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# Assortment of encounters and evolution of cooperativeness

**(altruism/evolutionary stable strategies/assortative meetings)**

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**ABSTRACT** The method of evolutionary stable strategies (ESS), in its current form, is confronted with a difficulty when it tries to explain how some social behaviors initiate their evolution. We show that this difficulty may be removed by changing the assumption made tacitly in game theory (and in ESS) of randomness of meetings or encounters. In reality, such randomness seems to be rare in nature. Family, population and social structure, customs, and habits impose various types of deviation from randomness. Introducing nonrandomness of meeting in a way formally similar to assortative mating, we show that the bar to initial increase of inherited cooperative or altruistic behaviors can be removed, provided there is sufficient assortment of meetings. Family structure may cause contacts predominantly between certain types of relatives, and one can reconstruct some results of classical kin selection in terms of evolutionary stable strategy with assortative meetings. Neighbor effects and group selection might be similarly treated. Assortment need not be a passive consequence of population and social structure, but it can also be actively pursued. Behaviors favoring the choice of cooperative companions will have the effect of favoring the evolution of cooperativeness. It can be shown that discrimination in the choice of companions, especially if combined with assortment, can favor the development of cooperativeness, making initial increase of cooperative behavior possible even at levels of assortment passively imposed which would not be adequate, *per se*, to guarantee the increase of cooperativeness. It is possible that, in some cases, cooperativeness and behavior favoring some type of assortment are coselected.

## 1. Introduction

The concept of evolutionarily stable strategies (ESS) as suggested by Maynard Smith and Price (1) is tightly, although usually tacitly, connected with the assumption of random encounters among individuals in a population, regardless of their strategy or phenotype. Only with this assumption, polymorphic and individually mixed strategies are equivalent in their effect on the individual payment function—a crucial prerequisite for the application of game theory, and especially of ESS, to population biology. In most natural situations, however, the assumption of random encounters is unlikely to be met. This may happen because of (*i*) nonpanmictic structure of the population and (*ii*) active choice of companions, especially in higher organisms. In the case of nonrandom encounters imposed by the population structure, they may tend to occur within the family. Moreover, in many populations, neighbors are likely to be more closely related than more widely separated pairs and thus more likely to choose the same strategy, independently of whether this choice is inherited genetically or culturally. Finally, even unrelated individuals sharing a similar strategy may tend to congregate because of their choice or avoidance of specific environments, or simply because they belong to the same social group.

In the case of nonrandom encounters due to active choice, individuals may actively seek or avoid encounters with other individuals of their phenotype or strategy. These choices may be the result of learning by the individual, or they may be genetically or culturally inherited traits that have spread in the population by natural selection. We saw that congregation of individuals with similar strategies might be the passive consequence of similar choice of habitats. One can also assume that the reverse can be true, so that the active choice of companions with similar strategies may be responsible for the choice of similar habitats.

The first objective of this work is to generalize the concept of evolutionary stability under the assumption of nonrandom encounters imposed by population and social structure, including within-family encounters (i.e., kin selection), group selection, and neighbor effect. We call this assortment "structural." Second, we study the evolutionary effects of nonrandom encounters due to active choice of companions and discuss the coevolution of this type of selective assortment, together with that of sociality.

## 2. Evolutionary stability with random and nonrandom encounters

We concentrate on a situation in which individuals in the population have two alternative strategies, $S_1$ and $S_2$. Paraphrasing the model by Maynard Smith and Price (1), the outcome of an encounter between two individuals in the population is measured in terms of some evolutionarily relevant payment function measured on the scale of Darwinian fitness. Let $V_{ij}$ be the expected increment to the fitness of an individual practicing strategy $i$ after an encounter with an individual of strategy $j$. Finally, let $x$ ($0 \leq x \leq 1$) be the proportion of individuals who choose the first strategy. With the tacit assumption that encounters are random and independent of strategy, the expected payment for individuals choosing strategy $i$ ($i = 1,2$) can be written, for Maynard Smith and Price's model (1):

$$V_i(x) = xV_{i1} + (1 - x)\, V_{i2}. \qquad [2.1]$$

We consider the general situation, in which $u_{ij} = u_{ij}(x)$ is the probability that an individual practicing strategy $S_i$ encounters an individual of strategy $S_j$ ($i,j = 1,2$; $u_{i1} + u_{i2} = 1$).

