# A Frequency-Dependent Natural Selection Model for the Evolution of Social Cooperation Networks

### (altruism/threshold effect/cooperative carnivore hunting behavior)

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**ABSTRACT** A model is presented for the evolution of several aspects of sociality based on reciprocal ties of social cooperation, modeling especially cooperative hunting behavior in carnivores. This model captures the possibility of a critical threshold in gene frequency, which, if reached, will lead to an explosion toward fixation of the "social" trait. This threshold phenomenon might be restated as follows: the precondition for evolution favorable to the specific form of social behavior considered is hard to satisfy, but—once this condition is satisfied—the tendency toward sociality is effectively irreversible. The simple model proposed appears to be highly robust, with most realistic changes additionally favoring the social gene.

There is growing evidence (surveyed in ref. 1) that formation of stable pair bonds between unrelated individuals other than mated pairs may be a behavioral basis for many vertebrate social adaptations, especially cooperative hunting behavior in carnivores (2) and the social structure of certain nonhuman primates (3). Looked at from the standpoint of its possible evolutionary origins, any predisposition for cooperative behavior cannot benefit a species member unless this individual happens to encounter and enter into a cooperative relation with another individual similarly adapted. The present note explores the problem of generating a critical mass of individuals with cooperative potential of this kind, assuming that such potential is genetically controlled. The process is developed from the standpoint of frequency-dependent selection in mathematical population genetics, and it is shown, as a consequence of this frequency-dependent structure (4, 5), that selection of social cooperation may have some interesting structural properties; more extensive mathematical developments will be published elsewhere. The concrete model proposed appears particularly suitable for study of the initial evolution of carnivore social behavior, though the applicability may extend quite generally throughout species where nonsexual pairbonding is identifiable and important. Moreover, insofar as the basic human adaptation may be more carnivore than primate (2), the model may be of interest for early human evolution.

The essence of our results is the prediction of a very fast increase in the frequency of an "altruist" allele once a certain critical threshold is exceeded. Specifically, consider a simple Mendelian dominant–recessive pair $(B,b)$ with the following postulated selection mechanism. Interpret the $bb$ recessives as having the capability for entering into a relation of co-

operation with other $bb$ individuals; a special case is what has been called (1) reciprocal altruism. Assume a population of highly mobile individuals that is randomly mixing within a generation (as is consistent with the predation behavior of many animal species), and suppose that each homozygous recessive individual in each generation makes $N \geq 1$ random contacts with other individuals of the species (for simplicity we assume $N$ fixed and generations nonoverlapping); these contacts define a random graph or network in each generation. Certain of these contacts will, in general, be with individuals of the dominant (uncooperative or solitary) phenotype; if the frequency of the $b$ allele is low and if $N$ is small relative to the total population, then most or all of the contacts will be with dominants. Now, in the simplest model, assume that the $bb$ phenotype is lethal if an individual of that phenotype fails to encounter (in the course of his random contacts with other species members) another individual who is also recessive; but assume that the $bb$ phenotype has superior fitness should linkup occur (the phenomenology being that the contact with another recessive individual allows a cooperative relationship to develop that raises the fitness of both species members in question).

Running the process out in time, the following phenomenon occurs. There exists a critical density of the cooperative allele, $\beta_{crit}$, such that, if the starting frequency of the allele exceeds this value, then the frequency of the cooperative phenotype will explode, and the cooperative trait will eventually fixate in the population. If the starting frequency falls below $\beta_{crit}$, then the frequency of $b$ will die away relatively slowly, and asymptotically the decay is algebraically slow like $1/n$, where $n$ is the number of generations (this slow decay occurs for the standard reason that most of the remaining recessive alleles stay hidden in the heterozygotes: see ref. 6). This asymmetry of the rates of genetic change above and below $\beta_{crit}$ is a very important conclusion that may be drawn from the present model. Crudely stated in qualitative terms, what this asymmetry entails is that, for $\beta$ even slightly exceeding $\beta_{crit}$, the social trait will move on a turnpike to fixation that minor environmental fluctuations are unlikely to reverse; whereas if a population, for whatever reason, achieves a significant frequency $\beta = \beta_0 < \beta_{crit}$, a significant frequency of the cooperative trait will persist for a very long time, and any of a wide variety of random environmental fluctuations (7) could act on this frequency to push the process over the critical threshold.

Fig. 1 gives a diagrammatic illustration of the general
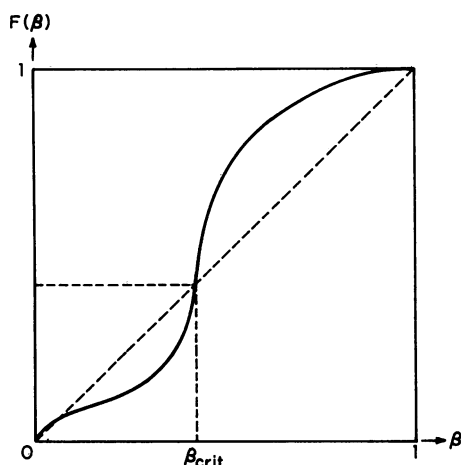
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FIG. 1. Graph of intergenerational frequency change $\beta \rightarrow F(\beta)$. $\beta_{crit}$ is the unique value of $\beta$ between 0 and 1 that is a fix-point of $F(\beta)$, i.e., for which $\beta_{crit} = F(\beta_{crit})$.

qualitative behavior of $F(\beta)$, defined to be the frequency of the recessive in the second generation given that this frequency is $\beta$ in the first. One can give a particularly simple analytic form to $F(\beta)$ by making the following assumptions:

(*1*) The population is large and is in Hardy–Weinberg equilibrium with $B$ having frequency $\alpha = 1 - \beta$ and $b$ having frequency $\beta$.

