THE THREE BROTHERS' PROBLEM: KIN SELECTION WITH MORE THAN ONE POTENTIAL HELPER. 1. THE CASE OF IMMEDIATE HELP

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Although the theory of kin selection (Hamilton 1964, 1972) has been introduced in terms of one individual (the donor) helping another (the recipient), altruistic behavior in general may involve more than two interacting individuals. An extreme (but maybe very common) example is that of an inherited physiological or biochemical trait that prevents the carrier from harming its neighbors (e.g., Eshel 1972; Cohen and Eshel 1976; Matessi and Jayakar 1976; Wilson 1979). Even situations of directed (active) altruism only rarely involve exactly two individuals, a donor and a recipient. In many situations an individual needs help, and this help can be provided, at some risk, by each of several relatives.

A natural question is what kind of behavior is favored by natural selection. Obviously, even when Hamilton's condition for altruistic behavior between two relatives is met, it is advantageous to stand by, letting another relative take the risk and provide the necessary help. If all are passive, however, then the original argument of Hamilton holds, and any potential helper can increase its own inclusive fitness by exclusively taking the risk and saving the relative in need. Once the helper takes the risk, the inclusive fitness of any other relative who decided to stand by will increase even more. Therefore, it seems that if any altruistic relative is in the vicinity, natural selection always favors the other selfish relatives.

In this paper, we attempt to show that simple arguments of evolutionary stability (Maynard Smith and Price 1973; Maynard Smith 1982) enable one to expand Hamilton's arguments of inclusive fitness to cases involving more than two interacting individuals. Our analysis of the evolutionarily stable strategy (ESS) model of multiple help, though apparently lacking some of the simplicity of Hamilton's original arguments, preserves much of the simplicity of his results.

An important quantitative result, which we hope contributes to the unification of the theory of kin selection, is that if Hamilton's condition for a one-to-one altruism is not met (i.e., if the ratio of the helper's risk to the recipient's benefit is

larger than the coefficient of relatedness), full selfishness is also the ESS when more than one potential helper is involved. If Hamilton's condition is satisfied, the only evolutionarily stable strategy is one that results in choosing to help, but only with some *positive* probability. Unlike the one-to-one case, in which this probability is always one (i.e., if Hamilton's condition is met, the ESS is full altruism), cases involving more than one potential helper rarely have full altruism as the ESS; most often the ESS is a mixed strategy of altruism and selfishness.

We present cases in which immediate help is needed, and each potential helper must independently decide whether or not to help. These models can also be applied to situations in which both the ability to help and the cost for it must be developed in advance (e.g., the case of physiological altruism). (Cases of delayed help are discussed in Motro and Eshel 1987. In these situations, each potential helper can wait in hope that another relative will volunteer; yet any delay decreases the efficiency of the help given to the recipient.)

The ESS model is accompanied by rigorous analysis of a simple genetic model of a one-locus, random-mating diploid population. The results of this simple genetic treatment coincide (at least in the case studied) with those of the ESS model, which is based on arguments of maximizing inclusive fitness.

IMMEDIATE MULTIPLE HELP: HAMILTON'S CONDITION FOR THE EXISTENCE
OF AN EVOLUTIONARILY STABLE MIXED STRATEGY

Assume a group of n symmetrical relatives, and let r (where $0 < r < 1$) be the degree of relatedness (measured by Wright's coefficient of relationship) between any two of them. We further assume that one individual in the group needs help, and that help may be given by k of the $n - 1$ other individuals in the group ($k = 0$, $1, \ldots, n - 1$). If k is greater than zero (at least one relative volunteers to help), the risk for each helper is a positive c_k, and the gain for the individual in need is b_k (risk and gain measured in terms of survival probability). For convenience, we define c_0 and b_0 equal to zero. Quite generally, one can assume that $\{c_k\}$ is a nonincreasing sequence and that $\{b_k\}$ is nondecreasing.

We consider the simple case in which the decision whether or not to offer help is made by each potential helper before information about other relatives' behavior is available. If p (where $0 \le p \le 1$) is the probability of a potential helper's offering help, then we seek a value of p that is an ESS, that is, a value of p that, when adopted by a large enough part of the population, becomes advantageous in terms of inclusive fitness over any alternative strategy adopted by the minority (Maynard Smith and Price 1973).

The concept of ESS can be directly applied to population biology only if random encounters among individuals in the population are assumed (Eshel and Cavalli-Sforza 1982). Then the probability of encountering a rare mutant is negligible both for a wild-type individual and for another identical mutant. Under this assumption, a necessary condition for a strategy p to be an ESS is that it must be a Nash solution of the game; namely, no mutant player that is the only mutant in its group can do better than a typical individual in a group consisting entirely of ESS players (Maynard Smith 1974). This is apparently not the case for situations involving

If $rv^{n-2}(1 - v) < c < r(1 - v)$, then no pure strategy is an ESS. In this case, since there are only two pure strategies, we know (Eshel 1982) that there must be a unique evolutionarily stable mixed strategy.

