ALTRUISM VIA KIN-SELECTION STRATEGIES THAT RELY ON ARBITRARY TAGS WITH WHICH THEY CO-EVOLVE

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Abstract

Hamilton's rule explains when natural selection will favor altruism between conspecifics, given their degree of relatedness. In practice, indicators of relatedness (such as smell) co-evolve with strategies based on these indicators, a fact not included in previous theories of kin recognition. Using a combination of simulation modeling and mathematical extension of Hamilton's rule, we demonstrate how altruism can emerge and be sustained in a co-evolutionary setting where relatedness depends on an individual's social environment, and varies from one locus to another. The results support a very general expectation of widespread, and not necessarily weak, conditional altruism in nature.

Hamilton's rule states that natural selection will favor altruism between conspecifics when $rb - c > 0$, where r is their genetic relatedness, b is the benefit to the recipient, and c is the cost to the donor (Hamilton 1964). In practice, indicators of relatedness (such as smell) co-evolve with strategies based on these indicators, a fact not included in previous theories of kin recognition (Reeve 1989; Crozier 1989; Ratnieks 1991; Agrawal 2001; Lehmann 2002). We show with an evolutionary model how contingent altruism can be sustained even when arbitrary heritable indicators of relatedness, called "tags", co-evolve with the strategies governing behavior. Discrimination based on tags is not assumed, but rather evolves endogenously in a viscous population (i.e., local reproduction and local interaction) and is selected for even when phenotypic matching is very coarse-grained. We also show how to extend Hamilton's Rule to establish the conditions under which kin recognition can support discriminating altruism even when co-evolution causes the reliability of indicators of relatedness to vary with each individual's evolving social environment. This multi-trait extension requires the calculation of different relatednesses for different traits. The simulation and the mathematical analysis show how discriminatory altruism can evolve in realistic settings where assessment of relatedness is based on weak and potentially deceptive indicators.

To explore the evolution of tag-based altruism, our model embodies three mechanisms. To allow altruism, but not direct reciprocity, fitness is determined by neighbors interacting in a one-move Prisoner's Dilemma. To allow behavior that is

conditioned on indicators of relatedness, strategies can take account of observable tags, such as odor. Tags differ from signals (Spence 1974; Grafen 1990) by being inflexible expressions of an individual's genotype rather than subject to individual control (Hochberg et al. 2003). To allow competition for scarce resources, the population is viscous, and the population size is fixed. Since the tags and strategies are not linked, the model allows for the possibility of "cheaters" who can be free riders in the group whose tag they carry. The resulting agent-based model is based on a model previously developed to study ethnocentrism in humans (Axelrod and Hammond 2003). The present model is not meant to be a literal representation of biological processes. Instead, our model is designed to illuminate the consequences of the fact that kin discrimination typically entails coevolution of three things: the strategies governing behavior, the reliability of the tags on which the behavior may be conditioned, and the population structure that determines who interacts with whom.

The model is very simple. An individual agent has three traits, each a haploid genetic locus. The first trait is a tag that can be one of four observable types, say smells. The second and third traits specify the agent's strategy. The second trait has two alleles to specify whether the agent cooperates or defects (i.e. is altruistic or selfish) when meeting an individual of its own smell. Likewise, the third trait specifies whether the agent cooperates or defects when meeting an agent of a different smell. For example, the discriminatory strategy is cooperation with agents of one's own smell and defection with others. In this model, the discriminatory strategy is only one of four possible strategies.

The simulation begins with a population of 2000 individuals (with random genotypes) each placed at random in its own site on a 50x50 lattice. The space has wrap

around borders so that each site has exactly four neighboring sites. Each period consists of two stages: interaction, and reproduction.

      1. Each agent in the population receives an initial value of 0.12 as its Potential To Reproduce (PTR). Each pair of adjacent agents interacts in a one-move Prisoner's Dilemma in which each player independently chooses whether or not to help the other. Giving help has a cost, namely a decrease in the agent's PTR by 0.01. Receiving help has a benefit, namely an increase in the agent's PTR by 0.03.