The expected payment for a strategy $S_i$ in this case is

$$V_i(x) = u_{i1}(x)V_{i1} + u_{i2}(x)V_{i2} \qquad i = 1,2. \qquad [2.2]$$

Assuming, further, that the expected number of encounters per individual is independent of its strategy, we also have

$$xu_{11} + (1 - x)u_{21} = x$$

(note that the left side gives us the proportion of encounters in which the second individual is of strategy $S_1$).

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Abbreviation: ESS, evolutionary stable strategies.

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Hence, for $x \neq 1$

$$u_{21} = \frac{x(1 - u_{11})}{1 - x}$$

$$u_{12} = 1 - u_{11} \qquad [2.3]$$

$$u_{22} = \frac{1 - 2x + xu_{11}}{1 - x}$$

(for $x = 1$, indeed $u_{11} = u_{21} = 1$, $u_{12} = u_{22} = 0$).

Note that all encounter probabilities are given by $x$ and $u_{11} = u_{11}(x)$. Payment function **2.2** can now be written as

$$V_1(x) = V_{12} + (V_{11} - V_{12})\, u_{11}(x) \qquad [2.4]$$

$$V_2(x) = V_{22} + (V_{21} - V_{22}) \frac{x}{1 - x}[1 - u_{11}(x)].$$

As a special case, if encounters are random, $u_{11} = x$. Therefore, $u_{21} = x$, $u_{12} = u_{22} = 1 - x$, and [**2.4**] immediately becomes [**2.2**].

In order to study the evolutionary kinetics of the frequency $x$ of individuals choosing strategy $S_1$, we consider a transmission model in which $x$ is increasing or decreasing from one generation to the next in proportion to the expected success of an individual choosing it at that specific generation. Thus, after one generation,

$$x' = \frac{xV_1(x)}{xV_1(x) + (1 - x)V_2(x)} = f(x). \qquad [2.5]$$

It can be shown that, in the special case of random encounters, the stable equilibria of transformation **2.5** are exactly the ESSs of the population game determined by the payment matrix $\|V_{ij}\|$, as being defined by Maynard Smith and Price (1). Thus, differentiating twice at the origin we see that $x = 0$ is a stable equilibrium if and only if either

$$V_{12} < V_{22}$$

or

$$V_{11} = V_{21} \text{ and } V_{12} > V_{22}, \qquad [2.6]$$

which is exactly the condition for $x = 0$ to be an ESS, as given by Maynard Smith (2, 3) and Bishop and Cannings (4). This can also be proven for an inner stable equilibrium, if it exists. Transformation function **2.5** corresponds to the simplest model of transmission—e.g., genetic transmission in haploids and vertical uniparental cultural transmission (5). However, in the case of random encounters one can extend the validity of the result to a wider class of transmission models, including one-locus $n$-allele random mating model when the payment function is viability (unpublished).

Extending definition **2.6** of evolutionary stability to nonrandom encounters, we again differentiate $f(x)$ twice at $x = 0$ and see that this equilibrium is stable if either

$$V_1(0) < V_2(0) \text{ [which means } f(0) < 1]$$

or

$$V_1(0) = V_2(0)\ [f'(0) = 1] \text{ and}$$

$$V_1'(0)\, V_2(0) - V_1(0)\, V_2'(0) + [V_2(0) - V_1(0)]V_1(0) < 0\ [f''(0) < 0].$$

The above are the conditions under which an evolutionary strategy is stable even if meetings are not random, and therefore we will refer to it as "generalized ESS." By using [**2.4**], the first condition becomes

$$V_{12} + (V_{11} - V_{12})\, u_{11}(0) < V_{22}. \qquad [2.7]$$

This is a sufficient condition for $x = 0$ being a generalized ESS. A weak version of [**2.7**] is a necessary condition for it.

A similar condition is required for $x = 1$ being a generalized ESS.

