Kin Selection

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Abstract

The theory of kin selection is the foundation for the study of social evolution. Here I discuss the historical origins of the theory, provide a mathematical overview, review the various mechanisms that give rise to kin selection, and explain its relevance to the understanding of eusociality.

The Origins of Kin Selection

The basic idea of kin selection was formulated by Charles Darwin, in *The Origin of Species* (Darwin, 1859; *see* Darwinism). It arose as the solution to a puzzle posed by sterile workers in social insect colonies; specifically, how to explain the striking adaptations of these individuals, given that they cannot reproduce and hence appear to be beyond the reach of natural selection. Darwin realized that this puzzle is similar to a problem faced by farmers who rear cattle for their meat. After slaughtering an animal, preparing the meat, and finally discovering that it is particularly delicious, the farmer is unable to breed from the slaughtered individual to ensure that subsequent generations of the herd will inherit the superior meat. However, he/she can breed from the slaughtered individual's close relatives who, on account of their co-ancestry, are likely to share the heritable tendency for delicious meat. Darwin suggested that something similar happens in the social insects. If a variant worker behavior or morphology arises that provides a reproductive benefit to the individual's fertile family members then, because those family members have a strong likelihood of sharing the same heritable tendency, it may be preserved for posterity by the action of natural selection.

Later, R.A. Fisher provided a kin selection explanation for the evolution of distastefulness in gregarious insect larvae in *The Genetical Theory of Natural Selection* (Fisher, 1930). He suggested that, although distastefulness provides no benefit to a predated larva, it may dissuade the predator from eating the larva's siblings. Fisher remarked that the ensuing selective benefit is only half as great as it would be had the individual herself avoided predation, and this appears to be the first use of a coefficient of relatedness to translate fitness effects for relatives into a selective benefit for a focal actor. However, Fisher did not elaborate the principle for more distant degrees of relationship. And he explicitly neglected such 'indirect effects' in the derivation of his fundamental theorem of natural selection, which he used as justification for the view that natural selection leads organisms to appear designed to maximize their personal reproductive success. In 1955, in a popular science article, J.B.S. Haldane gave a verbal account of how selection would operate on a rare gene that made its carrier jump into a river to save a drowning relative, showing that the gene could only be selectively favored if the degree of relationship were sufficiently close (Haldane, 1955). However, he seems not to have appreciated that this principle could be used to understand social evolution more generally.

Thus, it fell to W.D. Hamilton to develop and usefully apply a proper mathematical theory of kin selection, more than a century after Darwin had first formulated the idea. As an undergraduate at the University of Cambridge in the 1950s, Hamilton had been dismayed by the rampant 'for the good of the species' thinking that had come to dominate evolutionary biology in general and the study of social behavior in particular. So he took up the mantle of kin selection where Fisher had left it, focusing his doctoral studies upon the genetical evolution of altruistic behavior. In a series of articles published over 10 years during the 1960s and 1970s (Hamilton, 1963, 1964, 1967, 1970, 1972), Hamilton laid the theoretical foundations of kin selection, devised a classification of social behaviors, derived a general statement of how direct and indirect fitness effects jointly determine the response to natural selection, showed that this leads organisms to appear designed to maximize their inclusive fitness rather than their personal fitness, and applied this understanding to make seminal contributions to the topics of altruism, sex allocation, and eusociality. Spurred by Hamilton's work, John Maynard Smith coined the term 'kin selection' (Maynard Smith, 1964), and Eric Charnov immortalized Hamilton's contribution by naming the core mathematical result of kin selection theory 'Hamilton's rule' (Charnov, 1977). The theory of kin selection now provides the foundation for the study of social evolution (Frank, 1998).

