

# Kin recognition and the evolution of altruism

Aneil F. Agrawal

*Department of Biology and Center for the Integrative Study of Animal Behavior, Indiana University, 1001 East 3rd Street, Bloomington, IN 47405-3700, USA (aagraval@bio.indiana.edu)*

In 1964, Hamilton formalized the idea of kin selection to explain the evolution of altruistic behaviours. Since then, numerous examples from a diverse array of taxa have shown that seemingly altruistic actions towards close relatives are a common phenomenon. Although many species use kin recognition to direct altruistic behaviours preferentially towards relatives, this important aspect of social biology is less well understood theoretically. I extend Hamilton's classic work by defining the conditions for the evolution of kin-directed altruism when recognizers are permitted to make acceptance (type I) and rejection (type II) errors in the identification of social partners with respect to kinship. The effect of errors in recognition on the evolution of kin-directed altruism depends on whether the population initially consists of unconditional altruists or non-altruists (i.e. alternative forms of non-recognizers). Factors affecting the level of these error rates themselves, their evolution and their long-term stability are discussed.

**Keywords:** altruism; kin recognition; Hamilton's rule; recognition errors

## 1. INTRODUCTION

Although various exceptions to Hamilton's (1964*a,b*) rule have been noted when the simplifying assumptions of the theory are violated (e.g. Charlesworth 1978; Uyenoyama & Feldman 1982; Karlin & Matessi 1983), it remains a cornerstone of behavioural biology and social evolution (Grafen 1991; Queller 1992*a,b*; Frank 1998). Consistent with the predictions of Hamilton's rule, altruistic behaviours tend to be directed towards close relatives. In some systems, individuals predominantly interact with their kin as a by-product of spatial structure, but in many other systems individuals interact with both kin and non-kin, and preferentially direct altruistic behaviours towards the former (Fletcher & Michener 1987; Hepper 1991), using environmental and/or genetic cues to identify kin (reviewed in Sherman *et al.* 1997). Despite some earlier skepticism (Grafen 1990), the existence of kin recognition has now been demonstrated in a wide variety of taxa including mammals (e.g. Manning *et al.* 1992; Mateo & Johnston 2000), birds (e.g. Komdeur & Hatchwell (1999), and references therein), amphibians (e.g. Masters & Forester 1995; Pfennig 1999), fishes (e.g. Olsen *et al.* 1998), ascidians (Grosberg & Quinn 1986), spiders (e.g. Evans 1998, 1999), Hymenoptera (e.g. Moritz & Hillesheim 1990; Gamboa *et al.* 1996) and other insects (e.g. Joseph *et al.* 1999; Loeb *et al.* 2000). Although Hamilton discussed the possible importance of kin recognition in his classic work on the evolution of altruism (Hamilton 1964*a,b*), at the time he did not believe kin recognition to be as widespread as the empirical evidence now suggests (Hamilton 1987).

It is clear from kin-selection theory that altruism should evolve more readily in those animals that can accurately identify kin and direct their altruistic acts exclusively towards them. However, most recognition systems have some degree of error, and kin recognition is no exception (Keller 1997; Sherman *et al.* 1997). In kin recognition, two different types of error can occur; these errors are analogous to type I and type II errors in statistics (Reeve 1989). In statistics, a type I error occurs when the null hypothesis is wrongly rejected, whereas a type II error occurs when

the null hypothesis is wrongly accepted. In kin recognition, an acceptance error (type I error) occurs when an individual identifies a social partner as kin when it is non-kin, whereas a rejection error (type II error) occurs when an individual identifies a social partner as non-kin when it is kin. With acceptance errors, altruism is bestowed on non-relatives, whereas with rejection errors altruism is withheld from relatives.

As with type I and type II errors in statistics, there is some inherent degree of trade-off in minimizing both types of errors in kin recognition. When the function constraining the relationship between acceptance-error and rejection-error rates was specified, Reeve (1989) was able to solve for the optimal balance between type I and type II errors under a variety of different social conditions. In contrast, the purpose of the model presented here is to quantify how imperfect kin recognition changes the conditions for the evolution of an altruistic behaviour. I do not assume that the error rates are at their evolutionary optima or that they are evolving to be so; rather, I treat these error rates as constants. I extend Hamilton's (1964*a,b*) work by outlining when a population of unconditionally non-altruistic alleles can be invaded by an (imperfect) kin-recognizing altruistic allele. In particular, I show how the two types of error rates modify Hamilton's rule. I then model an alternative situation by outlining when a population of unconditionally altruistic alleles can be invaded by an (imperfect) kin-recognizing altruistic allele. I show that the relative importance of acceptance errors versus rejection errors changes in these different situations.