If $f(x)$ is an increasing function of $x$, and if neither $x = 0$ nor $x = 1$ are generalized ESSs, then at least one (but maybe more) mixed generalized ESS exists, satisfying the equation $V_1(x) = V_2(x)$. An analysis of models of transmission more complex than [**2.5**] for nonrandom encounters will not be given here.

For a complete description of nonrandom encounters one might want to specify a matrix indicating the numbers of encounters of the four possible pairs of types. In order to simplify the treatment, however, we concentrate on a model of nonrandomness of encounters that requires only one parameter and uses the shortcut often used in the analysis of assortative mating. We later suggest a further elaboration of this model which may cover some aspects of active choice.

## 3. Nonrandomness of encounters imposed by population structure

Simple cases of nonrandomness, imposed by population structure (for instance, in kin selection, group selection, and neighbor effect) may be approximated by a law of encounters similar to that used for assortative mating (6), which we will refer to as "assortative meeting or (encounter)." The frequency of meetings between individuals who both have strategy $S_1$ is then

$$P_{11} = (1 - m)x^2 + mx \qquad [3.1]$$

where $m > 0$ represents the portion of population that meets an individual of the same strategy, and $1 - m$ meets randomly. The probability that an individual practicing $S_1$ is met by another of its kind is

$$u_{11}(x) = \frac{P_{11}}{x} = m + (1 - m)x. \qquad [3.1a]$$

From [**3.1a**] and [**2.3**] we have

$$u_{22} = m + (1 - m)(1 - x). \qquad [3.1b]$$

Condition **2.6** for evolutionary stability of the fixation ($x = 0$) of strategy $S_2$ becomes

$$mV_{11} + (1 - m)V_{12} < V_{22}. \qquad [3.2]$$

The inverse inequality is the condition for initial increase of strategy $S_1$.

We are now interested in discussing a special class of social strategies whose evolutionary beginnings are difficult to explain on the basis of standard ESS theory. We will concentrate on strategies that we will call of the cooperative type. Strategy $S_1$ will be called "cooperative" if its adoption by both participants is more productive for both ($V_{11} > V_{22}$) but its adoption by one participant only is disadvantageous to the person adopting it ($V_{12} < V_{22}$)—i.e., it is better to be noncooperative if your opponent is noncooperative. Thus, formally

$$V_{11} > V_{22} > V_{12} \qquad [3.3]$$

are the conditions for cooperativeness, in agreement with Axelrod and Hamilton (7). Note that this definition includes, as a special case, the situation $V_{21} > V_{11}$ in which the chooser of $S_1$ always loses and his companion always gains (namely, the case of altruism) in agreement with Haldane (8) and Hamilton (9).

[**3.2**] shows that under random encounters ($m = 0$), the condition for initial increase of $S_1$ reduces to the classic ESS condition $V_{12} > V_{22}$, which is incompatible with [3.3], making the initial increase of cooperativeness impossible but, as $m$ increases, the left side of [3.2] increases and tends to $V_{11}$ as $m$ tends to 1, in which case the condition for initial increase of $S_1$ tends to become $V_{11} > V_{22}$ (which is part of our definition of cooperativeness).

From [3.2] and [3.3] we get:

COROLLARY. *For any situation of cooperativeness (altruistic or not) versus noncooperativeness, there are critical values* $0 < m^{**} < m^{*} < 1$ *such that, if* $m > m^{*}$ *(high rate of assortment), full cooperativeness* $(x = 1)$ *is the only ESS. If* $m < m^{**}$ *(low assortment), fixation of noncooperativeness is also an ESS and is the only one in the case of altruistic cooperativeness (Table 1).*

## 4. Cooperativeness and active choice of companions

Assortative meeting, passively imposed by the population structure (structural assortment), is always favorable for the evolution of cooperativeness. However, the evolution of cooperativeness may be more likely when there is an active choice of encounters with one's own sort (selective assortment). For clarity, for the purpose of this section we distinguish meetings and encounters, the latter being a chosen subset of the first in which individuals actually interact.