Moreover, in the special case C_1-B_2 for which only one helper is needed to save the relative's life, condition (2) for stability of the pure altruistic strategy is never satisfied if n is greater than 2. Hence, in this case, Hamilton's condition of $r(1 - v) > c$ is necessary and sufficient for the evolutionary stability of a mixed strategy, characterized by a probability p (where $0 < p < 1$), of helping the relative in need.

A mixed ESS cannot occur if n equals 2 (the case originally treated by Hamilton), but it appears to be quite common if n is greater than 2. As we see, Hamilton's condition for pure altruism when n equals 2 may serve as a criterion for the existence of a mixed selfish-altruistic ESS when n is greater than 2.

ANALYSIS OF THE EVOLUTIONARILY STABLE STRATEGY

Let the strategy of each individual in a group of relatives be denoted by a number p (where $0 \leq p \leq 1$), which is the probability of this individual's choosing to help a relative in need. Let n, r, c_k, and b_k also be defined as in the preceding section.

For any potential helper, if there are exactly k other volunteers ($k = 0, 1, \ldots, n - 2$), then volunteering to help entails a risk to self of c_{k+1}, an increase of $b_{k+1} - b_k$ in the benefit to the relative in need, and a decrease of $c_k - c_{k+1}$ in the risk to each of the k other helpers. Thus, if there are exactly k other volunteers and if the potential helper does provide help, then the inclusive fitness of the potential helper is

$$\Omega_k = -c_{k+1} + r[b_{k+1} - b_k + k(c_k - c_{k+1})]. \tag{5}$$

If the common strategy in the population is p, the probability that there will be exactly k other volunteers is

$$\pi_k = \binom{n-2}{k} p^k(1 - p)^{n-2-k}. \tag{6}$$

Hence, the unconditional inclusive fitness for a volunteer is

$$\Omega(p) = \sum_{k=0}^{n-2} \Omega_k \pi_k, \tag{7}$$

and specifically,

$$\Omega(0) = -c_1 + rb_1, \tag{8}$$

$$\Omega(1) = -c_{n-1} + r[b_{n-1} - b_{n-2} + (n - 2)(c_{n-2} - c_{n-1})]. \tag{9}$$

If pure selfishness ($p = 0$) is the common strategy, then condition (1) for the disadvantage of altruism follows from equation (8). Likewise, condition (2) for the evolutionary stability of altruism follows from equation (9). More interestingly, a mixed strategy ($0 < \hat{p} < 1$) is a Nash solution of the population game if and only if $\Omega(\hat{p}) = 0$. If $\Omega(\hat{p}) > 0$, then individuals having the strategy of pure altruism ($p = 1$) are at an immediate advantage (in terms of inclusive fitness). If $\Omega(\hat{p}) \leq 0$,

then the strategy of pure selfishness ($p = 0$) is advantageous. If $\Omega(\hat{p}) = 0$, no single individual can gain by having a different strategy.

We further claim that a mixed Nash solution ($0 < \hat{p} < 1$), if it exists, is an ESS if and only if the curve $\Omega(p)$ intersects the p-axis from above at the point where $p = \hat{p}$.

Assume that a small fraction of the population ($\epsilon > 0$) adopts a strategy $y > \hat{p}$. The probability that a random relative will volunteer to help is $p' = (1 - \epsilon)\hat{p} + \epsilon y > \hat{p}$. If $\Omega(p)$ intersects the p-axis at $\hat{p}$ from above, then the inclusive fitness resulting from the altruistic act is $\Omega(p') < \Omega(\hat{p}) = 0$. Thus, helping is disadvantageous, and $\hat{p}$ is more advantageous than y. Likewise, if $y < \hat{p}$, then $p' < \hat{p}$, $\Omega(p') > \Omega(\hat{p}) = 0$, helping is advantageous, and $\hat{p}$ is again more advantageous than y. Hence, $\hat{p}$ is an ESS.

Moreover, using the same argument, one can show that if $\Omega(p)$ does not intersect the p-axis from above (at $\hat{p}$), then $\hat{p}$ is not an ESS.

If we consider assumption C_1 (constant risk for the helper), equation (7) becomes

$$\Omega(p) = -c + r \sum_{k=0}^{n-2} \binom{n-2}{k} p^k (1 - p)^{n-2-k} (b_{k+1} - b_k). \qquad (10)$$

Thus, for the constant-risk additive-benefit model C_1-B_3, we get (not surprisingly)

$$\Omega(p) = -c + rb, \qquad (11)$$

which is either always positive or always negative, depending only on Hamilton's condition. (Indeed, this is a degenerate case of multiple help, since neither the helper's risk nor its gain depends on the number of other helpers.)