      2. Each agent is given a chance to reproduce asexually with probability equal to its PTR. An offspring receives the traits of its parent, with a mutation rate of 0.001 per trait. The expanded population of adults and infants is then culled at random to bring it back to its original size of 2000. The surviving offspring are then placed as close as possible to their parent's cell. Placement starts with "orphans" who are placed in their deceased parent's cell. Next to be placed are offspring who can find an empty cell *adjacent* to their surviving parent, and so on for increasing distances from the parent. (Distance is measured by "city-blocks").

The simulation results show that contingent altruism evolves even though there is no explicit bias for it in the model. Averaging over the final 100 periods of thirty 2000 period runs, 76.6% of the agents have the discriminatory strategy. This high rate of discriminatory altruism results in 91.6% of same tag interactions being cooperative, and 82.7% of different tag interactions being non-cooperative.

Notice that the model allows for deception by egoists who defect against everyone. In a region of discriminators of a certain smell, a lone egoist of the same smell will receive donations from its neighbors without itself donating. Analyzing the dynamics

of the simulation reveals how contingent altruism suppresses egoists. A successful agent and its offspring quickly form a more or less coherent region. Consider what happens when an agent belonging to a region of discriminatory agents with a common tag interacts with an agent belonging to a region of, for example, egoists of a different smell. In this case, the discriminatory agent will do better overall because it gets help from other agents in its own region, while the egoist gets no help from other agents in *its* own region. The result is that a region of discriminators will tend to expand at the expense of an adjacent region of egoists of a different smell. In fact, a region of discriminators will tend to expand at the expense of a region of a different smell that uses any one of the three other strategies. In this way, discriminators of one smell hold egoists of other smells in check. Since the tag (smell) locus does not go to fixation, egoism is controlled. (A Quicktime movie at umich.edu/~axe/AHG/ illustrates the spatial dynamics of the simulation.)

The success of contingent altruism is robust under a wide range of parameters. When any of the following parameters are either halved or doubled, at least 63% of strategies are discriminatory and at least 68% of the choices are cooperative: lattice width, number of alleles on the tag locus, mutation rate, or duration of the run (Table 1). **[TABLE 1 ABOUT HERE]** Changes in the size of the population relative to the lattice size also have minimal effect. For example, halving the proportion of empty space leads to an increase in the average distance between parents and their offspring, thereby weakening localism as a signal of relatedness. Even in this case, 58% of the agents use the discriminatory strategy, and 60% of the behavior is cooperative (Table 2). **[TABLE 2 ABOUT HERE]** The simulation results are also not very sensitive to the possibility

that an agent will occasionally misperceive whether or not the other agent in the interaction has the same smell. Even when agents make this mistake 10% of the time, the proportion of discriminatory strategy, level of contingent altruism, and the overall level of cooperation all remain over 75%.

Thus contingent altruism evolving from local reproduction and local interaction can support cooperation, even when the interactions are one-move Prisoner's Dilemma games. Indeed, some localism in both reproduction and interaction is necessary: if the simulation is run with either random placement of offspring or random interaction, fewer than two percent of the strategies are discriminatory, and less than one percent of the interactions are cooperative. (The small amounts of cooperation are due to mutation-selection balance.) Even with localism, cooperation requires a sufficiently high ratio of benefit to cost. When the benefit is no greater than the cost, cooperation fails and the egoist strategy is dominant; but as the benefit/cost ratio increases, egoism gives way to altruism (Fig 1). **[FIGURE 1 ABOUT HERE]**

A remarkable result of the simulation model is that discrimination based on an unreliable and potentially deceptive indicator of kinship can actually increase the total amount of cooperation in the population. As we have seen, when four alleles of the tag locus could be distinguished, 91.0% of all interactions were cooperative. In contrast, when all tags look alike, the rate of cooperation falls to 15.6%.

In this simulation, the indicator of relatedness evolves separately from the genes that control behavior, making the indicator potentially deceptive. Moreover, the indicator's reliability can vary throughout the population because reproduction and interaction are local. This variability is representative of an important class of biological reality.

