# Evolution of discrimination in populations at equilibrium between selfishness and altruism

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## HIGHLIGHTS

► Heritable variation in altruism allows discriminating altruists to evolve.
► Here we chart their evolution using diploid population genetic models.
► Help is assumed subject to diminishing returns.
► Selfishness and discriminating and non-discriminating altruism can evolve together.
► These predictions merit investigation by primatologists and psychologists.

## ABSTRACT

Where there is genetically based variation in selfishness and altruism, as in man, altruists with an innate ability to recognise and thereby only help their altruistic relatives may evolve. Here we use diploid population genetic models to chart the evolution of genetically-based discrimination in populations initially in stable equilibrium between altruism and selfishness. The initial stable equilibria occur because help is assumed subject to diminishing returns. Similar results were obtained whether we used a model with two independently inherited loci, one controlling altruism the other discrimination, or a one locus model with three alleles. The latter is the opposite extreme to the first model, and can be thought of as involving complete linkage between two loci on the same chromosome. The introduction of discrimination reduced the benefits obtained by selfish individuals, more so as the number of discriminators increased, and selfishness was eventually eliminated in some cases. In others selfishness persisted and the evolutionary outcome was a stable equilibrium involving selfish individuals and both discriminating and non-discriminating altruists. Heritable variation in selfishness, altruism and discrimination is predicted to be particularly evident among full sibs. The suggested coexistence of these three genetic dispositions could explain widespread interest within human social groups as to who will and who will not help others. These predictions merit experimental and observational investigation by primatologists, anthropologists and psychologists.

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## 1. Introduction

Variation among individuals in selfishness/altruism is a commonplace of everyday life and has recently been shown, by comparing the altruistic dispositions of monozygotic and dizygotic twins, to have in part a genetic basis in man (Cesarini et al., 2009; Gregory et al., 2009; Hur and Rushton, 2007; Knafo and Plomin, 2006; Rushton, 2004; Rushton et al., 1986; Scourfield et al., 2004) but cf. Krueger et al. (2002). However the evolutionary basis of genetic variation in selfishness/altruism is unclear. Variation is not predicted by Hamilton's kin selection theory with constant costs and benefits since if altruism and selfishness are genetically coded then either one allele or the other spreads to fixation as directed by Hamilton's rule (Hamilton, 1964). Clearly when the population is genetically homogenous with regard to altruism/selfishness, there is no advantage in discrimination.

Recently we provided a possible explanation for the heritability of altruistism/selfishness using a diploid population genetics model and Sewall Wright's definition of the coefficient of relatedness (Sibly and Curnow, 2011). Following Hamilton (1964) we supposed that there exist altruistic alleles that cause carriers to help relatives provided the individual fitness benefit obtained by the relative sufficiently exceeds the cost to the helper.

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In Hamilton's analysis the benefit provided by each individual is the same, and the evolutionary outcome is the elimination of either the altruistic or the non-altruistic allele. In our analysis we considered the case that as more individuals help the benefits each provides may decrease. Suppose I need shelter when injured, food when starving or rescue in battle. The first individual to help may save my life. Late comers may pay similar costs in attempting to help, but the additional benefit to me is less. There are diminishing returns because there are limits to how much individuals can be helped. Several possibilities are shown in Fig. 1A. In the case of near constant returns, the benefits per helper decrease little with the number of helpers (case 1 in Fig. 1A) and cumulative benefits increase almost linearly with the number who help (Fig. 1B). In cases 2–4 the diminution in returns is more severe. The existence of diminishing returns changes the operation of natural selection and the outcome can now be a stable evolutionary equilibrium with some individuals selfish and others altruistic (Sibly and Curnow, 2011).

The existence of innately selfish and innately altruistic individuals in the same population provides an opening for the evolution of discriminating individuals, who withhold help from selfish individuals and only help those who help others. We assume that all individuals can always recognise their relatives, and can recognise, by their social behaviour, which of their relatives are altruistic. Understanding what happens in this situation requires an explicit diploid population genetic model because, with diminishing returns, fitness depends non-additively on the number of encountered relatives who are altruistic and this depends on the alleles they carry, which in turn is determined by the genotypes of the individuals' forebears. Whether the other individuals reciprocate/provide help or not depends on their genotypes, and the proportions of the genotypes vary between sibships depending on the genotypes of the founders of the sibship. So it is necessary to enumerate all possible sibships, and to calculate the proportions of the different possible genotypes in each of them. Describing how to do this takes up the bulk of the paper.