We assume at the start that every individual has a constant number of meetings $N > 1$ (which may be random or with assortment at rate $m$) and will choose an encounter with one of them. A cooperative individual will always prefer another cooperative individual among the $N$ available candidates. As before, let $u_{11}(x)$ be the probability that a random individual, met by an $S_1$ individual, will be of the same type [with $u_{11} = m + (1 - m)x$ for assortative meeting]. If this is the probability for each of the $N$ individuals met by such an individual and if these meetings are independent, then the probability of finding at least one cooperative individual is

$$\hat{u}_{11}^{(N)}(x) = 1 - [1 - u_{11}(x)]^N. \qquad [4.1]$$

Thus, $u_{11}$ is the probability imposed by population structure, $\hat{u}_{11}^{(N)}$ is the actively obtained one, and $\hat{u}_{11}^{(1)} = u_{11}$ (i.e., $u_{ij}$ stands for meeting and $\hat{u}_{ij}$ stands for encounter).

If, more generally, $N$ is a random variable taking the value $k$ with probability $P(N = k) = P_k$ $(k = 1,2, \ldots)$ then

$$\hat{u}_{11}^{(N)}(x) = \sum_{k=1} P_k (1 - [1 - u_{11}(x)]^k)$$

$$= 1 - \phi[1 - u_{11}(x)], \text{ where} \qquad [4.2]$$

$$\phi(s) = \Sigma P_k s^k \qquad [4.3]$$

is the probability-generating function of the number of available candidates. (For models of active choice of mates, for comparison see ref. 10.)

Table 1. Evolutionary fate of cooperative strategies as influenced by assortment

| | High assortment ($m > m^*$) | Low assortment ($m < m^{**}$) |
|---|---|---|
| $S_1$ is altruism ($V_{21} > V_{11}$) | Fixation of $S_1$ only stable state | Fixation of $S_2$ only stable state |
| $S_1$ is nonaltruistic cooperativeness ($V_{21} < V_{11}$) | Fixation of $S_1$ only stable state | Fixation of $S_1$ or $S_2$ both stable |

If the imposed encounter probability is due to assortative meetings, then from [3.1a] and [4.2]

$$\hat{u}_{11}(x) = 1 - \phi(1 - m)(1 - x). \qquad [4.4]$$

Condition 2.6 for initial success of the cooperative strategy then becomes

$$V_{11} + (V_{12} - V_{11})\,\phi(1 - m) > V_{22}. \qquad [4.5]$$

The following results are immediately obtained from [4.5].

(*i*) If $m = 0$, Condition 4.5 for initial success of cooperativeness becomes $V_{12} > V_{22}$ and, therefore, it is never satisfied independently of the distribution of $N$.

If encounters are absolutely random, when a cooperative type is very rare it is not likely to find another cooperative candidate even with active search for one among many candidates.

(*ii*) On the other hand, by inserting [4.4] into [2.4] and expanding as a Taylor series of $x$, it is readily shown that, even for a small (but not infinitesimally so) frequency of the cooperative type in the population with absolutely random meetings ($m = 0$), the cooperative strategy becomes advantageous if the expected number of meetings $E(N)$ per individual is large and there is active choice of cooperative companions.

*i* and *ii* together may be usefully restated also in the following way. With $m = 0$ for any value of $E(N)$ (which may be viewed as a measure of selectivity of one's companion), a positive threshold frequency $x_0 > 0$ of the cooperative type is needed for it to become advantageous. Thus, it cannot be successful from its very beginning. However, in infinite populations this threshold becomes as small as we wish if $E(N)$ is sufficiently large, which means that in this case a relatively small frequency of the cooperative type may be sufficient for its success. Thus, in finite populations, high enough selectivity may permit initial increase even in the absence of assortment imposed by population structure.

(*iii*) If $m$ is small but positive (the imposed chance of a meeting between individuals of the same strategy is slightly above random), then by Taylor's expansion

$$\phi(1 - m) \approx 1 - m\,\phi'(1) = 1 - mE(N)$$

where $E(N)$ is the expected number of meetings per individual and [4.5] becomes

$$E(N) > \frac{1}{m}\frac{V_{22} - V_{12}}{V_{11} - V_{12}}. \qquad [4.6]$$

Recalling that $V_{11} > V_{22} > V_{12}$, the cooperative strategy will be initially successful if and only if the expected number of meetings per individual is larger than some critical value $N^*$ which depends on $V_{11}$, $V_{12}$, and $V_{22}$ and on $m$.