Previous models of altruism have assumed fixed relatednesses (Reeve 1989; Agrawal 2001; Lehmann and Perrin, 2002), or fixed levels of altruism (Crozier 1986; Ratnieks 1991). We now show how to extend Hamilton's Rule (henceforth "HR") to cover coevolving traits and variably reliable indicators of relatedness, accounting for the evolution of contingent altruism under these very general conditions.

We begin by analyzing the social environment of the individual, defining the following variables: m is one if there is a match (same tag) between two interacting individuals and zero if there is not; A_m is one if the individual is altruistic toward a neighbor of type m and zero if not; A'_m is the average A_m of neighbors, and N_m is the number of neighbors of type m. For example, $A_1=1$ indicates altruism toward matching neighbors, and $A_0=1$ indicates altruism toward non-matching neighbors. With these definitions, the individual's PTR is

$$P = a + b(A'_1 N_1 + A'_0 N_0) - c(A_1 N_1 + A_0 N_0)$$

where a is the initial PTR before social interaction. In the simulation, $a = 0.12$, $b = 0.03$, and $c = 0.01$. With hard selection, relative fitness is $W = (1 + P)/(1 + \overline{P})$, where $\overline{P}$ is the average P over the entire population for the period in question. Following Queller (Queller 1992) we substitute this formula for W into the population genetic Price equation (Price 1970) with perfect transmission

$$\Delta E[A_m] = \text{Cov}(A_m, W)$$

and obtain an expression for the expected change in the mean of A_m before mutation

$$k\Delta E[A_m] = b(\text{Cov}(A_m, A'_1 N_1) + \text{Cov}(A_m, A'_0 N_0)) - c(\text{Cov}(A_m, A_1 N_1) + \text{Cov}(A_m, A_0 N_0))$$

(eq. 1)

where $k = 1 + \overline{P}$.

HR has been shown to apply (Grafen 1985) if r is measured in terms of genetic similarity rather than kinship, where genetic similarity at a *single* locus, for a given allele (whose frequency is p), is defined as:

$$r = \frac{\sum_j H_j(R_j - p)}{\sum_j H_j(D_j - p)}$$

where D_j and R_j are the potential donor and potential recipient's genotype at that locus, and H_j equals one if a donation was made on the j'th occasion on which a donation might be made and zero otherwise.

We now extend this analysis and add subscripts to define r_{mn}, a relatedness at a locus m in relation to donations caused by locus n, to provide a two-locus (or as we shall see later more generally a two-trait) version of HR. Each directed pair of neighbors will be considered an 'occasion' and indexed by j. H_{nj} is defined as one if an altruistic act is made through locus n on occasion j, R_{mj} as one if the recipient on occasion j has the $A_m=1$ allele, and D_{mj} as one if the potential donor on occasion j has the $A_m=1$ allele; and each variable is zero otherwise. The generalization of r is

$$r_{mn} = \frac{\sum_j H_{nj}(R_{mj} - p_m)}{\sum_j H_{nj}(D_{mj} - p_m)}$$

We now show how this formula can be used to analyze the forces of selection. Let S_{mj} equal one if a donation would be made if the donor had allele $A_m=1$ and 0 otherwise,

so that $S_{1j} = 1$ if the pair have the same tag, and $S_{0j} = 1$ if the pair have different tags.

Noting that $H_{mj} = D_{mj} S_{mj}$, we obtain the following identities:

$$\sum_j H_{nj} = \sum_j D_{nj} S_{nj} = \sum_j R_{nj} S_{nj}$$

$$\sum_j H_{nj} R_{mj} = \sum_j D_{mj} R_{nj} S_{nj}$$

$$\sum_j H_{nj} D_{mj} = \sum_j D_{mj} D_{nj} S_{nj}$$

where we have sometimes reversed the role of donor and recipient, D_j and R_j. Such a reversal merely changes the order of the summation. It does not change the corresponding S_{nj} because reversing roles does not affect whether two given individuals match on a specific locus. These identities allow us to show that