The Genetical Theory of Kin Selection

The canonical elucidation of kin selection theory takes Price's (1970) equation of natural selection as its starting point (e.g., Hamilton, 1970). The following exposition owes heavily to Queller (1992) and is more fully developed by Gardner et al. (2011). Price's equation encapsulates the action of natural selection as the part of genetic change that is ascribable to the differential fitness of individuals:

$$\Delta_{NS}E(g) = \text{Cov}(v, g). \qquad [1]$$

This states that the change in the population average (or expectation, E) of any genetical character that owes to the action of natural selection is equal to the covariance (Cov) of relative fitness (v) and genetical character (g) across all the individuals in the population. Here, the genetical character

may represent the frequency of a particular gene in the individual's genome (in which case $E(g)$ is the population frequency of that gene), the heritable component of any phenotypic trait of interest (i.e., a genetic 'breeding' value), or any other weighted sum of genic values. That is, if individuals with a greater genetical character value tend to have higher fitness, then the covariance is positive ($Cov(v, g) > 0$) and natural selection acts to favor an increase in average character value ($\Delta_{NS}E(g) > 0$). Whereas, if individuals with a greater genetical character value tend to have lower fitness, then the covariance is negative ($Cov(v, g) < 0$) and natural selection acts to favor a decrease in the average character value ($\Delta_{NS}E(g) < 0$). If there is no tendency for individuals with a greater genetical character value to have higher or lower fitness, then the covariance is zero ($Cov(v, g) = 0$), and natural selection favors neither an increase nor a decrease in the average character value ($\Delta_{NS}E(g) = 0$).

Assuming that there is some heritable variance in the population (i.e., $Var(g) > 0$) then, without loss of generality, one can write $Cov(v, g) = \beta(v, g)Var(g)$, where $\beta(v, g) \equiv Cov(v, g)/Var(g)$. This coefficient $\beta(v, g)$ turns out to have a useful interpretation: if one were to make a plot of relative fitness (v) against genetic character (g) for all the individuals in the population, then $\beta(v, g)$ is equal to the slope of the straight line $E(v|g) = E(v) + \beta(v, g)(g-E(g))$ fitted through these (v, g) data by the method of least squares (**Figure 1(a)**). Since variances are non-negative, the condition for natural selection to favor an increase in average character value ($Cov(v, g) > 0$) may be written as:

$$\beta(v, g) > 0 \qquad [2]$$

Note that I have not assumed that there is a straight-line relationship between genes and fitness in the population. Indeed, there may be an arbitrarily complex relationship between genes and fitness, and the least-squares fit may fail to capture lots of this complexity (**Figure 1(a)**). However, it is only the least-squares fit that natural selection cares about. That is, natural selection favors an increase in the average character value if and only if the slope of the least-squares

linear regression is positive, and this translates into an actual response to selection in proportion to the heritable variance that is present in the population.

This association between genetic value and fitness is statistical and need not reflect a direct causal relationship. For example, if we consider that the genetic character leads the individual to enact altruism toward her neighbor, then the direct impact of the character on her own fitness will be negative, but she may enjoy an indirect benefit owing to her neighbor also carrying the gene and directing altruistic behavior back toward her. The overall slope of relative fitness against genetic character can be partitioned into these separate direct and indirect effects using multiregression methods. That is, instead of fitting a straight line through two dimensional data, as was described earlier, the idea is to fit a plane $E(v|g, g') = E(v) + \beta(v, g|g')(g-E(g)) + \beta(v, g'|g)(g'-E(g'))$ through the three-dimensional data set (v, g, g'), where g' denotes the genetic character of the focal individual's neighbor (**Figure 1(b)**). This leads to the multiregression partition:

$$\beta(v, g) = \beta(v, g|g') + \beta(v, g'|g)\,\beta(g', g). \qquad [3]$$

Considering an altruistic trait, the impact of the individual's character value (g) upon her own fitness (v), holding fixed the character value of her neighbor (g'), defines the cost of altruism for the actor, i.e., $\beta(v, g|g') \equiv -c$. The impact of the neighbor's character value (g') upon the focal individual's own fitness (v), holding fixed her own character value (g), defines the benefit of altruism for the recipient, i.e., $\beta(v, g'|g) \equiv b$. Finally, the association between the genetic character values of the focal individual (g) and her neighbor (g') defines the kin selection coefficient of relatedness, i.e., $\beta(g', g) \equiv r$. Hence, from eqn [3], the condition for natural selection to favor an increase in altruism – or, indeed, any genetic character of interest – is:

$$-c + br > 0, \qquad [4]$$

which is Hamilton's rule of kin selection. This formally separates the direct fitness effect of a character ($-c$) from the indirect
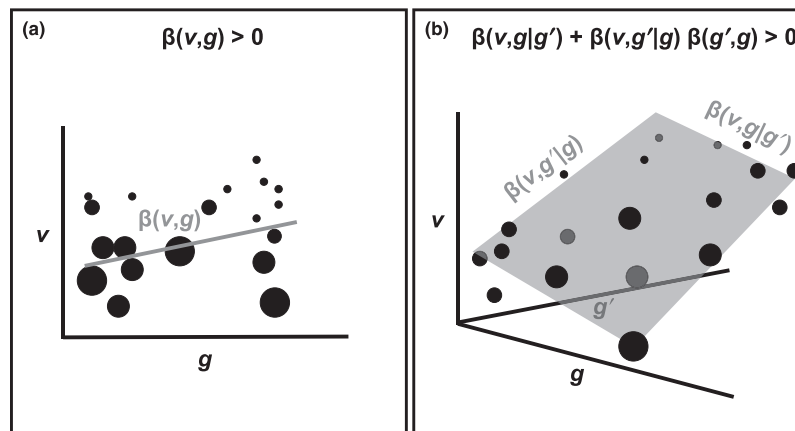

Figure 1 The genetical theory of kin selection. (a) Natural selection favors any heritable trait that is positively associated with fitness ($\beta(v, g) > 0$). (b) This association can be broken down into the direct impact of the trait on its bearer's fitness ($\beta(v, g|g')$) and the indirect impact of the trait on its bearer's fitness ($\beta(v, g'|g) \times \beta(g', g)$).

fitness effect of that character (rb). The part of natural selection corresponding to direct fitness effects may be termed 'direct selection,' and the part that corresponds to indirect fitness effects may be termed 'indirect selection' or 'kin selection.' That is, kin selection is a part of natural selection, driven by differences in individual fitness, rather than an additional evolutionary process.

In the above derivation, I have assumed that the focal individual has only a single social partner. However, the same methods are readily extended to consider multiple social partners, acting in a variety of roles. This yields a Hamilton's rule of the form $-c + \Sigma_{i \in I}\, b_i\, r_i$, where b_i and r_i are the benefit and relatedness, respectively, corresponding to the individual's ith social partner (Grafen, 2006). I have also assumed that the focal individual and her social partner are interchangeable. That is, they are exactly equivalent in all ways except for their genetic character values. More generally, social partners may belong to different classes, such as male and female or young and old or queen and worker. However, kin selection methods are also readily applied to such class structured populations (Taylor, 1990). Note that I have made no assumption that genes for altruism are additive in their action. There may be any degree of dominance within loci, epistasis between loci, synergy between individuals and frequency dependence at the population level and Hamilton's rule still holds. Recurring claims that Hamilton's rule breaks down in these scenarios are based upon a confusion between the additivity of a linear regression model versus the additivity of an evolutionary genetics model (reviewed by Gardner et al., 2011).

Here, I have focused on altruism, but Hamilton's rule applies when any heritable trait is favored by natural selection. Social behaviors are classified according to their impact on the fitness of the actor and the recipient (Table 1): altruistic behaviors decrease the fitness of the actor ($c > 0$) and increase the fitness of the recipient ($b > 0$); selfish behaviors increase the fitness of the actor ($c < 0$) and decrease the fitness of the recipient ($b < 0$); mutually beneficial behaviors increase the fitness of both the actor ($c < 0$) and the recipient ($b > 0$); and spiteful behaviors decrease the fitness of both the actor ($c > 0$) and the recipient ($b < 0$). In each case, the condition for natural selection to favor the social behavior is $-c + br > 0$. Note that spiteful behavior ($b < 0$ and $c > 0$) is only favored if there is negative relatedness between actor and recipient ($r < 0$, such that $-c + br > 0$). Negative relatedness sounds unusual, but simply means that the actor and recipient are less related than

average (Hamilton, 1970). Nonsocial behaviors are those that do not have fitness consequences for individuals other than the actor ($b = 0$), and hence are favored if they improve the fitness of the actor ($c < 0$) and are disfavored if they reduce the fitness of the actor ($c > 0$).