If superadditivity of benefit is assumed (model C_1-B_4), then $\Omega(p)$ is an increasing function of p. Hence, depending on the parameters, helping can be either always disadvantageous or always advantageous, or (for a nondegenerate set of parameters) it can be advantageous only if p, the tendency of other individuals to help, is large enough. No mixed ESS can exist in this model. The same results are obtained for the models C_2-B_3 and C_2-B_4. (Note the similarity of these results with those obtained by Cohen and Eshel [1976], who did not use any kin-selection arguments. For a prediction of such a similarity between compatible models of kin selection and group selection, see Matessi and Jayakar 1976.)

We find it more interesting, however, to lose some generality and concentrate on the situation that has originally motivated this work, namely, the model C_1-B_1. In this case, the need for one's help decreases as the number of other helpers increases, but the cost of altruism remains the same. A special case is model C_1-B_2, in which the help of a single helper is sufficient and the advantage of having someone else do the job is obvious.

Under C_1-B_1, equation (6) becomes

$$\Omega(p) = -c + r(1 - v)[1 - p(1 - v)]^{n-2}, \qquad (12)$$

which is a decreasing function of p. We already know from result 3 that in this model only one pure strategy, at most, can be an ESS. If $rv^{n-2}(1 - v) < c <$

$r(1 - v)$, no pure strategy is evolutionarily stable and a single mixed ESS exists, which is the solution of $\Omega(\hat{p}) = 0$, namely,

$$\hat{p} = \{1 - [c/r(1 - v)]^{1/(n-2)}\}/(1 - v). \tag{13}$$

Thus, $\hat{p}$ increases with r and decreases with c and n. Indeed, $\hat{p}$ tends to zero as n approaches infinity, not a surprising finding, since it agrees with both daily experience and documented results in the social sciences.

Less obvious is how the number of potential helpers affects the chances of the individual in need of being saved.

If Hamilton's condition for help between two relatives does not hold (i.e., if $r(1 - v)$ is smaller than c), the ESS is the pure selfish strategy. Hence, the probability of getting help is zero, independent of the number of potential helpers.

If Hamilton's condition holds, we discern between two possibilities. If, on the one hand,

$$n \leq 2 + \ln[c/r(1 - v)]/\ln v \equiv \tilde{n}$$

($\tilde{n}$ is larger than 2, since both v and $c/r(1 - v)$ are less than one), then $rv^{n-2}(1 - v) \geq c$ and $\hat{p} = 1$; hence, the probability of getting efficient help is

$$\Gamma_n = 1 - v^n, \tag{14}$$

which is an increasing function of n.

If, on the other hand, n is greater than $\tilde{n}$, then $\hat{p}$ is given by equation (13) and we get

$$\begin{aligned}\Gamma_n &= \sum_{k=0}^{n-1} (1 - v^k)\binom{n-1}{k} \hat{p}^k(1 - \hat{p})^{n-1-k} \\ &= 1 - [1 - \hat{p}(1 - v)]^{n-1} = 1 - [c/r(1 - v)]^{1+1/(n-2)},\end{aligned} \tag{15}$$

which is a decreasing function of n.

The probability of getting help is, therefore, maximal for some "optimal" group size n^*, which is either $[\tilde{n}]$ or $[\tilde{n}] + 1$. It tends to the positive value $1 - c/r(1 - v)$ as n approaches infinity. For the possible effect of such an argument on the evolution of family (or group) size in nature, the reader is referred to Parker and Hammerstein (1985). Note, however, that in their (quite different) model, the smaller the group size, the larger the chance of getting help. In the present model, the optimal group size, n^*, increases from 2 to infinity as v increases from 0 to 1 or as c decreases from $r(1 - v)$ to 0.

In the special case C_1-B_2, where v equals 0, the condition $rv^{n-2}(1 - v) \geq c$ for pure altruism is never satisfied when n is larger than 2, and Hamilton's condition is then a necessary and a sufficient condition for a mixed strategy. In this case, the probability Γ_n of getting efficient help decreases from 1 when $n = 2$ to $1 - c/r$ as n approaches infinity.

Since risk and gain are frequency-dependent for each helper, a generalized Hamilton's rule can be defined, which considers the *expected* value of $rb - c$. Using this generalized criterion, the mixed ESS, $\hat{p}$, can be obtained by solving the

equation $E(rb - c) = 0$. (This clarifying interpretation was suggested to us by one of the reviewers.)

Consider a diploid population and broods of a fixed size, n. An available sib will volunteer and help its brother in need according to its genetically determined, single-locus strategy.

Let AA be the wild type and let p be the probability that an individual of this type will help its sib in need. Let a be a rare mutation; Aa individuals have probability $y \neq p$ of helping the sib in need.

Note that in the kin-selection models of Cavalli-Sforza and Feldman (1978) and of Uyenoyama and Feldman (1980, 1981), the construction of the fitness functions implicitly assumes a single donor and a single recipient. Here we assume that all sibs in the brood are available when needed. (This assumption is relaxed in the next section.) We also assume that, in each generation, exactly one individual in a brood needs help. (This simplifying assumption is relaxed in the section "Multiple Help with Repetition and the Evolution of Reciprocal-like Altruism.")