$$r_{mn} = \frac{\sum_j D_{mj} R_{nj} S_{nj} - p_m \sum_j R_{nj} S_{nj}}{\sum_j D_{mj} D_{nj} S_{nj} - p_m \sum_j D_{nj} S_{nj}} = \frac{E[A_m A_n' N_n] - E[A_m] E[A_n' N_n]}{E[A_m A_n N_n] - E[A_m] E[A_n N_n]} = \frac{\mathrm{Cov}(A_m, A_n' N_n)}{\mathrm{Cov}(A_m, A_n N_n)}$$

Geometrically, r_{mn} is the regression coefficient of A_m' on A_m, using only data from directed pairs where a donation is caused by locus n; but forcing the line to pass through the point $(E[A_m], E[A_m])$ (Grafen 1985). The same approach defines a cross-locus regression that measures linkage disequilibria

$$\beta_{mn} = \frac{\sum_j H_{nj}(D_{mj} - p_m)}{\sum_j H_{nj}(D_{nj} - p_n)} = \frac{\mathrm{Cov}(A_m, A_n N_n)}{\mathrm{Cov}(A_n, A_n N_n)}$$

This is the slope of A_m on A_n among individuals that make a donation caused by locus n, forcing the line to pass through the point $(E[A_n], E[A_m])$.

Equation (1) can now be rewritten, assuming n is the other strategy locus from m, as

$$k\Delta E[A_m] = \text{Cov}(A_m, A_m N_m)(r_{mm}b - c) + \text{Cov}(A_n, A_n N_n)\beta_{mn}(r_{mn}b - c) \quad \text{(eq. 2)}$$

and we immediately interpret terms as

$$\text{Direct selection of } A_m = \text{Cov}(A_m, A_m N_m)(r_{mm}b - c)$$
$$\text{opportunity-weighted variation at } A_m = \text{Cov}(A_m, A_m N_m)$$
$$\text{HR term for } A_m \text{ over donations controlled by locus } m = r_{mm}b - c$$
$$\text{indirect selection } via\ A_n = \text{Cov}(A_n, A_n N_n)\beta_{mn}(r_{mn}b - c)$$
$$\text{opportunity-weighted variation at } A_n = \text{Cov}(A_n, A_n N_n)$$
$$\text{linkage disequilibrium with } A_n = \beta_{mn}$$
$$\text{HR term for } A_m \text{ over donations controlled by locus } n = r_{mn}b - c$$

The generalization of Hamilton's rule in equation (2) directs a biological interpretation of the simulation results. Each term can be calculated from each period of the simulation data to provide a numerical analysis of selection over time, and the analysis is exact in expectation apart from the effects of mutation. To obtain an exact analysis, the relatednesses have been specially constructed, and they measure genetic similarity and not co-ancestry. This is the first version of Hamilton's Rule to consider two traits simultaneously. We now turn to the interpretation.

First, it turns out that indirect selection is small enough to be neglected compared to direct selection. Thus, whether selection favors altruism toward matching neighbors

($A_1 = 1$) depends on the sign of the HR term $r_{11}b - c$, and whether selection favors

altruism toward non-matching neighbors ($A_0 = 1$) depends on the sign of the HR term

$r_{00}b - c$. Inequality between the two relatednesses is necessary to achieve

$r_{11}b - c > 0 > r_{00}b - c$, the condition for selection for discrimination.

This focuses attention on the relatednesses, r_{11} and r_{00}. They can be compared to a

third measure of relatedness based on the tag locus, say r_t. The ordering of relative

relatedness is $r_{11} > r_t > r_{00}$, numerically after 2000 periods in the standard case, 0.328

(± 0.014) > 0.222 (± 0.036) > -0.047 (± 0.074), where the standard errors derive from 30

replications of the simulation. The explanation is as follows. The relatednesses are

measured over the opportunities for action, so r_{11} is measured between same-tag

neighbors while r_{00} is measured between different tag neighbors. Within the relatively

stable blocks composed of the same tag, neighbors are likely to share much recent

common ancestry. By contrast, different tag neighbors are likely to descend from

different tag parents, on either side of a tag-boundary, except in the relatively rare

instances of recent mutation at the tag locus. This difference between relatednesses

allows the evolution of discriminating altruism.

