within kin groups

Although high relatedness favors high levels of co-operation, potential conflicts persist in groups composed of kin, whether they are co-operative breeding birds or eusocial insects. Potential conflicts arise because, in contrast to cells of an organism, group members are not genetically identical. Hence, kin selection predicts that individuals with partially divergent genetic interests may attempt to favor the propagation of their own genes, possibly to the detriment of other group members. Group members can compete over direct reproduction or over how to allocate group resources to various relatives, and the potential conflict may translate into actual conflict or may remain unexpressed (Ratnieks and Reeve 1992). Interestingly, the study of conflicts provides some of the best tests of kin selection, as illustrated by the patterns of allocation of resources to the production of male and female reproductives in social Hymenoptera.

Kin selection theory predicts that the value of new queens and males is influenced by their relatedness to other colony members (Hamilton 1964). The haplodiploid sex-determination system in social Hymenoptera results in asymmetries in the relatedness of workers to females and males with, in colonies headed by a single queen, workers being three times more related to new sister queens than they are to their brothers. Thus, the equilibrium is a 3:1 biased population sex-investment ratio in favor of females if workers control colony sex ratios. In contrast, because queens are equally related to their sons and daughters, the equilibrium ratio should be an even investment in males and females if queens control colony sex ratios. Therefore, kin selection predicts a conflict between queens and workers over sex investment ratios (Trivers and Hare 1976).

Cross-species comparison of population-level sex investment ratios in ants that generally have a single queen per colony showed that the population sex investment ratio is globally female-biased (1.7:1). This indicates that workers have some control over colony sex ratios and that, as predicted by kin selection, they bias sex investment toward females. Unfortunately, it is very difficult to reliably assess the relative cost of production of males and queens, and a proportion of the ant species in this comparative study probably depart from the simple family structure expected when the colony is headed by one queen mated with a single male. As a result, interspecific comparisons of this type do not allow precise determination of the theoretically expected and observed population-wide investment sex ratios and thus the relative power of queens and workers in biasing colony sex ratios to their advantage.

The most complete demonstration of queen-worker conflict over sex allocation and an all important role of kin selection comes from a study in the ant *Formica exsecta* (Sundström et al. 1996). The study population consists of colonies headed by single queens mated with either one or multiple males. Multiple mating by queens decreases the relatedness between workers and the new queens to be raised but does not influence the relatedness of workers to males. Theory shows that, under such conditions, worker maximize their inclusive fitness by producing the sex to which they are most related compared to the population average, that is new queens in nests headed by a singly-mated queen and males in colonies with a multiple-mated queen (Boomsma and Grafen 1990). The queen controls the primary proportion of males and females by regulating the proportion of haploid and diploid eggs she lays. However, workers may subsequently modify the sex investment ratio by selective rearing of the brood. Comparison of sex ratio at the egg and adult stage showed that workers eliminated a high proportion of males in colonies headed by single-mated queens, leading these colonies to produce mostly females. By contrast, males were kept alive in colonies headed by a multiple-mated queen (Sundström et al. 1996). Hence, in this population, workers win the conflict against the queen and bias colony sex ratio so as to maximize their inclusive fitness. A similar pattern of relatedness-induced split sex ratio has been documented in 16 other species of social Hymenoptera (Queller and Strassmann 1998). In some

other species, however, there is apparently no association between sex ratio and colony level relatedness, suggesting that queens may also have some means to achieve their colony sex ratio interests, for example by limiting the number of female eggs produced (Pamilo 1982; Reuter and Keller 2001; Aron et al. in press).

Overall, studies of sex allocation in social Hymenoptera and other within-group conflicts (e.g., Pfennig 1993) demonstrate that the nature and expression of many conflicts depends on the genetic structure of the group, as predicted by kin selection theory. Paradoxically, the outcomes of within-group conflicts strongly support kin selection theory, a theory which was first proposed to explain the evolution of co-operation! More generally, these conflicts also reflect the most basic principle of Darwinian evolution, namely that organisms are selected to maximize the number of copies of their own genes transmitted to the next generation.

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Vignette 1: Computing relatedness from genetic data

Relatedness can be computed from genetic data as follows (Queller and Goodnight 1989; Reeve et al. 1992): Let A be the average frequency of the altruism gene in altruists, p be the population-average frequency of the altruism gene, and R be the average frequency of the altruism allele in the kin group within which an altruist interacts. Then it can be shown that $Ar + (1-r)p = R$ (Grafen 1985, 1991), where r is the "regression measure of relatedness" (so called because it is equal to the slope of the regression of the gene frequency of an individual's group on the gene frequency within the individual). Rearranging the latter equation, $r = (R - p)/(A - p)$. The regression measure of relatedness is essentially identical to the genealogical measure of relatedness r when selection is not too strong (Grafen 1985, 1991). This measure of relatedness nicely illustrates that relatedness depends on above-background genetic similarity ($R - p$), not only on the absolute genetic similarity (R) between altruists and recipients.

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