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Indiscriminate altruism: unduly nice parents and siblings

Laurent Keller

Kin recognition, defined here as the differential treatment of relatives, occurs in a large number of species (see Refs 1–3 for review). The two traditionally hypothesized benefits of kin recognition are (1) to favour fitness of more-related individuals (nepotism), and (2) to ensure an optimal balance between inbreeding and outbreeding⁴. The benefits of an efficient kin-recognition system are illustrated by the simple case of a worker ant. By helping the queen increase her reproductive success, the worker indirectly passes on to future generations copies of genes that are identical by descent⁵. The benefits of such altruism rely on the workers being related to the queen that receives the help, which indeed is the case in most species^{6,7}. A common chemical label among nestmates is an important factor that maintains colony cohesion. This signature comes from a combination of genetically specified and environmentally acquired cues that are transferred among colony members. By learning the colony-specific

Many animals can identify their relatives and bias altruistic behaviour in their favour. However, recent studies have also uncovered cases where nepotism might be expected but is weak or absent within social groups. For instance, in some bird and mammal species, males apparently feed offspring that have been sired by other males at the same rate as their own offspring. Similarly, social insect workers fail to favour more closely related individuals within their colony. Why is this so?

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chemical signature, workers can accurately discriminate nestmates from non-nestmates¹.

However, situations occur where nepotism seemingly ought to be favoured but is absent. Here I consider two such situations and discuss the causes that might be responsible for the paradoxical existence of indiscriminate altruism.

Nice parents

Most benefits of parental behaviour depend on the recipient of care being related to the care giver^{5,8,9}. However, molecular techniques have revealed that multiple paternity is frequent in species with parental care¹⁰. In such a situation, the ability of a male to recognize and preferentially care for its own offspring would provide substantial benefits, yet several experi-

ments suggest that both in birds and in mammals males appear not to assess their genetic relationship with the recipient of their care (Table 1). In addition, Kempnaers and Sheldon¹¹ review several studies providing indirect evidence that male birds do not exhibit kin discrimination among

Table 1. The occurrence of nepotistic behaviour during parental care in vertebrates^a

Species	Subjects	Measure	Nepotism	Refs
Birds				
<i>Prunella modularis</i>	male-chick	allocation of food	no	36
<i>Agelaius phoeniceus</i>	male-chicks	allocation of food	no	40
<i>Hirundo rustica</i>	male-chicks	allocation of food	no	^b
Mammals				
<i>Mus musculus</i>	male-pups	infanticide	unlikely ^c	41
<i>Homo sapiens</i>	father-offspring	recognition	unknown	12

^aData in this Table are restricted to within-family discrimination when broods are of mixed paternity. In such a situation, males would have to rely on phenotype matching to assess their genetic relationship to particular young⁴².

^bA.P. Møller and N. Saino, pers. commun.

^cOne study⁴³ reported increased infanticide of unrelated pups, but other experiments, including one with the same experimental procedure, failed to demonstrate nepotistic behaviour by males.

chicks within the nest. For instance, brood manipulation experiments where offspring are cross-fostered show that fostered offspring do no worse than offspring being fed by true parents.

It has recently been suggested that nepotism may possibly occur in humans. Christenfeld and Hill¹² showed that humans are able to match one-year-old babies to photos of their father but not their mother. The authors suggested that the resemblance between babies and their fathers might be in the interest of the babies. While a mother can be confident that the child is hers, regardless of what it looks like, the father cannot. It may then be to a baby's advantage to look like the father if this encourages paternal investment. However, there was a high error rate in the matching of babies and fathers. More studies are necessary to determine whether fathers indeed discriminate against children that look different from themselves.