The time course of development of the relatednesses is also of interest. Unlike the

analytical relatednesses employed by Taylor and Irwin (2000), our relatednesses, like

those of Hamilton (1970), are statistical within the model, and so do not rely on an

assumption of weak selection. Their statistical nature does mean that the mechanisms

underlying them need to be studied. As the simulations begin with randomly placed

random genotypes, both relatednesses begin at zero. After 25 generations, r_{11} has climbed

to 0.626 ($\pm$0.006) while r_{00} still remains near zero: clusters of same-tagged individuals are forming so that same-tag neighbors share common ancestry, while opposite-tag neighbors do not. This value of r_{11}, if sustained, would result in $A_1=1$ going very close to fixation. However, as noted above, by 2000 generations, r_{11} has fallen to 0.328 ($\pm$0.013), around the value of c/b, stabilizing the frequency of $A_1=1$. This fall must arise from the increased size of the same-tag clusters. The parents of same-tag neighbors may now be some distance away, even if in the same cluster. Further, individuals on the inside of clusters have the highest fitness as they benefit most from altruism. Thus there is higher pressure of offspring within a cluster to fill the gaps caused by culling than on its boundary. Large clusters have relatively larger 'insides', and so their offspring will on average be placed further from parents than in small clusters, and so reduce neighbor-neighbor relatednesses. This effect of cluster-size on relatedness has a negative feedback effect and holds the population back from complete same-tag altruism.

There is an important extension not required for the simulations, but which adds to the importance of the analysis of selection presented here. Provided the expected fitness is linear in the variables A_m, we can relax the requirement that A_1 and A_0 are each determined by a single haploid locus. Instead, A can be any 'p-score' (Grafen 1985). Thus, there can be any number of alleles at the locus, specifying arbitrary numerical values for A. The population could be diploid (or more generally polyploid), provided the value of A is obtained by adding the numerical values of the alleles present. A could even be determined by adding up numerical values from the alleles present at more than one locus, provided all the loci have the same inheritance pattern. The analysis of selection retains exactly the same form, and the interpretations of the terms as regression

coefficients of relatedness, regression measures of genetic covariance, and measures of genetic variation, remain the same. Mitteldorf and Wilson (2000) study simulations that also have local competition and limited dispersal, and introduce non-inclusive fitness arguments to supplement the original form of HR. In contrast, our analysis generalizes HR, and so incorporates the effects of local competition and dispersal into the overall framework of inclusive fitness, thus preserving the one conceptual framework with the capacity to embrace all work on selection of social traits.

The algebraic method above is the first published analysis of selection for kin recognition with simultaneous variation at the indicator and altruistic loci. This method helps us understand the conditions under which kin recognition can support discriminating altruism even when the reliability of indicators of kinship depends on the individual's social environment. The simulation was specially designed to make net fitness linear in the values of the altruistic loci, so that benefits and costs of altruism in the algebraic analysis can be calculated directly from the specification of the simulation. The analytical approach can be applied in simulations with non-linear fitnesses by following Queller in obtaining 'empirical' estimates of b and c from a linearized fitness function.

The value of being able to distinguish tags can be understood in terms of inclusive fitness theory that takes into account the degree of relatedness between two agents (Hamilton 1964; Lacy and Sherman 1983; Riolo et al. 2001). While proximity alone can be an indication of relatedness, being able to distinguish among heritable tags, as in the "armpit effect" (Dawkins 1982; Hauber et al. 2000; Hauber and Sherman 2000; Mateo and Johnson 2000; Isles et al. 2001), allows a still better indication of relatedness, for

example among sessile cnidarians (Grosberg and Quinn 1989; Grafen 1990). The discriminatory abilities required for the armpit effect are likely to be widespread. The self-recognition required for multicellularity provides them from intimate contact, and the need to distinguish conspecifics for mating provides them more generally for animals. In both cases, a hardwired comparison known as the green beard effect (Hamilton 1964; Dawkins 1976; Haig 1996; Grafen 1998; Keller and Ross 1998) would seriously slow evolution and make speciation almost impossible.