(*iv*) From the definition of cooperativeness, $V_{12} < V_{11}$, and since $\phi(s)$ as a generating function is always increasing, the left side of [4.5] is an increasing function of $m$. Thus, it follows from *ii* that, for all $0 < m < 1$, if $E(N)$ is sufficiently high, cooperativeness is successful from its very beginning.

(*v*) With all other parameters being equal, a high value of $E(N)$ is typical of both high population density and high mobility of individuals with it (10). Thus, quite surprisingly, condition 4.6 for initial success of the cooperative strategy is roughly the opposite of most conditions for the evolution of altruism, obtained by group-selection models (11–14).

Note, however, that all these models are concerned with altruism equally shared by all people of the same group as the altruist. This is exactly the opposite of the assumption made in this section. We therefore think it worth making a clear distinction between altruism in which there is, or is not, a choice of companions—namely, between selective and nonselective altruisms. The same can be said for cooperativeness.

*Remark:* The results obtained so far assume that the number of encounters per individual is constant. This is not the case in certain social situations. For instance, there are behaviors that make individuals gregarious, or solitary, which will affect the number of meetings and encounters. The formalism above can be extended to cover different numbers of encounters, if we incorporate into the payment function $V_{ij}$ the price of solitude due to a failure of $i$ to encounter $j$. For example, if two individuals of type $S_2$ are not able to interact at all, then $V_{22}$ may stand for the fitness of solitariness.

## 5. Co-evolution of assortment and cooperativeness

In the previous section we assumed that the number of individuals $N$ whom one meets and from whom a companion is chosen is constant or, more likely, is distributed according to a given probabilistic law. We see that a selectively cooperative type is always more successful whenever the number of meetings increases. It is therefore reasonable to expect that a selectively cooperative trait will evolve more easily if associated with some other behavioral tendency that increases the individual's ability for selective encounters.

In the same way it is possible that nonselectively cooperative traits will evolve better when associated with behavioral changes that, although not directly connected with cooperativeness, affect the rate of assortment. Lowering the individual's mobility, a tendency to spend more time with the family, or a preference for a less-attractive habitat are examples of such behavior. Adoption of such behavior may be favorable for the cooperative type, especially when rare, even if it inflicts some immediate cost. In such cases, a natural question is: What is the rate $m$ of assortment resulting from some idiosyncratic behavior that is most favorable for the evolution of cooperativeness, in the sense of making its initial increase most likely? If the cost associated with a rate of assortment is $G(m)$ where $G(m)$ is any convex function, then from [**2.7**] and [**3.1a**] it follows that the condition for initial increase of the cooperative is

$$[mV_{11} + (1 - m)V_{12}] - G(m) > V_{22}. \qquad [5.1]$$

Thus, there is a single value $m$ with $G'(m) = V_{11} - V_{12}$ that maximizes the left side of [**5.1**] and is the optimal one for initial increase of the cooperative type.

In the same way, the expected payment for the cooperative type when in frequency $x > 0$ and when investing $G(m)$ in assortment is

$$V_1^{(m)}(x) = [m + (1 - m)x]V_{11} + (1 - m)(1 - x)V_{12} - G(m). \qquad [5.2]$$

The value $m(x)$ which maximizes this is readily calculated and, at least for the nonaltruist, cooperation is shown to decrease with $x$. When $x = 1$, no investment to increase assortment is favorable for the cooperative type. Thus, some change in behavior increasing the rate of assortment is shown to be favorable for the cooperative type when rare and may be associated with it. This is not the case when the cooperative type becomes common.

A possible route for the evolution of a cooperative type may thus be characterized by first taking over small or isolated habitats, making it possible to have a large assortment, and then invading the mainland (15).