Nice siblings

Colonies of social insects frequently consist of a number of genetically distinct lineages: in many species, queens mate with multiple males^{13,14}, resulting in colonies consisting of full sisters ($r = 0.75$) and half sisters ($r = 0.25$). Earlier studies of honeybees (*Apis mellifera*) suggested that workers behave nepotistically by favouring full sisters over half sisters

in interactions with other workers, including swarming and queen brood rearing (e.g. Refs 15, 16). However, these studies have been justifiably criticized either because (1) the preference for full sisters may be an artifact of the use of heritable phenotypic markers to distinguish sub-families, (2) task specialization among lineages was not controlled for, (3) faulty statistical analyses were used, and/or (4) colony genetic diversity was artificially low because queens were experimentally inseminated with the sperm of only two to three males, although they usually mate with between seven and 17 males¹⁷⁻¹⁹. Based on a review of the current data, Breed *et al.*²⁰ suggested that within-colony kin recognition in queen-rearing plays no role, or at best only a minor role, in the biology of the honeybee. A critical analysis of the evidence for nepotism and possible alternative explanations for results suggesting within-family nepotism in the honeybee can be found in the recent debate between Sherman²¹ and Alexander²².

Further studies of other species of social insects have also failed to show nepotism within colonies. In several ant and wasp species, queens may cooperate to initiate new colonies, but not in a nepotistic way. Queens of the wasp *Polistes annularis* do not prefer to cooperate with closest relatives to initiate new colonies²³. Cooperation between founding queens is also common in the fire ant (*Solenopsis invicta*), but queens start fighting soon after the eclosion of the first workers, ending with the death of all but one queen. The first eclosed workers may also take part in the fights, but they do not favour their mother or increase her probability of survival^{24,25}. Finally, mature colonies of some ant and wasp species are headed by several queens (see Ref. 26 for review), but the workers fail to favour sisters over workers from other matriline, or to behave nepotistically towards their mother compared with other queens (Table 2).

The logic of indiscriminate altruism

There are at least two, non-mutually exclusive, general explanations for the apparent lack of nepotism in paternal behaviour and reproductive altruism within insect societies. The first explanation posits that the benefits of preferential treatment of more-closely related individuals are offset by the cost incurred by other less-related group members²⁷. The second asserts that kin-biased behaviours are disfavoured because of the cost of recognition errors^{3,28}.

The first explanation is that selection has favoured universal treatment of family or colony members because differential treatment of kin classes incurs costs that outweigh the benefits to the altruistic individual. When all individuals receiving help are related (to a variable degree) to the altruist, the benefits resulting from the increased fitness of more-related individuals is mitigated by the decrease in fitness of the less-related individuals (costs and benefits being weighted by the coefficient of relatedness between care giver and recipients). Thus, Ratnieks and Reeve²⁷ considered the case of an insect colony headed by a multiply-mated queen in which workers may help

Table 2. The occurrence of nepotism within colonies of social insects

Species	Subjects	Measure	Nepotism	Refs
<i>Apis mellifera</i>	worker-larvae	rearing of new queens	unlikely	17-22
	worker-worker	swarming behaviour	unlikely	17-22
<i>Polistes annularis</i>	queen-queen	joining of other queens	no	20
<i>Formica argentea</i>	worker-worker	grooming and feeding	no	44
	worker-queen	"	no	44
<i>Camponotus planatus</i>	worker-worker	food exchange, grooming, antennation and jerking	no	45
	worker-queen	"	no	45
	worker-virgin queen	"	no	45
<i>Solenopsis invicta</i>	worker-queen	queen survival, queen-worker fights	no	24,25
	worker-queen	queen tending	no	46
	worker-virgin queen	food exchange	no	46

either full or half sisters. They pointed out that differential treatment of colony members would inevitably lead to losses in colony efficiency, for example, because time is wasted in assessment of patriline status. Therefore, if nepotism is associated with a decrease in colony efficiency, all patrilines may experience a net decrease in inclusive fitness, and kin discrimination might be selectively disfavoured. In general, smaller differences in relatedness between colony members should tend to select against nepotism. This is because smaller differences in relatedness between altruists and classes of individuals receiving help result in smaller potential benefits for nepotistic behaviours. It is important to note that the explanation that selection may favour universal treatment of group members does not generally apply to social groups in which altruistic individuals are completely unrelated to some of the potential recipients of the help (see Box 1). Thus, in the case of a brood of mixed paternity, it pays for the male to discriminate against offspring fathered by other unrelated males since there is no cost associated with decreased fitness of these unrelated individuals.