## 2. EVOLUTION OF KIN-DIRECTED ALTRUISM AMONG NON-ALTRUISTS

I use a haploid model because this analysis provides the same result as would a game-theoretical approach. Consider a haploid organism with a kin-recognition locus having two alternative alleles. Individuals with the  $k_{UNA}$  allele do not discriminate between individuals and never act altruistically with respect to the behaviour of interest

(i.e. they are unconditionally non-altruistic, UNA). Individuals with the  $K$  allele perform kin-directed altruistic behaviours (i.e. they act altruistically but only towards individuals identified as kin). The altruistic action provides a fitness benefit,  $B$ , to the recipient but there is a fitness cost,  $C$ , incurred by the donor. Acceptance (type I) errors and rejection (type II) errors occur with probabilities  $\alpha$  and  $\beta$ , respectively. I assume that a constant fraction,  $f$ , of social interactions occur between kin. The conditional probability that the kin of a  $K$  individual will also have genotype  $K$  is  $p_{K|K}$ . The conditional probability that the kin of a  $k_{UNA}$  individual will have genotype  $K$  is  $p_{K|k_{UNA}}$ . The global frequency of  $K$  individuals is  $p$ .

Using these parameters, the fitnesses of the genotypes are given by

$$W(k_{UNA}) = 1 + f(1 - \beta)(p_{K|k_{UNA}}B) + (1 - f)\alpha p B \quad (1)$$

and

$$W(K) = 1 + f(1 - \beta)(p_{K|K}B - C) + (1 - f)\alpha(pB - C). \quad (2)$$

The second term in each equation is a result of interactions that occur with kin while the third term is a result of interactions with non-kin. For altruism to be favoured,  $K$  individuals should derive higher fitness from interacting with their kin than  $k_{UNA}$  individuals will derive from interacting with their kin (i.e. the second term in equation (2) should be greater than the second term in equation (1)). However,  $K$  individuals will derive lower fitness from interacting with non-kin than will  $k_{UNA}$  individuals (i.e. the third term in equation (2) will be less than the third term in equation (1)). Kin-directed altruism evolves through natural selection when the fitness of  $K$  individuals is greater than the fitness of  $k_{UNA}$  individuals, i.e.  $W(K) > W(k_{UNA})$ . This condition is met when

$$\frac{f(1 - \beta)}{\alpha(1 - f) + f(1 - \beta)} r > C/B, \quad (3)$$

where  $r$  is the probability of identity by descent. The probability that the kin of a  $K$  individual will also have the  $K$  allele is equal to the probability of identity by descent plus the probability of identity by chance (not descent), i.e.  $p_{K|K} = r + (1 - r)p$ . The probability that the kin of a  $k_{UNA}$  individual will have the  $K$  allele is equal to the probability of non-identity by chance, i.e.  $p_{K|k_{UNA}} = (1 - r)p$ . The  $r$  in equation (3) arises because  $K$  and  $k_{UNA}$  individuals have different probabilities of having altruistic kin due to relatedness, i.e.  $p_{K|K} - p_{K|k_{UNA}} = r$ . Thus,  $p_{K|K} - p_{K|k_{UNA}}$  is equivalent to classic measures of relatedness (e.g. it is 0.5 between full-sibs or between parents and their offspring, it is 0.25 between half-sibs, etc.).

Figure 1 shows the maximum cost-benefit ratio for altruistic behaviour that will allow the spread of the  $K$  allele. If an individual recognizes everyone as kin and therefore always acts altruistically, then  $\alpha = 1$  and  $\beta = 0$ . Thus, the corner of the graph where  $\alpha = 1$  and  $\beta = 0$  gives the conditions for the spread of an unconditionally altruistic allele. Note that other combinations of  $\alpha$  and  $\beta$  can either expand or reduce the conditions under which the  $K$  allele will spread. Low values of  $\alpha$  and  $\beta$  (i.e. more-accurate kin recognition) allow kin recognition to evolve more easily. Conversely, if kin recognition is highly