The above derivation of Hamilton's rule has taken the 'personal fitness' or 'neighbor-modulated fitness' approach to kin selection (Figure 2). This considers the impact of an individual's own genetic character (g) and that of her social partner (g') upon her own fitness (v). An alternative – but exactly equivalent – approach is the 'inclusive fitness' approach, which considers the impact of an individual's own genetic character (g) upon her own fitness (v) and the fitness of her social partner (v'; Figure 2). The only difference between these two approaches is that the benefit term, conceptualized as $b = \beta(v,\ g'|g)$ under the personal fitness view, is reconceptualized as $b = \beta(v',\ g|g')$ under the inclusive fitness view. Thus, the response to selection may be written as $\beta(v, g|g') + \beta(v', g|g')r = \beta(v + v'r, g|g')$. This describes the partial effect of the individual's own genetic character (g) upon the relatedness-weighted sum of the individual's relatives' fitnesses ($v + v'r$), i.e., the impact that the individual has upon her own inclusive fitness.
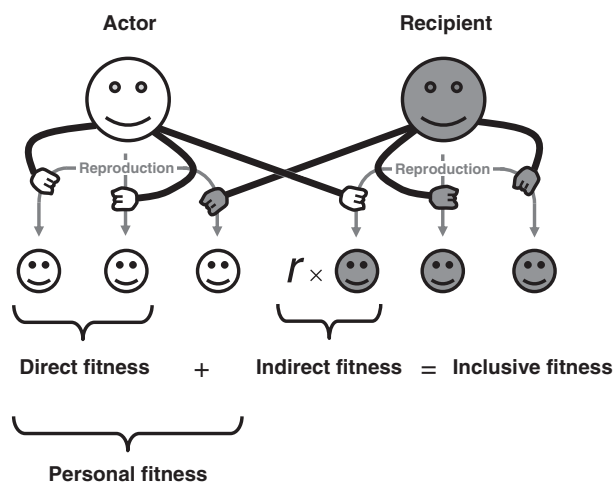

Figure 2   Personal and inclusive fitness. Personal (or neighbor-modulated) fitness describes a focal individual's lifetime reproductive success (unshaded offspring), some of which may be attributed to the action of the individual's own genes (unshaded hands), and some of which may be attributed to the action of the genes carried by the individual's social partners (shaded hands). A necessary and sufficient condition for genes to be favored by natural selection is that they are positively associated with personal fitness. However, individuals do not behave as if they are trying to maximize their personal fitness, because they do not have complete control over this quantity. Inclusive fitness describes the impact that a focal individual's genes (unshaded hands) have on her own fitness (unshaded offspring) and the fitness of her genetic relatives (shaded offspring), each increment or decrement being weighted by the coefficient of relatedness between the individual and her recipient. A necessary and sufficient condition for genes to be favored by natural selection is that they are positively associated with inclusive fitness. Moreover, individuals do behave as if they are trying to maximize their inclusive fitness, because they have complete control over this quantity.

Table 1   Classification of social behaviors

		Impact upon recipient	
Impact upon actor		+	−
	+	Mutual benefit	Selfishness
	−	Altruism	Spite

Behaviors that increase the fitness of both actor and recipient ($+/+$) are termed *mutually beneficial*; behaviors that increase the fitness of the actor and decrease the fitness of the recipient ($+/-$) are termed *selfish*; behaviors that decrease the fitness of the actor and increase the fitness of the recipient ($-/+$) are termed *altruistic*; and behaviors that decrease the fitness of both actor and recipient ($-/-$) are termed *spiteful*. See West et al. (2007) for more discussion.

Inclusive Fitness

The dynamics of natural selection – operating via direct and indirect (kin selected) effects – can be understood either in terms of personal fitness or in terms of inclusive fitness. These two approaches are exactly equivalent and yield the same predictions. However, the adaptive design that emerges from the action of natural selection can only be understood in terms of inclusive fitness. The organism is not generally adapted to maximize her personal fitness, because – in the context of social interactions – she does not have full control over this quantity. However, she is adapted to maximize her inclusive fitness, which is under her sole control, the effects of her social partners having been explicitly stripped away. Consequently, inclusive fitness is a crucial concept in the study of Darwinian adaptation (see Adaptation, Fitness, and Evolution). The formal connection between the dynamics of natural selection and the optimization of inclusive fitness has been shown by Grafen (2006).