We consider the model C_1-B_1, treated in the preceding section. A typical brood consists of AA individuals exclusively. For any one of them (call it I), the probability of being the one in need is $1/n$, and it has a probability $[1 - p(1 - v)]^{n-1}$ of not getting efficient help and therefore dying. If someone else needs help (the probability of that event is $1 - 1/n$), the probability that I will volunteer is p and the probability that I dies in its attempt to help is c. Hence, for any sib in the brood, the probability of dying is

$$1 - \omega_1 = [1 - p(1 - v)]^{n-1}/n + (1 - 1/n)pc. \tag{16}$$

If the frequency $\epsilon > 0$ of allele a is small enough, the viability of a random AA individual is $\omega_1 + o(\epsilon)$. The rare allele a is usually carried (with probability $1 - o(\epsilon)$) by a heterozygote Aa, which is an offspring of a mating of AA and Aa. The probability that Aa will have exactly k Aa brothers (and $n - 1 - k$ AA brothers) is $\binom{n-1}{k} 1/2^{n-1}$. Hence, the probability that an individual of type Aa will die either from a lack of help or in an attempt to help a sib is

$$1 - \omega_2(y) = \sum_{k=0}^{n-1} \binom{n-1}{k} \{[1 - y(1 - v)]^k[1 - p(1 - v)]^{n-1-k}/n$$
$$+ (1 - 1/n)yc\}/2^{n-1} \tag{17}$$
$$= [1 - (y + p)(1 - v)/2]^{n-1}/n + (1 - 1/n)yc.$$

The viability of a random Aa is $\omega_2 + o(\epsilon)$. Natural selection operates for Aa, when it is rare, if $\omega_1 < \omega_2$, and against Aa when $\omega_1 > \omega_2$. But $\omega_2(p) = \omega_1$, and at $y = p$,

$$d\omega_2(y)/dy|_{y=p} = (1 - 1/n) \{(1 - v)[1 - p(1 - v)]^{n-2}/2 - c\} = (1 - 1/n)\Omega(p),$$

where $\Omega(p)$ is defined as in equation (12), and $r = \frac{1}{2}$.

If $\frac{1}{2}(1 - v) < c$, then $\Omega(p) < 0$ for all $0 \le p \le 1$. Hence, $\omega_2(y)$ is a decreasing function of y at $y = p$.

If $\frac{1}{2}v^{n-2}(1 - v) > c$, then $\Omega(p) > 0$ for all $0 \le p \le 1$, and $\omega_2(y)$ increases at $y = p$.

If $\frac{1}{2}v^{n-2}(1 - v) < c < \frac{1}{2}(1 - v)$, then $\Omega(p) < 0$ (and $\omega_2(y)$ decreases at $y = p$) if $p > \hat{p}$; but $\Omega(p) > 0$ ($\omega_2(y)$ increases at $y = p$) if $p < \hat{p}$, where $\hat{p}$ is the ESS defined in equation (13). If $p = \hat{p}$, then $d\omega_2/dy = 0$ at $y = \hat{p}$. But

$$d^2\omega_2/dy^2 = -(1 - 1/n)(n - 2)[(1 - v)/2]^2 [1 - (y + p)(1 - v)/2]^{n-3} < 0 \,.$$

Hence, $\omega_2(y)$ has a global maximum at $y = \hat{p}$; $\omega_2(y) < \omega_2(\hat{p}) = \omega_1$ for all $y \ne \hat{p}$.

If $\omega_2(y)$ decreases at $y = p$, then a mutant with a tendency to help y slightly larger than p is selected against, whereas if y is slightly smaller than p, Aa has a selective advantage. The reverse holds if $\omega_2(y)$ increases at $y = p$. In both cases, natural selection favors mutations that cause their carrier to choose a strategy slightly closer to the ESS. If $p = \hat{p}$, natural selection operates against any mutant with a different strategy.

Result 4: The ESS of the preceding section is 0 if $\frac{1}{2}(1 - v) < c$; 1 if $\frac{1}{2}v^{n-1}(1 - v) > c$; and $\hat{p}$, defined in equation (13), if $\frac{1}{2}v^{n-1}(1 - v) < c < \frac{1}{2}(1 - v)$. This ESS has the property of evolutionary genetic stability (EGS; see Eshel and Feldman 1982; Eshel 1985). It is the only strategy that, when fixed in the population, is immune to any mutation that determines a different tendency to help. Moreover, if the population is fixed on a different strategy, that strategy is always unstable with respect to mutations that determine (at least in a heterozygous form) a strategy slightly closer to EGS.

MULTIPLE HELP WITH A RANDOM NUMBER OF HELPERS: THE ESS MODEL

In the previous sections, we assumed that the number of potential helpers is constant ($n - 1$, where n is the group size). The analysis remains virtually intact if the number of potential helpers changes from one situation to another, provided that each time every potential helper is fully aware of that number. The ESS then determines different helping probabilities for different situations, depending not only on the risk, c, but also on the actual number of potential helpers.