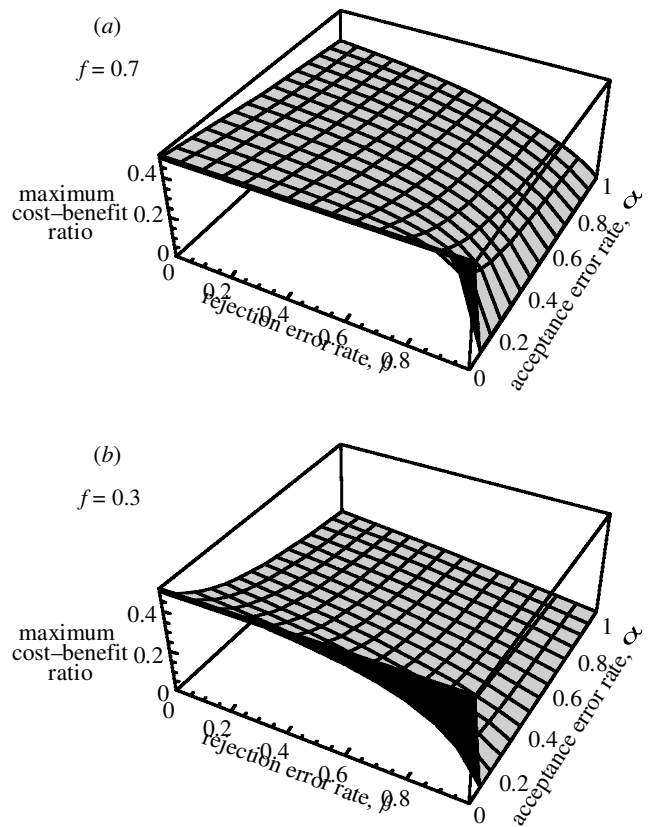


Figure 1. The maximum cost-benefit ratio permitting the evolution of kin-directed altruism in a population of unconditionally non-altruistic individuals. The maximum cost depends on the accuracy of kin recognition, measured by the rates of acceptance errors,  $\alpha$ , and rejection errors,  $\beta$ . The greater the space under the surface, the easier it is for kin recognition to evolve. This plot assumes that the kin are full-sibs so that  $r = 0.5$ ; (a) 70% of social interactions occur between kin,  $f = 0.7$ ; and (b) 30% of social interactions occur between kin,  $f = 0.3$ .

inaccurate (high values of  $\alpha$  and  $\beta$ ) then an unconditionally altruistic behaviour may be favoured over a behaviour based on kin recognition.

The extent to which a particular combination of  $\alpha$  and  $\beta$  expands or contracts the conditions for the evolution of altruism using a kin-directed strategy relative to the unconditional strategy also depends on the fraction of social interactions that occur with kin,  $f$  (equation (3); figure 1a,b). When a greater fraction of interactions occur between non-kin (i.e. lower values of  $f$ ), the cost of unconditional altruism increases and kin-directed altruism evolves more easily than unconditional altruism over a wider range of  $\alpha$  and  $\beta$  than when  $f$  is high. However, it becomes more difficult for any form of altruism to invade a population of non-altruists when the fraction of interactions that occur between kin is reduced, unless there are no acceptance errors (see below).

If kin-recognizers always identify kin correctly ( $\beta = 0$ ) but always incorrectly identify non-kin as kin ( $\alpha = 1$ ), then  $K$  individuals are actually unconditionally altruistic, as in the case considered by Hamilton. Under these conditions, the equation (3) becomes

$$fr > C/B. \quad (4)$$

Equation (4) is equivalent to Hamilton's rule,  $\bar{r} > C/B$ , where the average relatedness of individuals receiving acts of altruism is  $\bar{r} = fr$ . The average relatedness is equal to  $fr$  because a fraction  $f$  of social partners have a relatedness of  $r$ , while the remaining fraction  $(1-f)$  are completely unrelated.

If both acceptance errors and rejection errors occur (as in equation (3)),  $K$  individuals encounter non-relatives with frequency  $1-f$  and act altruistically towards them with probability  $\alpha$ , and they encounter relatives with frequency  $f$  and act altruistically towards them with probability  $1-\beta$ . In total,  $K$  individuals act altruistically with frequency  $\alpha(1-f) + f(1-\beta)$ . The term  $\{f(1-\beta)\}/\{\alpha(1-f) + f(1-\beta)\}$  therefore represents the fraction of altruistic acts that  $K$  individuals direct towards their kin. When both types of errors occur, the product  $\{f(1-\beta)\}/\{\alpha(1-f) + f(1-\beta)\}r$  found in equation (3) can be viewed from the perspective of Hamilton's rule as the average relatedness of the recipients of altruistic acts,  $\bar{r}$ .

When there are no acceptance errors (i.e.  $\alpha = 0$ ),  $K$  individuals never act altruistically towards non-relatives; their altruism is exclusively directed towards kin (i.e. 100% of a  $K$  individual's altruistic acts are directed towards their kin). In this case, the rate of rejection errors,  $\beta$ , and the proportion of interactions that occur between kin,  $f$ , no longer affect the conditions for the evolution of altruism (figure 1) and equation (3) reduces to

$$r > C/B. \quad (5)$$

The frequency with which  $K$  individuals encounter kin and act altruistically towards them,  $f(1-\beta)$ , affects only how often kin receive altruism and not the average relatedness of the recipients of altruism. Consequently, the magnitude of the difference in fitness between  $K$  and  $k_{\text{UNA}}$  individuals depends on  $f$  and  $\beta$ , but the sign of the difference (i.e. the direction of evolution) does not. The case of no acceptance errors (i.e.  $\alpha = 0$ ) allows altruism to evolve more easily than in any other case and sets an upper bound on the cost-benefit ratio of altruistic behaviours (figure 1).