The second explanation asserts that kin-biased behaviours are disfavoured because of the cost of recognition errors. Since no recognition system is perfect, the decision of an individual to behave nepotistically depends on the probability of correctly identifying desirable and undesirable recipients and the benefits versus costs of correct and incorrect assessment^{3,28}. The efficiency of any type of kin recognition system rests on the types of cues available. Males would have to rely on genetically specified cues to recognize their offspring in the case of broods with mixed paternity¹¹. Similarly, because they share the same environment, workers in an insect colony cannot use environmental cues to distinguish genetic lineages.

Evidence suggests that recognition mediated by genetic cues might be unstable and error prone. First, theoretical studies indicate that allelic diversity of recognition should decrease over time because more-frequent alleles will be continually favoured until fixation^{29,30}. Thus, other selective forces such as gamete compatibility, disease resistance or prevention of intraspecific parasitism must operate to maintain the genetic diversity of recognition cues^{29,30}. Consistent with this idea, several vertebrates have been shown to use MHC-induced odours to recognize relatives; the extremely high allelic variability at MHC loci is maintained because of their role in immune defence and, most importantly, the avoidance of kin-matings³¹. Although no genetic system of kin recognition has been identified in social insects, sex determination alleles, which are maintained at high diversity by frequency-dependent selection in Hymenoptera⁷ could provide useful polymorphic loci for kin recognition²⁹. However, it is still unknown whether or not these alleles have a recognizable phenotypic effect³⁰.

Second, the use of genetically specified cues might be associated with relatively high rates of recognition errors since recombination results in different combinations of segregating alleles in family members³²⁻³⁵. In the case of paternal behaviour, acceptance errors (feeding of non-descendants) and rejection errors (non-feeding of descendants) could have very asymmetric consequences. Acceptance errors are costly since food intended for true descendants would be allocated to others. However, rejection errors are probably much more costly since descendants might starve if they receive less or no food at all. Thus, the fitness consequences of rejection errors may constrain the evolution of nepotism by males feeding chicks. Moreover, the job of males is made even more difficult because in many cases

Box 1. Indirect benefits of help and punishment

There are, however, at least two factors that may select against nepotism in groups, where potentially altruistic individuals are completely unrelated to some of the potential recipients of their help. First, nepotism might be selected against when help to unrelated recipients is associated with *indirect* benefits. Consider, for example, a colony with multiple unrelated queens where workers do not behave nepotistically. A mutant allele inducing workers to behave nepotistically would provide benefits to females carrying this allele since they are more likely to get help from their sisters. However, the 'nepotistic' allele also induces a cost to its bearers because it reduces the number of non-nepotistic workers (i.e. those who do not carry the nepotistic allele) produced. This is, of course, because non-nepotistic workers are valuable to all colony members since they help indiscriminately. Thus, nepotism will be favoured only if it is not too costly in terms of the production of workers from other matrilines.

The second factor that may select against nepotism is punishment by other group members. In birds, for example, males may be prevented from discriminating against offspring fathered by other unrelated males if, by so doing, they are punished by females. Similarly, punishment of discriminating workers might effectively prevent nepotistic behaviour in insect societies, particularly when there are many patrilines and/or matrilines (i.e. a high ratio of individuals, which should police nepotistic workers). Apart from in primates, the possible role of punishment as a factor maintaining within-group cooperation has received very little empirical scrutiny⁴⁷.

non-descendant offspring will be in the minority, thus increasing further the relative cost of rejection errors²⁸.