(*2*) $N$ is constant, uniform over individuals, and is small relative to the population size.

(*3*) The fitness of a recessive who links up with another recessive is 1; the fitness of all dominants is a constant $\sigma$, with $0 < \sigma < 1$, which may be interpreted as a survival probability per individual per generation; the fitness of a recessive that fails to link up is 0 (i.e., in this case the recessive phenotype is lethal).

(*4*) The contact network in each generation is random (random mixing).

(*5*) Mating is random, and is uncorrelated with the contact network.

Under these baseline assumptions, the probability that a given recessive will link up with some other recessive can be well approximated in the interesting $\beta$ ranges (not too near 0 or 1) by the expression

$$f(\beta,N) = 1 - (1 - \beta^2)^N, \qquad [1]$$

which ignores sampling without replacement considerations and certain other statistical subtleties.

Then it can be shown that

$$F(\beta) = \left[ \beta\left( \alpha + \beta\frac{f(\beta,N)}{\sigma} \right) \right] \Big/ \left[ \alpha + \beta\left( \alpha + \beta\frac{f(\beta,N)}{\sigma} \right) \right] \qquad [2]$$

'and the qualitative behavior of $F(\beta)$ in Fig. 1 may be deduced. The value $\beta_{crit}$ is given by the unique internal fixed point of the mapping $\beta \rightarrow F(\beta)$; above $\beta_{crit}$ the growth is essentially exponential, while for $\beta < \beta_{crit}$ the decay is asymptotically algebraic and $F(\beta)$ is tangent to the 45° line at the origin, so that at very low $\beta$ values decay is very slow indeed.

In this simplest model, the effects of social cooperation networks have been developed as a special case of frequency-dependent invididual (Mendelian) selection, which as a pure concept is quite old, going back to studies by Wright (sur-

veyed in ref. 8). As Levins (7) has pointed out, however, frequency-dependent selection as a concept has in general lacked motivation, and the main contribution of the present model from this standpoint lies in its use of network connectivity considerations in generating a concrete frequency-dependent *mechanism*. Moreover, most existing work on possible frequency-dependent selection effects stresses circumstances in which such effects lead to *stable* polymorphism, which is most relevant to a set of problems quite different from those involved in modeling social evolution (though see ref. 9). The utility of the present model lies in the fact that it is able to relate a threshold effect based on frequency-dependence to the possible evolution of a very specific and important form of sociality, namely, pairwise ties of social cooperation, i.e., to a primitive form of social networks.

It can be shown that the basic qualitative form of $F(\beta)$ displayed in Fig. 1 remains invariant for much more general $f(\beta,N)$ than that given by Eq. [1]. Specifically, the behavior shown in Fig. 1 is present if $f = f(\beta;\mathbf{p})$ where $f'(\beta) > 0$ ($f$ is strictly monotone increasing) and $f(0) < \sigma < f(1)$, $\mathbf{p}$ being any fixed vector of parameters. In consequence, the basic mathematical behavior of the model is extremely robust, and the evolution of a wide variety of more complicated social network and group structures could be modeled along similar lines.

Moreover, it is important to stress that many perturbations of the null assumptions *1–5* actually help the recessive, essentially by pulling down the effective $\beta_{crit}$. Thus, in particular, if one considers nonrandom contacts owing to population viscosity, preferential mating (assortative between phenotypes), or positive correlation between the mating structure and the pattern of contacts between species members in a given generation—all of these assumptions being highly realistic—the result is a decreased value of $\beta_{crit}$ and a general increase in the relative advantage of the recessives. In particular, in an island-like system consisting of a large number of small and weakly coupled populations that are internally panmictic (10, 11), if the *bb*s manage to take over even one local population, then eventual conquest of the whole metapopulation by diffusion outward from this secure base is essentially assured for appropriate migration rates, even though such conquest may take a long time. Further analysis of these qualitative statements involves interaction between sampling-with-replacement considerations necessary in the analysis of small local populations, stepping-stone models, drift effects, and comparison of relative time scales.

The present model has some resemblance to the models of Scudo and Karlin (12) dealing with the superior fertility of homogamous matings, which also may lead to thresholds of allele frequency, but has the crucial difference that these last models reduce or, in the limit, eliminate fertile interphenotype pairings, whereas the present model does not. One specific consequence of this asymmetry is that, in the Scudo–Karlin model, the dominant phenotype is in a symmetric position with the recessive one as far as the death of its alleles in cross-phenotype matings is concerned, and is, in this sense, likewise disadvantaged. The present model, by contrast, stresses the asymmetries between a solitary dominant and a social recessive.

At the same time that it is reasonable for social carnivores and certain other social vertebrates, it should be stressed that the whole thrust of the present network mechanism goes

strongly against much known data for social insects where pair bonding based on individual recognition plays a much smaller role (13, 14). As far as applications of the model are concerned, the main unsolved problem is differentiating the effects of a pairwise cooperation mechanism of the kind we have delineated from kin selection effects that are certainly present in most carnivore packs and social vertebrate groups in general (15). This differentiation remains largely an unsolved problem. It should be stressed, however, that the present model is like kin selection in that it postulates no group selection mechanism involving competition between intrinsically higher-order units such as colonies or populations (11, 16, 17). If higher-order units are involved in the present considerations, they should be thought of as networks, which are based on kin ties in kin selection and ties of cooperation in models along the lines of the present paper.

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