Acceptance errors (and  $f$ ) affect the conditions for the evolution of altruism even when there are no rejection errors:

$$\frac{f}{\alpha(1-f) + f} r > C/B. \quad (6)$$

The  $\alpha$  term in the denominator indicates that acceptance errors always reduce the average relatedness of the recipients of altruism, making it more difficult for altruism to evolve.

### 3. EVOLUTION OF KIN-DIRECTED ALTRUISM AMONG ALTRUISTS

When the cost of an altruistic behaviour is less than the benefit weighted by the average relatedness of social partners, Hamilton's rule is satisfied (equation (4)) and an unconditionally altruistic gene can spread to fixation. We can then ask under what conditions a kin-recognition allele,  $K$ , can invade a population of unconditionally altruistic alleles,  $k_{\text{UA}}$ . We do this by comparing the fitness

of the  $K$  and  $k_{\text{UA}}$  alleles when only these two alleles exist in the population. The fitnesses of the alleles are given by

$$W(k_{\text{UA}}) = 1 + f(B(1 - \beta p_{K|k_{\text{UA}}}) - C) + (1-f)(B(1 - (1-\alpha)p) - C) \quad (7)$$

and

$$W(K) = 1 + f(B(1 - \beta p_{K|K}) - C(1-\beta)) + (1-f)(B(1 - (1-\alpha)p)C\alpha). \quad (8)$$

Note that the fitness of the  $K$  allele depends on whether it is competing against the  $k_{\text{UNA}}$  or the  $k_{\text{UA}}$  allele (i.e. equation (2) and equation (8) are not the same). Because  $K$  individuals do not always identify their kin as such (rejection errors), they should derive lower fitness from interacting with their kin than  $k_{\text{UA}}$  individuals will derive from interacting with their kin (i.e. the second term in equation (8) should be less than the second term in equation (7)). However,  $K$  individuals will derive higher fitness from interacting with non-kin than will  $k_{\text{UA}}$  individuals because  $k_{\text{UA}}$  individuals always act altruistically, even to non-kin (i.e. the third term in equation (8) will be greater than the third term in equation (7)). Kin-directed altruism will evolve when  $W(K) > W(k_{\text{UA}})$ . This condition is met when

$$\frac{f\beta}{1 - (\alpha(1-f) + f(1-\beta))} r < C/B. \quad (9)$$

Note the reversal in the direction of the inequality in equation (9) relative to that in equation (3). This reversal is not surprising: higher costs of altruism make it easier for an alternative strategy to invade a population of unconditional altruists. If the cost of altruism is too high, Hamilton's rule (equation (4)) will be violated and unconditional altruists will be quickly supplanted by unconditional non-altruists. In that case, we would return to the analysis in §2 for the evolution of  $K$  in a population of unconditional non-altruists. For the present case, we are most interested in intermediate levels of costs, specifically (combining equations (4) and (9)).

$$\frac{f\beta}{1 - (\alpha(1-f) + f(1-\beta))} r < C/B < fr. \quad (10)$$

This inequality identifies the conditions under which unconditional altruism is favoured over unconditional non-altruism but where a kin-directed altruism is superior to both.

Figure 2 shows the minimum cost-benefit ratio for altruistic behaviour that will allow the spread of the  $K$  allele. If  $\alpha = 0$  and  $\beta = 1$  then an individual recognizes everyone as non-kin and therefore never acts altruistically. Thus, the corner of the graph where  $\alpha = 0$  and  $\beta = 1$  gives the conditions for the spread of an unconditionally non-altruistic allele; this corner therefore gives the maximum cost-benefit ratio specified by equation (10). Combinations of  $\alpha$  and  $\beta$  that require higher minimum cost-benefit ratios than the value at this corner represent cases where equation (10) is violated (i.e. cases in which unconditional non-altruism would supplant unconditional altruism). Combinations of  $\alpha$  and  $\beta$  that require a lower minimum cost-benefit ratio than  $\alpha = 0$  and  $\beta = 1$  are regions where an unconditionally non-altruistic allele