In this section, we consider a situation in which the number of potential helpers (e.g., the number of relatives hearing the cry for help) is a random variable, X. The decision by each of them to provide help or not must be made before any information on X is available to the potential helper.

More specifically, we assume that the group of potential helpers is drawn at random from a larger population of relatives, that each relative has the same chance of being included in that group (not necessarily independently of others), and that the size of the group, X, in each situation is independent of past events.

Let $P(X = n) = \pi_n$ ($n = 0, 1, 2, \ldots$) be the probability that the number of potential helpers is n, and let $\phi(s)$ denote the generating function of X such that

$$\phi(s) = E(s^X) = \sum_{n=0}^{\infty} \pi_n s^n \,.$$

As we have seen, the decision of each potential helper to offer its help or not heavily depends on the number of potential helpers present. In the situation analyzed here, however, the only information available to the decision maker is the probability distribution of the number of potential helpers, X, and the realization of the event E that the decision maker itself belongs to that group. But from the assumption that any individual in the larger population of relatives has the same probability of being included in the random group of potential helpers, it immediately follows that the a priori probability that one belongs to such a group is proportional to the group size n, say, θn. Hence,

$$P(X = n/E) = \theta n P(X = n) \Big/ \sum_{k=0}^{\infty} \theta k P(X = k) = n\pi_n / E(X).$$

The appropriate generating function for the conditional distribution of X, given E, is, therefore,

$$\psi(s) = E(s^X/E) = \sum_{n=1}^{\infty} \frac{n\pi_n s^n}{E(X)} = \frac{s\phi'(s)}{E(X)}.$$

Considering the model C_1-B_1, we already know that if there are exactly n potential helpers including I, the decision maker, the inclusive fitness of the decision maker if it volunteers to help is (eq. 12)

$$\Omega_{n+1}(p) = -c + r(1 - v)[1 - p(1 - v)]^{n-1}.$$

Hence, if an individual volunteers, its unconditional inclusive fitness is

$$\Omega(p) = \sum_{n=1}^{\infty} \Omega_{n+1}(p)P(X = n/E) = -c + \frac{r(1 - v)\phi'[1 - p(1 - v)]}{E(X)}. \quad (18)$$

Since $\phi'(1) = E(X)$, we have

$$\Omega(0) = -c + r(1 - v)$$

and

$$\Omega(1) = -c + r(1 - v)\phi'(v)/E(X).$$

The inclusive fitness $\Omega(p)$ is a decreasing function of p, which means that the higher the willingness of others to help, the less advantageous it is for an individual to volunteer. Consequently, the system maintains one and only one ESS, either pure or mixed.

Result 5: (a) Hamilton's condition that $c < r(1 - v)$ is, in this case, a necessary and sufficient condition for having *some* altruistic behavior (i.e., for having the ESS $\hat{p} > 0$).

(b) The condition for pure altruism is always strictly stronger than Hamilton's condition, namely, $c < r(1 - v)\phi'(v)/E(X)$.

(c) If $r(1 - v)\phi'(v)/E(X) < c < r(1 - v)$, then the (unique) ESS, $\hat{p}$, is mixed. This ESS is the solution of

$$\phi'[1 - \hat{p}(1 - v)] = c E(X)/r(1 - v). \quad (19)$$

If the number of available helpers is a random variable, pure altruism can be maintained even under the assumption that $v = 0$ (provided that c is small enough); this is not the case when the number of available helpers ($n > 2$) is fixed.

An example of the ESS model for multiple help with a random number of helpers is the situation in which the number of available helpers has a Poisson distribution. Assume that $\pi_n = e^{-\lambda} \lambda^n/n!$. This corresponds to a very large group of relatives (e.g., a tribe) that move around such that each of them has a small chance of being available when needed, independently of others. (Here, λ is the expected number of available helpers.)

In this case,

$$\phi(s) = e^{\lambda(s-1)},$$

$$\phi'(s) = \lambda e^{\lambda(s-1)}, \tag{20}$$

$$\Omega(p) = -c + r(1 - v)e^{-\lambda p(1-v)}.$$

The condition for full altruism is

$$c < r(1 - v)\phi'(v)/E(X) = r(1 - v)e^{-\lambda(1-v)}. \tag{21}$$

If λ approaches infinity (i.e., the population of relatives is dense), the right-hand side of equation (21) tends to zero and the condition for full altruism is never satisfied. If, however, λ approaches zero (i.e., the population of relatives is sparse), equation (21) tends to coincide with Hamilton's condition.

The ESS is mixed if $r(1 - v)e^{-\lambda(1-v)} < c < r(1 - v)$, and it is then

$$\hat{p} = [1/\lambda(1 - v)] \ln[r(1 - v)/c]. \tag{22}$$

The probability in this case that an individual in need will get help is

$$\Gamma = \sum_{n=0}^{\infty} \pi_n \{1 - [1 - \hat{p}(1 - v)]^n\} = 1 - e^{-\lambda\hat{p}(1-v)}$$
$$= 1 - c/r(1 - v), \tag{23}$$

which is independent of λ.