This point is best explained with an illustration. Consider a gene that makes an insect worker lay fewer eggs and work harder to improve the reproductive success of her queen. From a personal fitness approach we would say that sometimes the gene will be present in a worker, in which case it will be associated with reduced fitness, because it makes her lay fewer eggs; but sometimes the gene will be present in a queen, in which case it will be associated with increased fitness, because the workers in the queen's colony will also tend to carry the gene, which makes them work harder. Consequently, the gene for worker altruism will be favored if the former direct effect is outweighed by the latter indirect effect. However, we cannot regard the insect worker as striving to maximize her personal fitness, as this would never allow for worker altruism to evolve. Instead, we can take an inclusive fitness approach and say that altruism enacted by the worker reduces her direct fitness, by making her lay fewer eggs; but it also improves her indirect fitness as a consequence of increasing the reproductive success of the queen; and, consequently, worker altruism is favored if the former direct effect is outweighed by the latter indirect effect. Crucially, the worker can be regarded as striving to maximize her inclusive fitness, as it is under her complete control.

Often, the personal fitness approach is the easier option when the aim is simply to capture the dynamics of natural selection in a mathematical model. However, by emphasizing an actor and the causal impact that her social behavior has upon the reproductive success of her social partners, the inclusive fitness approach is more useful for empirical research in behavioral ecology. Moreover, because humans are naturally better at reasoning about agents and strategies than about the dynamics of gene frequencies, the inclusive fitness approach – which yields a simple maximizing agent interpretation – provides a powerful way of thinking about social evolution. The notion of an agent with an agenda is implicit within the intentional language employed by evolutionary biologists: selfishness, altruism, conflicts of interest, etc. For these reasons, the inclusive fitness approach to kin selection has dominated the empirical study of social evolution.

Mechanisms of Kin Selection

Kin selection occurs whenever there is a genetic association between the actor and the recipients of her social behavior. Hamilton (1964) suggested three basic mechanisms for ensuring such a genetic association: population viscosity; kin recognition; and the greenbeard effect (Figure 3).

First, population viscosity occurs when individuals do not disperse far from their place of origin, so that neighboring individuals tend to be closely related, and hence even indiscriminate social behavior can lead to kin selection (Figure 3(a)). Because this requires no special cognition or recognition mechanism, population viscosity has been suggested to provide a very general explanation for cooperative behavior. However, a problem with this idea is that viscosity may also be associated with intense local competition for resources, which can inhibit the evolution of cooperative behavior. In fact, in the simplest models of viscous populations the relatedness-enhancing and competition-enhancing effects of reduced dispersal exactly cancel so that there is no overall impact of the rate of dispersal on the evolution of cooperation (Taylor, 1992). This surprising result has generated a great deal of theoretical interest in exploring factors that act to decouple the relatedness and competition consequences of dispersal, so that cooperation can evolve in viscous populations.

One such factor is budding dispersal. If individuals disperse in groups, alongside social partners, then they may maintain high relatedness with their neighbors while also enjoying the competition-relaxation benefits of dispersal. This idea has been tested empirically, using experimental evolution of
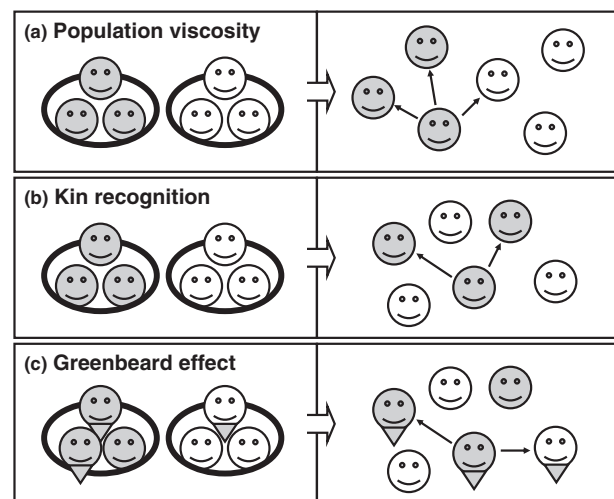

Figure 3 Mechanisms of kin selection. (a) Population viscosity: if individuals do not move far during their lifetime, then they will tend to be surrounded by kin (shaded), and hence even indiscriminate social behavior will give rise to kin selection. (b) Kin recognition: if individuals use cues that carry information about kinship to mediate their social behavior, such as remembering with whom they shared a nest (shaded) and acting altruistically toward those individuals, then this will give rise to kin selection. (c) Greenbeard effect: if the gene controlling social behavior is associated with a phenotypic marker, such as a beard, then carriers of the gene can identify which of their social partners also carry copies, independently of whether or not these social partners are kin (shaded).