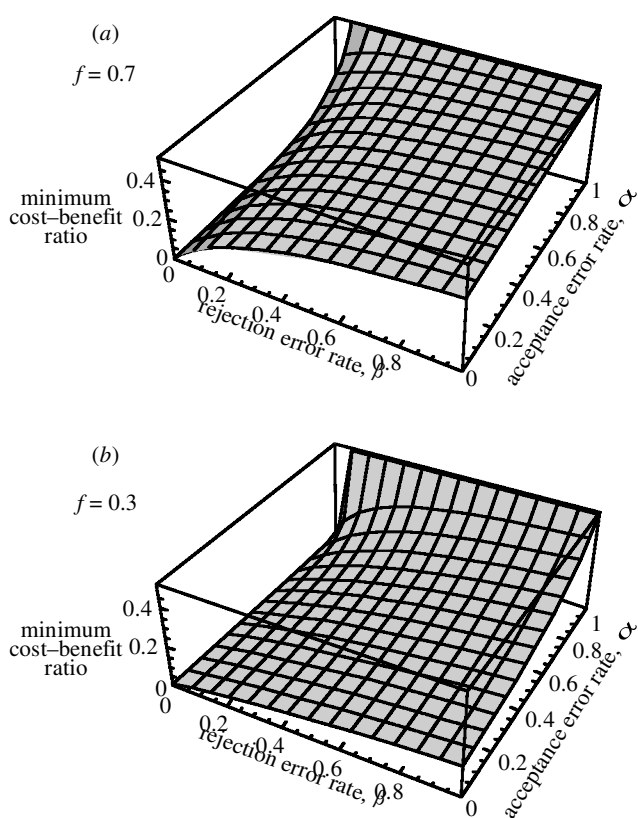


Figure 2. The minimum cost-benefit ratio permitting the evolution of kin-directed altruism in a population of unconditionally altruistic individuals. The minimum cost depends on the accuracy of kin recognition, measured by the rates of acceptance errors,  $\alpha$ , and rejection errors,  $\beta$ . The greater the space above the surface, the easier it is for kin recognition to evolve. This plot assumes that the kin are full-sibs so that  $r = 0.5$ ; (a) 70% of social interactions occur between kin,  $f = 0.7$ ; and (b) 30% of social interactions occur between kin,  $f = 0.3$ .

would be unable to invade a population of unconditionally altruistic alleles but where a  $K$  allele could do so.

The term  $f\beta/\{1 - (\alpha(1-f) + f(1-\beta))\}$  in equation (10) represents the fraction of non-altruistic acts that  $K$  individuals direct towards kin. When there are no rejection errors (i.e.  $\beta = 0$ ),  $K$  individuals never act non-altruistically towards kin and equation (10) no longer depends on the acceptance-error rate:

$$0 < C/B < fr. \quad (11)$$

When they make no rejection errors,  $K$  individuals receive the same benefit from interacting with kin as  $k_{UA}$  individuals receive from interacting with their kin. Unlike  $k_{UA}$  individuals,  $K$  individuals do not always pay the cost of altruism when interacting with non-kin. This case of no rejection errors allows altruism based on kin recognition to evolve in a population of unconditional altruists more easily than any other condition and sets a lower bound (i.e. zero) on the minimum cost-benefit ratio for altruistic behaviour.

The existence of rejection errors affects the evolution of kin-directed altruism even in the absence of acceptance errors:

$$\frac{f\beta}{1 - f(1 - \beta)} r < C/B < fr. \quad (12)$$

Rejection errors prevent  $K$  individuals from acting altruistically towards their relatives and thus reduce the benefit received through kin interactions below the level received by  $k_{UA}$  individuals.

#### 4. DISCUSSION

Almost 40 years ago Hamilton (1964*a,b*) explained how altruistic behaviours could evolve if the recipients of such actions were relatives. Since then, a growing body of empirical evidence has shown that many animals identify and respond differentially to relatives. The accuracy of kin identification has been modelled for a variety of possible kin-recognition systems (e.g. Crozier & Dix 1979; Getz 1981; Lacy & Sherman 1983). The evolutionarily optimal balance between type I and type II errors has also been calculated for various ecological scenarios (Reeve 1989). However, the direct connection between kin recognition and the evolution of altruism has not previously been modelled. Here, I have outlined the conditions for the evolution of kin-directed altruism in populations of unconditional altruists and unconditional non-altruists. The extent to which kin recognition relaxes the conditions for the evolution of altruism depends on the probabilities that kin and non-kin are identified correctly as well as the proportion of interactions that occur between kin. From the perspective of Hamilton's rule, these factors can be viewed as determining the average relatedness of the recipients of altruism.

Not surprisingly, the range of conditions under which kin-directed altruism evolves expands with increasing accuracy of kin recognition (i.e. decreasing error rates). Ironically, if kin recognition is too inaccurate, kin-recognizing altruists may be unable to invade a population of unconditional non-altruists even in cases where unconditional altruists would be able to do so. When the error rates are such that the  $K$  individuals recognize everyone as kin and, consequently, always act altruistically, this model recovers Hamilton's rule (equation (4)). When the error rates are not constrained in this way, their effects on the conditions for the spread of the  $K$  allele depend on whether the  $K$  allele is evolving in a population of unconditional non-altruists (figure 1) or unconditional altruists (figure 2). When evolving in a population of unconditional non-altruists, the inequality depends on the fraction of altruistic acts that  $K$  individuals direct towards their kin. In contrast, when evolving in a population of unconditional altruists, the inequality depends on the fraction of non-altruistic acts that  $K$  individuals direct towards kin. In the first case acceptance errors,  $\alpha$ , play a larger role while in the second case rejection errors,  $\beta$ , are more important.