Result 6: Let Hamilton's criterion for altruism, $c < r(1 - v)$, hold, and let the number of available helpers be distributed as a Poisson random variable with expectation λ.

(a) Then the evolutionarily stable probability of altruism ($\hat{p}$) is always positive.

(b) If the relatives' population is sparse enough (i.e., if $\lambda < \ln[r(1 - v)/c]/(1 - v) \equiv \lambda^*$), full altruism is the only ESS in the population. In this case, the probability that an individual in need receives help is

$$\Gamma_\lambda = 1 - e^{-\lambda(1-v)},$$

which is an increasing function of λ. This result is identical to that obtained by Boorman and Levitt (1980) in their "one-one" combinatorial model.

(c) If the relatives' population is dense (i.e., if $\lambda > \lambda^*$), the ESS is mixed. It is a decreasing function of λ, tending to zero as λ approaches infinity.

Quite surprisingly, however, in this case the probability that an individual in need will get help does not change with λ. This result differs from that obtained for a fixed number of potential helpers in the above "Analysis of the Evolutionarily Stable Strategy." In that case, the probability of getting help is a decreasing function of the number of potential helpers (which, as it increases, tends to a limit that is exactly Γ of eq. 23).

MULTIPLE HELP WITH A RANDOM NUMBER OF HELPERS: A SIMPLE GENETIC MODEL

Assume a diploid population divided into large groups (each of size $N + 1$) of relatives. Let r be the degree of relatedness between any two individuals in a group, and assume that mating is random between individuals belonging to different groups. Suppose that in each generation exactly one individual in each group needs help. Let ρ ($\rho \ll 1$) be the probability that any other individual in the group is available when needed. Thus, the number of available helpers is, approximately, Poisson-distributed with $\lambda = N\rho$. We consider model C_1-B_1 and assume that λ is not smaller than λ^* of the preceding section.

We further assume that the tendency to help is genetically determined by a single locus, which has a common allele A and a rare mutation a (at a small but positive frequency, $\epsilon > 0$). Let p be the probability that an available AA individual will help its relative in need, and let $y \neq p$ be that strategy for Aa.

A random AA individual has relatives of type AA with probability $1 - o(\epsilon)$. If this individual is the one who needs help (the probability of that event is $1/[N + 1]$), then its probability of not getting efficient help and dying is

$$\sum_{n=0}^{\infty} e^{-\lambda}\lambda^n [1 - p(1 - v)]^n/n! + o(\epsilon) = e^{-\lambda p(1-v)} + o(\epsilon).$$

The probability that this individual will lose its life while helping a relative in need is ρpc. Hence, the death probability of AA is

$$1 - \omega_1 = e^{-\lambda p(1-v)}/(N + 1) + [1 - 1/(N + 1)]\, \rho pc + o(\epsilon)$$

$$= (e^{-\lambda p(1-v)} + \lambda pc)/(N + 1) + o(\epsilon).$$

A random Aa individual comes from a group in which the proportion of AA's is, approximately, $1 - r$ and the proportion of Aa's is r. (Here we used both the assumption of random mating and the assumption of large groups of r relatives.) If Aa needs help, it will die because of lack of help with probability

$$\exp\{-\lambda(1 - v)[ry + (1 - r)p]\} + o(\epsilon).$$

The total death probability of Aa is

$$1 - \omega_2(y) = e^{-\lambda(1-v)[ry+(1-r)p]}/(N + 1) + [1 - 1/(N + 1)]\, \rho yc + o(\epsilon)$$

$$= (e^{-\lambda(1-v)[ry+(1-r)p]} + \lambda yc)/(N + 1) + o(\epsilon).$$

Natural selection operates for (against) allele a, when rare, if $\omega_2 > \omega_1$ ($\omega_2 < \omega_1$).

Employing analysis similar to that for sib-sib multiple help, we arrive at the following result.

Result 7: The ESS probability $\hat{p}$, defined in equation (22), has the property of evolutionary genetic stability (see result 4).

MULTIPLE HELP WITH REPETITION AND THE EVOLUTION
OF RECIPROCAL-LIKE ALTRUISM

Trivers (1971) was the first to suggest that reciprocation provided the basis for the evolution of altruism. If encounters are frequent enough, then helping an individual in trouble may be advantageous to the donor in the long run, provided that the recipient tends to repay kindness in kind once its help is needed. The possibility of future encounters can also increase the level of mutual help established between relatives to a higher degree than expected because of their respective relatedness (Eshel and Cohen 1976; Eshel and Motro 1981). This higher level of mutual help does not require the existence of gratitude or even of memory; it is a direct consequence of kin selection itself. If some amount of help is expected, following simple tenets of kin selection, from individual A toward B, then (by the same argument) the same amount of help is expected from B toward A. Thus, for A, the death of B means not only the direct loss of their common genes, but also the loss of any future help from B. Analysis of mutual help between two individuals has shown (Eshel and Motro 1981) that a high degree of mutual help may be established between distantly related (and, sometimes, even unrelated) individuals when interactions are frequent.