Viscosity is ubiquitous because few populations completely mix from one generation to the next. Hamilton (1964) believed that simple viscosity was a widespread sufficient cause of fairly weak altruism, and various models have found that viscosity can indeed foster cooperation (Getty 1987; Pollock 1989; Nowak and May 1992; Nakamaru et al. 1997). However, this general claim is now considered doubtful. The balance between increased relatedness and increased competition between neighbors may tilt towards or away from cooperation (Taylor 1992; Wilson et al. 1992; West et al. 2002). Taylor and Irwin (2000) have suggested that with overlapping generations, and with altruism dispensed as benefits to fecundity, there is a tendency for population viscosity to support altruism. The 15.6% cooperation found in our model with one tag is on the one hand more than zero, supporting Taylor and Irwin, but on the other hand is rather limited. Adding observable tags shows that proximity can sustain cooperation based on contingent altruism, even if the very correlation of tags and relatedness evolves. By putting both the matching and the altruism under explicit genetic control, the model shows how altruism conditional on heritable tags can evolve despite substantial costs of cooperation. Thus the present model, which combines viscosity, the armpit effect, and

endogenous use of discrimination in a genetically explicit way, creates a very general

expectation of widespread, and not necessarily weak, conditional altruism in nature.

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Table 1. Robustness of the Simulation Model

The data are averaged over the last 100 iterations of the 30 replications of each variant. .

The base case parameter settings are: cost = 0.01, benefit = 0.03, number of colors = 4,

mutation rate = 0.001, lattice size = 50x50, run length = 2000, proportion empty space =

20%.

Variant	Discriminatory strategy		Cooperative behavior	
	%	Standard Error	%	Standard Error
base case	**76.6%**	2.2%	**91.0%**	0.9%
colors: 2	**65.5%**	3.6%	**85.9%**	2.3%
colors: 8	**67.2%**	3.0%	**91.8%**	0.8%
mutation rate: .0005	**80.1%**	2.8%	**95.8%**	0.5%
mutation rate: .002	**63.6%**	2.2%	**80.2%**	1.5%
lattice size: 25 x 25	**79.7%**	4.2%	**93.2%**	2.6%
lattice size: 100 x 100	**62.9%**	2.9%	**67.5%**	2.7%
run length: 1000	**78.6%**	1.6%	**90.7%**	0.9%
run length: 4000	**70.8%**	2.7%	**91.7%**	0.8%

Table 2. Effects of variation in proportion of vacant space

The less crowded the environment, the closer the offspring can be placed to their parents, resulting in higher levels of cooperation. Conversely, the more crowded the space, the further the offspring tend to be from their parents, and the more the results resemble the case of completely random placement. The data are averaged over the last 100 iterations of the 30 replications of each variant.

Variant	Discriminatory strategy		Pure Altruist Strategy		Cooperative behavior	
	%	Standard Error	%	Standard Error	%	Standard Error
ε (random offspring placement)	**1.3%**	0.2%	**0.0%**	0.0%	**0.1%**	0.0%
10%	**57.5%**	5.6%	**3.9%**	0.9%	**60.0%**	5.9%
20% (standard case)	**76.6%**	2.2%	**14.6%**	2.0%	**91.0%**	0.9%
30%	**70.4%**	3.6%	**24.6%**	3.7%	**94.5%**	0.5%
40%	**74.0%**	3.2%	**22.2%**	3.1%	**95.8%**	0.4%

Figure 1. Effect of variation in benefit/cost ratio

The benefit parameter (b) is systematically varied from 0.01 to 0.10 by increments of 0.01, with the cost parameter held constant at c = 0.01. The strategy distribution data are averaged over the last 100 iterations of the 30 replications of each variant.

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