Increasing the fraction of interactions that occur between kin,  $f$ , expands the conditions under which (either unconditional or kin-directed) altruists can invade a population of unconditional non-altruists. This effect occurs because with increasing  $f$  a greater fraction of the recipients of altruism are kin. However, increasing  $f$  can reduce the parameter space in which kin-directed altruism is favoured over unconditional altruism. At high

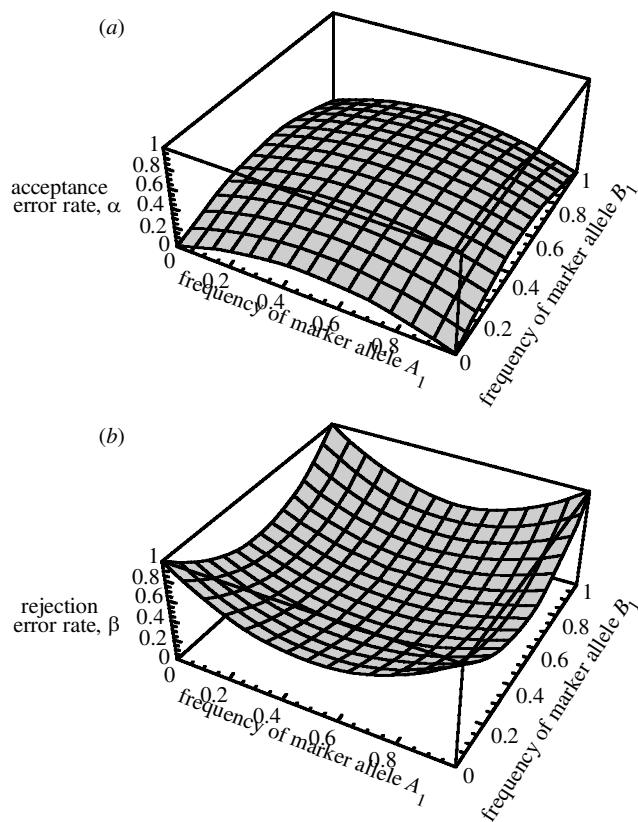


Figure 3. The accuracy of kin recognition as a function of the frequency of marker alleles: (a) the acceptance-error rate,  $\alpha$ , and (b) the rejection-error rate,  $\beta$ .

values of  $f$ , a  $K$  individual can suffer more by wrongly denying altruism to kin than an unconditional altruist suffers by being altruistic towards non-kin.

The acceptance-error and rejection-error rates discussed in this model can be empirically estimated. The type I error rate,  $\alpha$ , can be estimated by measuring the fraction of interactions with non-kin in which a focal individual acts altruistically. Similarly, the type II error rate,  $\beta$ , can be estimated by measuring the fraction of interactions with kin in which a focal individual acts non-altruistically. In both cases, a population average estimate could be obtained by averaging estimates for a variety of individuals from different families.

#### (a) Identification of kin using genetic cues

Environmental and/or genetic cues could be used to assess the relatedness of a social partner (Sherman *et al.* 1997). Although the analysis described in §§2 and 3 applies to any type of kin recognition, I now focus on systems that rely on genetic cues. There is a growing body of evidence that, in many systems, animals have ways of assessing the genotypes of their social partners at marker loci (e.g. Manning *et al.* 1992; Masters & Forester 1995; Olsen *et al.* 1998). The term 'marker loci' is used to indicate that these loci are not directly involved with the tendency of an individual to act altruistically; they are other loci in the genome that perhaps perform unrelated functions but that can be used to assess relatedness.

There are a number of ways in which animals could evaluate genetic cues to assess relatedness (Crozier 1987; Sherman *et al.* 1997). An individual could regard a social

partner as kin only if the social partner has a certain number of alleles at the marker loci in common with the focal individual. Golden hamsters appear to use such a self-referent matching system to identify kin (Mateo & Johnston 2000). In other systems, individuals may use kin-referent templates learned in the nest to identify kin in other contexts (Sherman *et al.* 1997).