In this section, we consider the possibility that the situation in which an individual needs help may happen again in the future (not necessarily with the same players), and we see how this possibility affects the ESS of multiple help.

We restrict our analysis to a situation in which the members of a large group of relatives move around, such that each of them has a small chance of being available when needed. Hence, the number of potential helpers has approximately a Poisson distribution. We consider the model C_1-B_2. (Treatment of the more general model C_1-B_1 is technically more complicated, and no qualitatively new results are obtained by that generalization.)

Assume now that for each individual in the population there is a small probability α that it will be the next one to need help (in a similar future situation). The death of a relative in the present situation entails a small decrease in the expected number of potential helpers in the future, from $\rho N = \lambda$ to $\rho(N - 1) = \lambda - \rho$ (using the same notation as in the preceding section). Consequently, if p, the tendency in the population to help a relative, is $0 \le p \le 1$, the death of a relative increases the death probability of an individual in need from $\exp(-\lambda p)$ to $\exp[-(\lambda-\rho)p]$. The probability that an individual will die in helping any of its relatives in the future remains $\alpha \rho p c$. Hence, the probability of death while helping in a future situation decreases, with the death of the individual in need at the present situation, from $N\alpha\rho pc$ to $(N - 1)\alpha\rho pc$. Thus, with the death of the relative in need, the probability of death for each of the N remaining individuals increases by

$$\alpha(e^{-(\lambda-\rho)p} - e^{-\lambda p}) - [\alpha\lambda pc - \alpha(\lambda - \rho)pc] \approx \alpha\rho p(e^{-\lambda p} - c).$$

The total loss to I (in terms of inclusive fitness) as a result of its relative death is

$$\beta = r + [1 + r(N - 1)]\alpha\rho p(e^{-\lambda p} - c).$$

The total loss to I (in terms of inclusive fitness) due to its own death is

$$\gamma = 1 + rN\alpha\rho p(e^{-\lambda p} - c).$$

Under the assumption C_1-B_2, if I volunteers to help, the survival probability of the individual in need increases from $1 - e^{-(\lambda - \rho)p}$ to 1, while I has a probability c of losing its life in that act. Hence, the inclusive fitness of I, if it volunteers, is

$$
\begin{aligned}
\Omega_\alpha(p) &= e^{-(\lambda - \rho)p}\, \beta - c\gamma \approx e^{-\lambda p}\, \beta - c\gamma \\
&= -c + re^{-\lambda p} + \alpha\rho p(e^{-\lambda p} - c)[(1 - r)e^{-\lambda p} + rN(e^{-\lambda p} - c)].
\end{aligned}
\tag{24}
$$

As an immediate result, Hamilton's condition for the stability of $p = 0$ (full selfishness) remains unchanged; $r < c$. (Indeed, if nobody helps, there is no point in saving someone else's life in the hope that that individual will save your life or your relative's life in the future.)

If, however, a mixed ESS, p_α, exists (where $0 < p_\alpha < 1$), then $\Omega_\alpha(p_\alpha) = 0$ and $\partial\Omega_\alpha(p)/\partial p|_{p = p_\alpha} < 0$ (see "Analysis of the ESS"). From equation (24) it is clear that if $\Omega_\alpha(p) = 0$, then $\exp(-\lambda p) - c > 0$ (and $r\exp(-\lambda p) - c < 0$). Hence, by using the implicit-function theorem, we get $dp_\alpha/d\alpha > 0$.

Result 8: If not zero, the evolutionarily stable probability of altruism is an increasing function of α, the probability of a need for help in the future.

Our analysis of mutual help with repetition between two individuals (Eshel and Motro 1981) indicated the possibility of more than one ESS, with each ESS established at a different level of altruism. In the case of multiple help with repetition, this possibility also exists. Moreover, even in the sub-Hamiltonian situation $r < c$, a positive ESS can be maintained in addition to the ESS of pure selfishness (which always exists in the sub-Hamiltonian case). To show this, choose any positive value of p_0, keep the parameters r, c, ρ, and α fixed (provided that $r > 0$), and let λ approach infinity. From equation (24) we get

$$\lim_{\lambda \to \infty} (1/\lambda)\Omega_\alpha(p_0) = \alpha p_0 rc^2 > 0.$$

Hence, for sufficiently large λ, $\Omega_\alpha(p_0)$ is greater than zero. Thus, either $\Omega_\alpha(p)$ intersects the p-axis from above at some point p_1 ($p_0 < p_1 \leq 1$) or $\Omega_\alpha(p)$ is greater than zero for all $p_0 \leq p \leq 1$. In the first case, p_1 is a positive ESS, whereas $p = 1$ is an ESS in the second case. In both cases, if $r < c$, $p = 0$ is also an ESS.