Third, the rate of recognition errors might be increased when there are conflicts of interests between family members. Whereas a father should favour his own offspring, a mother would normally benefit if the father would treat all chicks equally^{11,36}. This conflict between parents sets in motion a race between the father trying to discriminate between offspring and the mother attempting to reduce or eliminate information about kinship within the family (i.e. 'scramble' recognition cues³⁷). Chicks themselves should be on the side of their mother in this conflict when they are uncertain about whether they are the offspring of the resident males (which may almost always be the case). This is because for a chick the fatal cost of being rejected, even if small, probably exceeds the benefit, even if likely, of receiving extra food^{3,11}.

Individuals in social insect colonies may also benefit by scrambling recognition labels, particularly when close relatives constitute only a small fraction of the total pool of interactants³⁷. This is because accurate signalling of kin status would produce some increased help from (rare) more-closely related individuals but reduce the benefits provided by the (most common) less-related individuals. Moreover, when nepotism entails cost for colony productivity, all members may benefit by reducing or eliminating information about kinship within the group. This could be achieved by transferring odours between colony members, as indeed has been observed in many ant species¹. However, it is not yet clear if the role of chemical cue transfer is to remove information about kinship within colonies or to provide a better system of recognition between members of different colonies. A direct prediction of the scrambling hypothesis is that odour transfer should be absent or less frequent in colonies where there is usually a single matriline and patriline (colonies with one singly-mated queen), than in colonies with different genetic lineages, since no nepotism is predicted to occur in the former.

A schematic representation of the combined effects of factors selecting against nepotism is given in Box 2. Whether or not nepotism will be favoured depends on the factors affecting the efficiency of the recognition system, and also on the factors setting the minimum recognition efficiency required for nepotism to be favoured.

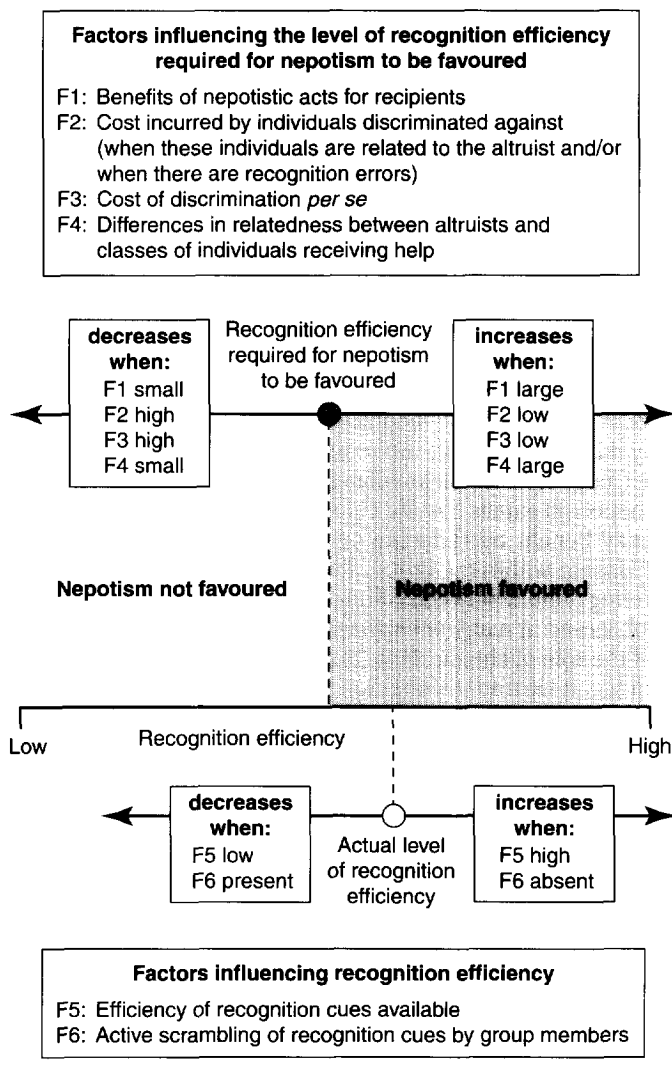
Conclusion and perspectives

The advent of 'selfish-gene' thinking has led to the view that nepotism should be commonplace in social groups consisting of different kin classes. Yet, recent studies indicate that potential conflicts do not always translate into actual conflicts, as exemplified above by the cases of parental and sibling care. For instance, lack of an efficient system of recognition, cost of recognition errors, decreases in efficiency within groups consisting essentially of related individuals, and active conflicts of interest between care provider(s) and receiver(s), may all work in concert to select against nepotism.