Pseudomonas aeruginosa bacteria. In iron-limited medium, bacterial cells may release iron-scavenging molecules called siderophores that bind iron and facilitate its uptake by cells. However, the cell that takes up the bound iron need not be the cell that manufactured and released the siderophore, so siderophore production is a form of public-goods cooperation and cheating cells that do not produce siderophores may free-ride on the cooperation of the other cells in the medium. Kummerli et al. (2009) varied the pattern and rate of dispersal of cells between flasks of medium and showed that, while cooperation was disfavored under both high and low individual dispersal, it was favored under budding dispersal.

Second, kin selection may also occur when individuals use environmental or genetic cues to recognize which of their social partners are their genealogical kin and adjust their social behavior according to this information (Figure 3(b)). Environmental kin recognition occurs when an individual makes use of an environmental cue that is associated with her having greater kinship to her social partners. For example, the rule 'behave altruistically toward individuals who are in my nest, and behave aggressively toward individuals who are not in my nest' uses the position of the recipient relative to the individual's own nest as a proxy for degree of kinship. In contrast, genetic kin recognition occurs when an individual makes use of a genetic cue. For example, if blue eyes were relatively rare in the population, then it is likely that two neighbors who shared blue eyes would do so because they were genealogically close kin, rather than simply by chance. Consequently, individuals may be favored to behave altruistically toward those neighbors whom they most closely resemble.

However, genetic kin recognition appears to be inherently unstable. This is because, while only relatively rare genetic markers provide a good indicator of genealogical closeness, common genetic markers may enjoy a selective advantage owing to their carriers being more often identified as kin and receiving benefits of altruism. Hence, the polymorphism at marker loci that is required for genetic kin recognition to work may be eroded by natural selection, until every individual carries the same alleles, which no longer give any information about genealogical kinship (Crozier, 1986). This may explain why genetic kin recognition is relatively rare in the natural world. One possibility for maintaining genetic kin recognition is if the genetic marker loci mediate host–parasite interaction, as this is a potent source of balancing selection that can help to maintain rare alleles. This may explain why genetic kin recognition, when it does occur, appears to be based on immune-system genes such as the multihistocompatibility complex in humans (Wedekind et al., 1995) and extraembryonic-membrane genes in parasitoid wasps (Giron and Strand, 2004).

Third, the greenbeard effect is similar to genetic kin recognition, but occurs when the same gene (or two closely linked genes) encodes both the marker and the social behavior (Figure 3(c)). The idea here is that two individuals who share a genetic marker in common may also share genes for social behavior that are linked to that marker, irrespective of whether they are genealogically close kin. The greenbeard mechanism was devised by Hamilton (1964) as a thought experiment to illustrate that genetic similarity, and not genealogical kinship per se, is the key to kin selection. The name was coined by Dawkins (1976), who gave a hypothetical example of a gene that causes its carrier to grow a green beard and to act altruistically toward other individuals with green beards. However, empirical examples have been found in the natural world. For example, bacteriocins are toxins produced by bacteria, often at great cost to the producer cell, that poison neighboring cells. The bacteriocin gene is tightly linked to a gene for immunity to that bacteriocin (they are often carried together on a plasmid), and so other carriers of the bacteriocin gene survive the killing and benefit from reduced competition for resources (Gardner and West, 2010). Greenbeards are susceptible to invasion by 'falsebeards,' that enjoy the benefits of bearing a beard but without paying the costs of the social behavior (Gardner and West, 2010). For example, a bacterium that enjoys immunity to bacteriocins without committing itself to the costs of bacteriocin production. Such falsebeards are readily created by sex and recombination between beard and behavior loci, and this may explain why most empirical examples of greenbeards are found in the asexual world of microbes.