## 6. A genetic example—first appearance of a dominant cooperative allele due to sib selection

Consider a rare cooperative type $Aa$ in a randomly mated diploid population in which the common type is the noncooperative $aa$. Assume that encounters that matter for this sort of cooperativeness occur only among sibs. If the frequency of the cooperative type $Aa$ in the parent population is $\varepsilon$, then $2\varepsilon + 0(\varepsilon)$ of all matings will be of type $aa \times Aa$. Almost all cooperative offspring are born to such a mating, and the probability that a cooperative individual born in such a mating meets another cooperative individual (sib) is $m = 1/2$. Thus

$$u_{11}(\varepsilon) = \frac{1}{2} + 0(\varepsilon).$$

From [**2.4**] the expected fitness of a cooperative offspring is

$$V_1(\varepsilon) = \frac{V_{11} + V_{12}}{2} + 0(\varepsilon)$$

which may be written as

$$V_1(0) = \frac{V_{11} + V_{12}}{2}.$$

The noncooperative fixation therefore is stable if and only if

$$V_{22} > \frac{V_{11} + V_{12}}{2}. \qquad [6.1]$$

Hence, although we have assumed $V_{22} > V_{12}$, the cooperative strategy $S_1$ can still be successful from its very beginning if $V_{22} < (V_{11} + V_{12})/2$. This example of the effect of nonrandom encounter is exactly what is traditionally referred to as "kin selection."

Thus, for the simplest altruism model in which $Aa$ always gives up a proportion $\gamma > 0$ of its fitness, thereby increasing that of its companion by $\beta > 0$ (17),

$$V_{11} = 1 - \gamma + \beta \qquad V_{21} = 1 + \beta$$

$$V_{12} = 1 - \gamma \qquad V_{22} = 1.$$

Here, condition **6.1** becomes

$$\gamma > \beta/2 \qquad [6.2]$$

which is the well-known Hamilton result, and in this case corresponds also to the condition for stability of fixation of the selfish in the exact genetic model, as proved by Cavalli-Sforza and Feldman (15). In the same way the assortative-meeting model leads to the conditions $3\beta/4$ and $\beta/4$ for initial increases of a dominant allele for sister-to-sister altruism in haplodiploid genetic determination and for half-sib altruism in a diploid population. These results coincide again with the exact genetic model (15, 16).

## Discussion

In a recent paper, Axelrod and Hamilton (7) described a well-known dilemma of a strategy that is advantageous to all participants if they are inclined to accept it to start with but is disadvantageous to anybody adopting it on its own. They refer to it as "cooperativeness," a term we use here, and ask about the problem of its initial increase. By employing standard methods of ESS, it is indeed shown that both fixation of cooperativeness and noncooperativeness are evolutionarily stable. Thus, the natural question arises of how this cooperativeness can initially increase. We find that the problem of the type discussed by Axelrod and Hamilton disappears once one departs from the standard assumption of random encounters, which is implicit in current applications of the ESS method. Kin, deme, niche, and social group structure, neighbor effect, idiosyncratic behavior, and discrimination in the choice of companions are some of the possible sources of deviation from randomness that seem to us crucial for understanding evolutionary stability of social structure.

The concept of assortative encounters suggested in this paper is aimed at integrating this factor into the theory of ESS. The problem described by Axelrod and Hamilton (7) exists only for too-low rates of assortment. We find that fixation of the non-cooperative types ceases to be evolutionarily stable once the rate of assortment exceeds a given threshold value. In this work we distinguish between two modes of assortment, structural and selective, the first resulting from the social population structure because of stratifications of kin, deme, social group, niche, class, caste, colony, etc., and the second, due to active choice of companions. They can coexist.

We introduced an example of how the ESS method modified by the introduction of structural assortment can explain the initial increase of altruism versus sibs, a classical kin-selection problem, but the method can also be applied to other situations in which a family structure is less obvious. Thus, Axelrod and Hamilton's suggestion (7) that initial progress of a cooperative trait may be due to some sort of kin selection can be stated more safely in the more general terms of structurally assorted encounters. Note, however, that this method (like inclusive fitness) cannot give conclusions as precise as those obtainable with exact genetic models.

The possibility of selective assortment, however, may have effects that are shown to be qualitatively different from those achieved by methods of kin selection, group selection, etc., which generate the structural assortment. We do not attempt to exemplify the existence of social selectivity among animals. We note, however, that there is likely to be so much evolutionary feedback between selectivity and cooperativeness that the possibility of co-evolution emerges naturally. In the general case, arguments of assortative meeting can serve only as first approximations to an exact genetic model. They need not coincide with it—for example, when applied to interior (polymorphic) equilibria.

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