Discrimination is not possible unless there is variation in the character used as the basis for discrimination. In our model character variation is attributed to the effects of genes at one or two loci. The variation at the loci arises initially from mutation but we do not need to assume recurrent mutation to show that, under certain conditions, a genetic evolutionary equilibrium occurs in which altruistic, selfish and discriminating individuals

co-exist. Recurrent mutation is posited as the source of continuing genetic variation in the models of discrimination (choosiness) of McNamara et al. (2008), but it is debatable how much variation this would provide in reality. McNamara et al. (2008)'s treatment did not model genetic relatedness between individuals so did not need a kin selection approach such as that adopted here. Current treatments of kin selection are not expressed in terms of specific population genetic models but in terms of a general correlation between the occurrence of character values in related individuals. Our population genetics treatment has the advantage that it is expressed in measurable terms and shows how the proportions of the various types of allele in the population relate to Sewall Wright's coefficient of relatedness and benefits and costs expressed in terms of increments to individual fitness. This provides opportunities for testing the validity of the model. It is not clear how this can be achieved in other treatments of kin selection including the 'direct fitness' approaches developed using the methods of quantitative genetics (see, e.g., Fletcher and Doebeli, 2006; Frank, 1998; Queller, 1985, 1992a, 1992b; Taylor and Frank, 1996), and the evolutionary game theory approaches (e.g., Grafen, 1979; Hauert et al., 2006; Marshall, 2009; McNamara et al., 2008; Sigmund, 1993).

Most direct fitness treatments have been based directly or indirectly on Price's covariance equation, which requires knowledge of the genetic covariance between individuals' relative fitnesses and the characters of interest (Gardner et al., 2011; Marshall, 2011; Price, 1970), here altruism and discrimination. However these covariances cannot be calculated for the situations studied here without an explicit population genetic model. Calculating the covariances would allow application of Price's theory, but this step is not necessary to achieve our objective of calculating evolutionary trajectories.

Our approach has a superficial resemblance to Queller (1984) which, using a game theoretic analysis, provides short-cut approximate answers to some generalised frequency-dependent problems, including a model with diminishing returns, that are difficult to address using population genetics. Our model differs in that diminishing benefits apply to selfish as well as altruistic individuals, three strategies are considered rather than the two discussed by Queller (1984) and testable equilibrium conditions are derived for a specific genetic model.

Here we analyse the evolution of genetically-based discrimination in populations initially in evolutionary equilibrium between
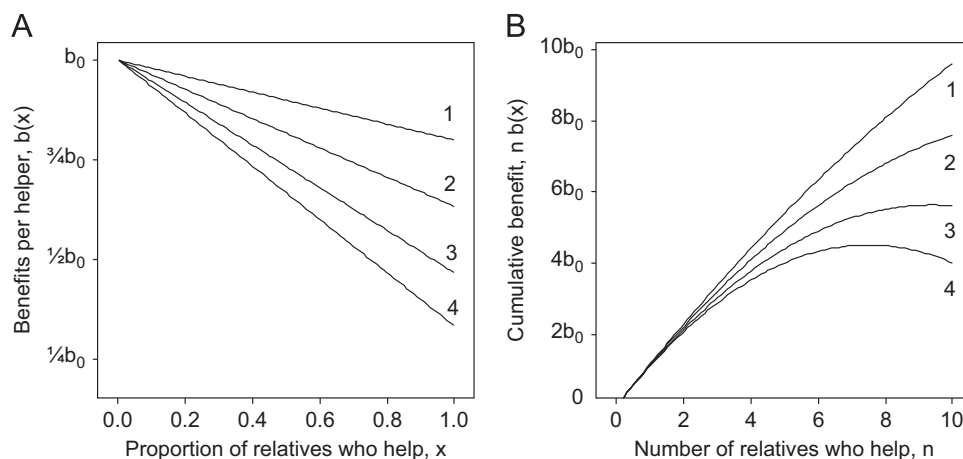


**Fig. 1.** Four cases of diminishing returns from helping. A. Benefit per helper in relation to the proportion of relatives who provide help. Benefits are in multiples of the cost of help. In case 1 the benefits per helper diminish only a little with the proportion of relatives who provide help, and the cumulative benefits increase nearly linearly with the number of helpers as shown in B. In cases 2–4 the benefits decline more sharply with the proportion of relatives who help and the diminutions in cumulative returns are more marked. In the calculations reported in Fig. 2 we took $b_0 = 3c$ for full sibs, $6c$ for half sibs and $12c$ for first cousins, so $rb_0 = 1.5c$ in each case ($r$ is the coefficient of relatedness, $= 1/2$ for full sibs, $1/4$ for half sibs, and $1/8$ for first cousins). $b_1/b_0 = 0.8$ in case 1, 0.6333 in case 2, 0.4666 in case 3 and 0.3333 in case 4.