Kin Selection and Eusociality

Obligate eusociality is a permanent division of reproductive labor, whereby both reproductive and helper castes are required for totipotency. This system of biological organization is known only in the social hymenoptera (ants, wasps, and bees) and the social cockroaches (termites). The problem of eusociality is to explain why individuals of the helper caste have evolved to give up any chance of future reproductive success in order to serve the needs of their reproductive colony mates. This is the most striking example of altruistic behavior in the natural world and has consequently received much attention from kin selection researchers.

Historically, most attention has been given to the 'haplodiploidy hypothesis' for eusociality. Most of the origins of obligate eusociality have occurred in the social Hymenoptera, a group that is noted for its haplodiploid mode of inheritance. These organisms produce diploid daughters sexually, with one genome being contributed from the mother and one from the father. But they produce haploid sons asexually, from unfertilized eggs. Hamilton (1964, 1972) famously suggested that the apparent predisposition for haplodiploid organisms to eusociality owes to the inflated relatedness between full sisters that emerges under this mode of inheritance. Under both diploidy and haplodiploidy, the relatedness of a female to her daughter is one half ($r = 1/2$), but whereas the relatedness between sisters under diploidy is also one half ($r = 1/2$) the relatedness between sisters under haplodiploidy is three quarters ($r = 3/4$). Hence, while females in diploid populations are ambivalent over whether to rear a sister or a daughter, females in haplodiploid populations prefer to rear sisters over daughters, and this potentially paves the way for the evolution of eusociality.

However, this argument does not really work. Hamilton (1964, 1972) was aware that the relatedness between sister and brother is correspondingly lower under haplodiploidy, and Trivers and Hare (1976) pointed out that this actually cancels any benefit of rearing siblings (sisters and brothers)

rather than own offspring (daughters and sons), assuming an even sex ratio. Craig (1979) subsequently showed that even a female-biased sex ratio does not resolve this problem, as the increased relatedness to siblings (mostly sisters) is exactly countered by the increased reproductive value of males (which is higher, owing to the rarer-sex effect, in a population with a female-biased sex ratio). Haplodiploidy can be made to promote altruistic sib-rearing if there are 'split sex ratios,' whereby some colonies are relatively female biased and others are relatively male biased (Grafen, 1986), but it can also be made to inhibit altruistic sib-rearing, and in most cases its impact is meager (Gardner et al., 2012).

Instead, the key to eusociality appears to be strict lifetime monogamy, which ensures that maternal siblings are full siblings, and hence – on average – as related to the actor as are her own offspring (Boomsma, 2009). That is, it is not necessary for relatedness of siblings to exceed that of offspring, but only that relatedness of siblings match that of offspring, such that any slight efficiency benefit of sib-rearing is sufficient to provide a selective advantage for eusociality. Although not all eusocial organisms are strictly monogamous – the highly polyandrous honeybee providing a striking counterexample – phylogenetic analysis reveals that strict lifetime monogamy is the ancestral state for all eusocial hymenoptera and was the mating system in which eusociality always initially arose (Hughes et al., 2008). The predisposition for the hymenoptera to evolve eusociality may simply be due to their ancestral sperm-storage ability, which enables a singly mated female to produce multiple batches of offspring without needing to remate. Moreover, the monogamy hypothesis also explains why termites have evolved eusociality (their societies are founded by a monogamous mating pair), despite their diploid mode of inheritance.

Summary

Darwin formulated the concept of kin selection in *The Origin of Species*. More than a century later, Hamilton developed a mathematical theory of kin selection, and showed that natural selection leads organisms to appear designed to maximize their inclusive fitness. Hamilton's rule of kin selection emerges as a simple partition of natural selection into its direct and indirect components and is as general as the genetical theory of kin selection itself. There are three major mechanisms by which kin selection operates: population viscosity, kin recognition, and the greenbeard effect. Kin selection is the key to understanding altruistic behavior and the evolution of eusociality.

See also: Adaptation, Fitness, and Evolution; Human Cooperation, Evolution of; Kinship, Evolution of; Sociobiology: Overview.

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