Box 2. Factors favouring/disfavouring nepotism

The level of recognition efficiency required for nepotism to be favoured is set by four main factors (F1–F4). For example, nepotism is less likely to evolve if discrimination is a costly process (F3) and if the differences in relatedness between altruists and classes of individuals potentially receiving help are small (F4). By contrast, nepotism will be favoured even when recognition efficiency is relatively low provided that the following four conditions are met: (1) important benefits for recipients of nepotistic acts (F1); (2) low costs for individuals discriminated against (F2); (3) low cost of discrimination between kin classes for the altruist (F3); and (4) large differences in relatedness between altruists and potential recipients of help (F4).

The actual efficiency of a recognition system depends on the nature of recognition labels available (F5) and whether or not active scrambling of these labels by group members occurs (F6). Of course, nepotism cannot evolve if individuals lack the ability to discriminate between kin classes. However, such a situation is probably unlikely in many animal species – mammals and insects frequently have good genetically specified odour cues. For example, two recent studies^{48,49} show that ant workers are able to determine whether their queen is singly or multiply mated, which requires workers to determine the diversity of genetically determined odour cues within their colony^{30,46,48}.



An interesting avenue for investigating the selective forces that prevent nepotism in social groups would be to study whether discrimination between kin classes occurs when the cost of rejection error is small or when there is no benefit for group members to scramble recognition cues. For instance, one could test whether queens avoid mating with brothers in ant colonies where mating occurs within the nest. The harmful effects of inbreeding have been documented in a variety of organisms and they are likely to be particularly important in the numerous species of Hymenoptera, where matings between kin result in the production of non-fertile diploid males⁷. Consistent with the idea that inbreeding might have detrimental effects, a recent study suggested that sexuals of the Argentine ant (*Linepithema humile*) prefer to mate with unrelated individuals³⁸.

Another topic that would be worth investigating is to what extent some group or family members actively scramble recognition cues. This could be investigated, for instance, by observing whether a female mammal that experienced extra-pair copulation does transfer more odours between offspring than a female that has not mated with another male. Similarly, when ant queens cooperate to initiate a new colony, the queens who produce fewer offspring should attempt to make the odour of immature individuals uniform³⁷. This is because the queen with the lowest fecundity should avoid worker detection of its lower participation in brood production, because workers may favour the queen with the highest fecundity as an effective rule of thumb for identifying their mother queen.

Finally, one cannot consider within-family conflicts without being struck by the close analogies with intragenomic conflicts. The potential benefits for individuals to scramble recognition cues in order to increase their inclusive fitness are much the same as the benefits received by organisms that evolve mechanisms preventing or reducing intragenomic conflicts³⁷. Thus, a driving allele that increases its probability of being passed into the gamete by destroying non-distorting alleles on the homologous chromosome will generally inflict a cost on the whole organism since fewer gametes are produced. Hence, a modifier gene that deactivates a driving allele will be favoured. Interestingly, Haig and Grafen³⁹ suggested that recombination might have been selected to decrease the possibility that closely linked genes might cooperate to bias their transmission during meiosis. In the same manner, scrambling of recognition cues may benefit all workers in a social insect colony if it increases the colony productivity. Thus, the benefits of the group as a whole may sometimes win over the selfish interest of each group member. This increased group productivity is, however, not the product of group selection – in the strict sense – but rather reflects the selfish interest of some group members in preventing other group members from behaving selfishly.

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