When the number and frequency of alleles at each marker locus, as well as the rules of the recognition system, are known, it is possible to calculate parameters  $\alpha$  and  $\beta$  for a given mating system. For example, assume that there are only two di-allelic marker loci,  $A$  and  $B$ , and that an individual regards a social partner as kin only if the social partner has exactly the same marker-loci genotype as itself. Figure 3 shows the values of  $\alpha$  and  $\beta$  as functions of the allele frequencies under these conditions and assuming that females mate randomly but singly, producing families of full siblings. When marker alleles become fixed,  $\alpha$  is minimized and  $\beta$  is maximized. Under these conditions, all individuals have the same marker alleles so everyone recognizes everyone else as kin. As with type I and type II errors in statistics, there is some inherent degree of trade-off in minimizing both  $\alpha$  and  $\beta$  for kin recognition (compare figure 3a and figure 3b). This trade-off between rates of acceptance errors and rejection errors occurs whenever there is some degree of overlap in the distributions of genetic cues presented by kin and non-kin (Reeve 1989). The existence of a trade-off indicates that not all combinations of  $\alpha$  and  $\beta$  are equally likely; the exact nature of this trade-off (and therefore the constraints on  $\alpha$  and  $\beta$ ) will depend on the rules of the recognition system.

Just as increasing the sample size mitigates this trade-off in statistics, so increasing the number of loci and the number of alleles per loci mitigate this trade-off for kin recognition. The more loci that serve as markers and the higher the degree of polymorphism at each locus, the more accurately relatedness will be assessed (Crozier & Dix 1979; Getz 1981; Lacy & Sherman 1983). Because more information leads to increased identification accuracy, selection should favour modifier alleles that cause the kin-recognition system to detect and use a greater number of polymorphic marker loci in the assessment of relatedness. An upper limit is set by the number of cues presented by a social partner. In addition, there may be costs associated with attempting to perceive a more accurate measure of a social partner's genotype. These costs could manifest as an increase in the time required to assess these additional cues or an increase in the perception or processing power required to use these additional cues.

#### (b) The stability of genetic cues

The existence of altruistic behaviours based on kin recognition should tend to eliminate polymorphism at marker loci, making kin recognition continually less accurate (Crozier 1987). Positive frequency-dependent selection occurs because those individuals with common marker genotypes will commonly be mistaken for kin and thus become the recipients of altruistic acts. If we consider the kin-recognition system based on two di-allelic loci described in §4(a) and assume multi-locus Hardy-Weinberg equilibrium, the fitness difference between the two alleles,  $A_1$  and  $A_2$ , at the first marker locus is

$$W(A_1) - W(A_2) = \frac{1 - 3a + 2a^2}{1 - a} (C - B)(1 - 2b(1 - b) - 0.5f(1 - 3b(1 - b))), \quad (13)$$

where  $a$  and  $b$  are the frequencies of the  $A_1$  and  $B_1$  alleles, respectively. When the two  $A$  alleles are equally common (i.e.  $a = 0.5$ ) then  $W(A_1) - W(A_2) = 0$  and these marker alleles are selectively neutral. However, this situation is unstable. Assuming, as should be true, that  $C - B < 0$ , when the  $A_1$  allele is rare (i.e.  $a < 0.5$ ) then  $W(A_1) - W(A_2) < 0$ , leading to the elimination of this allele. When  $A_1$  is common (i.e.  $a > 0.5$ ) then  $W(A_1) - W(A_2) > 0$ , leading to the fixation of the  $A_1$  allele. An analogous situation holds for the second marker locus. Although the mathematical details of equation (13) depend on the rules of kin recognition, the number of alleles and loci involved, as well as the mating system, the principle remains the same: altruism based on kin recognition generates positive frequency-dependent selection on marker loci. This process will tend to eradicate polymorphism, making genetically based identification of kin impossible. For kin-directed altruism to persist over evolutionary time, recognition systems must depend on marker loci that are maintained at high levels of polymorphism for other reasons, such as disassortative mating and/or coevolving parasites (Crozier 1987).

## 5. CONCLUSIONS

Imperfect kin-recognition systems modify the relatedness coefficient in Hamilton's rule. The relative importance of acceptance errors versus rejection errors depends on (i) whether the kin-recognizing altruist is competing against unconditional altruists or unconditional non-altruists, and (ii) the fraction of interactions that occur between kin.

E. D. Brodie III and M. J. Wade improved the presentation of these ideas. Two anonymous reviewers provided helpful comments. I thank a reviewer for pointing out the relationship between the conditional genotype probabilities and relatedness. This work was supported by the Natural Sciences and Engineering Research Council of Canada.