The possibility of more than one ESS distinguishes the case of multiple help with repetition from the case without repetition. In the latter case, $\Omega(p)$ is a decreasing function of p, which entails the existence of only a single ESS.

A case of special interest is that of mutual help among nonrelatives. Putting $r = 0$ in equation (24) yields

$$\Omega_\alpha(p) = -c + \alpha\rho p e^{-\lambda p} (e^{-\lambda p} - c) \tag{25}$$

and

$$\Omega_\alpha(0) = -c < 0;$$

absolute selfishness is, indeed, stable. Yet, for a sufficiently small (but positive) value of c,

$$\Omega_\alpha(1) = -c + \alpha\rho e^{-\lambda} (e^{-\lambda} - c) > 0.$$

Hence, full altruism can also be an ESS.

If $c < \exp(-\lambda)$, then $\Omega'_\alpha(1) < 0$ and $\Omega_\alpha(1) > \Omega_\alpha(0)$. Thus, there exists $\bar{p}$ $(0 < \bar{p} < 1)$ for which $\Omega_\alpha(p)$ obtains its maximal value. By choosing c small enough (but not too small), we can get $\Omega_\alpha(\bar{p}) > 0$ and $\Omega_\alpha(1) < 0$. Hence, there is a value $\hat{p}$ $(\bar{p} < \hat{p} < 1)$ for which $\Omega_\alpha(p)$ intersects the p-axis from above. Thus, $\hat{p}$ is a mixed ESS. Using the implicit-function theorem, we get that $\hat{p}$ is an increasing function of α and ρ and a decreasing function of c and λ.

Result 9: The evolutionarily stable probability of altruism within a group of nonrelatives is an increasing function of α, the probability of future need, and of ρ, the probability that a group member will be available when needed. As expected, the ESS is a decreasing function of the risk, c, but, quite interestingly, it is also a decreasing function of λ, the parameter that reflects the intensity of meetings within the group. Since λ equals $N\rho$, the ESS is indeed a decreasing function of group size; but however big the group is, altruism can be maintained, provided that c is small enough.

DISCUSSION

The possibility that an individual in trouble can be saved by each of *several* relatives has long been considered a criticism of Hamilton's theory of kin selection. The criticism arises because if Hamilton's condition for altruism between two relatives is fulfilled, any potential helper can always benefit from leaving the risky task of saving the individual in need to any of its other relatives. Hence, since desertion is advantageous, it seems that selfish behavior will always prevail in such situations.

As shown in this paper, the weakness of this argument lies in its ignoring the possibility of mixed strategies. Indeed, if Hamilton's condition for altruism between two relatives is not satisfied, full selfishness is also the only evolutionarily stable strategy for the case of more than one potential helper. However, the fulfillment of Hamilton's condition in the one-to-one situation implies, in the multiple-help case, the evolutionary stability of a mixed strategy of altruism and selfishness, that is, of a strategy by which help is provided only with a certain positive probability.

As expected, the evolutionarily stable probability of altruism increases with the degree of relatedness, it decreases as a function of the risk involved in providing the necessary help, and it also decreases as a function of the number of potential helpers (it tends to zero as the number of potential helpers tends to infinity). If Hamilton's condition holds and if the population is fixed on the ESS, the probability that the individual in need will be saved is maximal for a certain group size. Unlike the evolutionarily stable probability of providing help, the probability of getting help does not tend to zero as the number of potential helpers tends to infinity.

If a situation in which an individual needs help can be repeated in the future (in such a way that each group member has the same small chance of being the next one to need help), the evolutionarily stable probability of altruism increases as the chance of future repetition increases. In this case, a positive evolutionarily stable probability of altruism can exist even among nonrelatives. The existence of mutual help in a group of nonrelatives requires neither any tendency for gratitude among group members nor any memory or ability to distinguish between group members (though they must recognize a group member as such). Note, however, that if Hamilton's condition for one-to-one altruism does not hold, then even if some positive probability of altruism is evolutionarily stable, full selfishness is always stable. One must still consider how (and whether) a population (or a group) can evolve from the selfish evolutionarily stable state into the (at least partly) altruistic state (see, e.g., Axelrod and Hamilton 1981).

SUMMARY

In situations involving a single relative in distress and several potential helpers, the advantage of leaving the risky job of aiding the relative in need to any of the other potential helpers is quite obvious. Hence, even if Hamilton's condition for altruism in the one-to-one situation is satisfied, it might seem that altruistic behavior would not evolve if there is more than one potential helper.

In this paper we investigate the evolutionarily stable strategy (ESS) of helping behavior in situations involving several potential helpers and a necessarily instantaneous response. The main result is that if Hamilton's condition is met, the ESS is usually a *mixed* strategy of altruism and selfishness, with a decreasing (yet positive) probability of helping as the number of potential helpers increases.

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