## REFERENCES

- Charlesworth, B. 1978 Some models of the evolution of altruistic behaviour between siblings. *J. Theor. Biol.* **14**, 268–280.
- Crozier, R. H. 1987 Genetic aspects of kin recognition: concepts, models, and synthesis. In *Kin recognition in animals* (ed. D. J. C. Fletcher & C. D. Michener), pp. 55–73. New York: Wiley.
- Crozier, R. H. & Dix, M. W. 1979 Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. *Behav. Ecol. Sociobiol.* **4**, 217–224.
- Evans, T. A. 1998 Offspring recognition by mother crab spiders with extreme maternal care. *Proc. R. Soc. Lond. B* **265**, 129–134.
- Evans, T. A. 1999 Kin recognition in a social spider. *Proc. R. Soc. Lond. B* **266**, 287–292.
- Fletcher, D. J. C. & Michener, C. D. 1987 *Kin recognition in animals*. New York: Wiley.
- Frank, S. A. 1998 *Foundations of social evolution*. Princeton University Press.
- Gamboa, G. J., Grudzien, T. A., Espelie, K. E. & Bura, E. A. 1996 Kin recognition pheromones in social wasps: combining chemical and behavioural evidence. *Anim. Behav.* **51**, 625–629.
- Getz, W. 1981 Genetically based kin recognition systems. *J. Theor. Biol.* **92**, 209–226.
- Grafen, A. 1990 Do animals really recognize kin? *Anim. Behav.* **39**, 42–54.
- Grafen, A. 1991 Modelling in behavioural ecology. In *Behavioural ecology: an evolutionary approach*, 3rd edn (ed. J. R. Krebs & N. B. Davies), pp. 5–31. Oxford, UK: Blackwell Scientific Publications.
- Grosberg, R. K. & Quinn, J. F. 1986 The genetic control and consequences of kin recognition by the larvae of a colonial marine invertebrate. *Nature* **322**, 457–459.
- Hamilton, W. D. 1964a The genetical evolution of social behaviour. Part I. *J. Theor. Biol.* **7**, 1–16.
- Hamilton, W. D. 1964b The genetical evolution of social behaviour. Part II. *J. Theor. Biol.* **7**, 17–52.
- Hamilton, W. D. 1987 Discrimination nepotism: expectable, common, overlooked. In *Kin recognition in animals* (ed. D. J. C. Fletcher & C. D. Michener), pp. 417–437. New York: Wiley.
- Hepper, P. G. 1991 *Kin recognition*. Cambridge University Press.
- Joseph, S. B., Snyder, W. E. & Moore, A. J. 1999 Cannibalizing *Harmonia axyridis* (Coleoptera: Coccinellidae) larvae use endogenous cues to avoid eating relatives. *J. Evol. Biol.* **12**, 792–797.
- Karlin, S. & Matessi, C. 1983 Kin selection and altruism. *Proc. R. Soc. Lond. B* **219**, 327–353.
- Keller, L. 1997 Indiscriminate altruism: unduly nice parents and siblings. *Trends Ecol. Evol.* **12**, 99–103.
- Komdeur, J. & Hatchwell, B. J. 1999 Kin recognition: function and mechanism in avian societies. *Trends Ecol. Evol.* **14**, 237–241.
- Lacy, R. C. & Sherman, P. W. 1983 Kin recognition by phenotype matching. *Am. Nat.* **121**, 489–512.
- Loeb, M. L. G., Diener, L. M. & Pfennig, D. W. 2000 Egg-dumping lace bugs preferentially oviposit with kin. *Anim. Behav.* **59**, 379–383.
- Manning, C. J., Wakeland, E. K. & Potts, W. K. 1992 Communal nesting patterns in mice implicate MHC genes in kin recognition. *Nature* **360**, 581–583.
- Masters, B. S. & Forester, D. C. 1995 Kin recognition in a brooding salamander. *Proc. R. Soc. Lond. B* **261**, 43–48.
- Mateo, J. A. & Johnston, R. E. 2000 Kin recognition and the 'armpit effect': evidence of self-referent phenotype matching. *Proc. R. Soc. Lond. B* **267**, 695–700.
- Moritz, R. F. A. & Hillesheim, E. 1990 Trophallaxis and genetic variance of kin recognition in honey bees, *Apis mellifera* L. *Anim. Behav.* **40**, 641–647.
- Olsen, K. H., Grahn, M., Lohm, J. & Langefors, A. 1998 MHC and kin discrimination in juvenile Arctic charr, *Salvelinus alpinus* (L.). *Anim. Behav.* **56**, 319–327.
- Pfennig, D. W. 1999 Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate. *Proc. R. Soc. Lond. B* **266**, 57–61.
- Queller, D. C. 1992a A general model for kin selection. *Evolution* **46**, 376–380.
- Queller, D. C. 1992b Quantitative genetics, inclusive fitness and group selection. *Am. Nat.* **139**, 540–558.
- Reeve, H. K. 1989 The evolution of conspecific acceptance thresholds. *Am. Nat.* **133**, 407–435.
- Roff, D. A. 1997 *Evolutionary quantitative genetics*. New York: Chapman & Hall.
- Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997 Recognition systems. In *Behavioural ecology: an evolutionary approach*, 4th edn (ed. J. R. Krebs & N. B. Davies), pp. 69–96. Oxford: Blackwell Scientific Publications.
- Uyenoyama, M. K. & Feldman, M. 1982 Population genetic theory of kin selection. II. The multiplicative model. *Am. Nat.* **120**, 614–627.