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ALTRUISM IN MENDELIAN POPULATIONS DERIVED FROM SIBLING GROUPS: THE HAYSTACK MODEL REVISITED

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Abstract.—A group-selection model is presented in which each group is initiated by a single fertilized female and persists for several generations before dispersal. Maynard Smith (1964) concluded that altruism could not plausibly evolve under these circumstances. I show that his conclusion is an artifact of a simplifying assumption that amounts to a worst-case scenario for group selection. When the standard donor-recipient equations for altruistic behavior are used in Maynard Smith's model, Mendelian populations derived from sibling groups are often more favorable for the evolution of altruism than are the sibling groups themselves. In general, long-term and large-scale aspects of population structure may at times be important in the evolution of altruistic and other group-advantageous behaviors.

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The early 1960's marked two important events in evolutionary biology. One was the publication of W. D. Hamilton's inclusive-fitness theory (Hamilton, 1963, 1964*a*, 1964*b*; relabelled kin selection by Maynard Smith [1964]), which predicted the evolution of altruistic behavior among genetically related individuals. The second was the publication of V. C. Wynne-Edwards's (1962) *Animal Dispersion in Relation to Social Behavior,* which claimed that altruistic population regulation is common in nature and that it evolves by the process of group selection. Wynne-Edwards's argument was based mostly on a review of possible examples and did not include an explicit model of the group selection process.

The case for group selection was so overstated and rested on such a weak theoretical foundation that it seemed important to distinguish it from the better specified and more limited process of kin selection. For this purpose, Maynard Smith (1964) built a group-selection model in which an imaginary mouse species lives within haystacks. Each haystack is colonized by a single fertilized female, and the population within each haystack grows for an unspecified number of generations, after which all individuals disperse to colonize a new set of haystacks. Two alleles, which code for altruistic and selfish behavior, exist at a single locus. The altruistic allele declines in frequency within each haystack but also increases the number of mice from that haystack that enter the pool of dispersers. Thus, the allele is opposed by individual selection and favored by group selection. Maynard Smith concluded that the haystack model cannot plausibly explain the evolution of altruism, and that altruism in nature is probably restricted to close relatives, as predicted by Hamilton's theory.

In recent years the perceived relationship between kin selection and group selection has substantially changed (Michod, 1980, 1982; Uyenoyama and Feldman, 1980; Wade, 1979, 1980; Wilson, 1977, 1980, 1983). Kin selection is seen not as a separate mechanism for the evolution of altruism but, rather, as a group-selection process itself. Exactly as in the haystack model, the altruistic allele is selected against within each kin group but also increases the contribution of that kin group to the global population. The evolution of altruism by kin selection requires the differential productivity of kin groups.

If kin selection is itself a group-selection process, then why does the haystack model appear to be so ineffective? Since each group is founded by a single fertilized female, interactions are exclusively among siblings during the first generation. If dispersal occurred at this stage the haystack model would be identical to kin selection among siblings. It is tempting to conclude that the haystack model works poorly because sibling groups do not disperse but, instead, grow into Mendelian populations. Maynard Smith's conclusions could then be revised to state that group selection becomes weak when several

generations are spent within groups between dispersal episodes.

A close look at the haystack model reveals, however, that this conclusion is unjustified. To test the effect of group duration it would be necessary first to specify fitness functions, and then to follow the consequences of those fitness functions for group and individual selection as the number of generations spent within groups is increased. Maynard Smith did not do this but, instead, made a simplifying assumption that amounts to a worst-case scenario for group selection. He assumed that, for all groups that are polymorphic at colonization, the selfish allele drives the altruistic allele extinct before dispersal. Individual selection is as strong as it can possibly be, and the altruistic allele survives only in groups initiated by a homozygous female carrying the sperm of a homozygous male.

The evolution of altruism in Mendelian populations derived from sibling groups is therefore a surprisingly neglected topic. It has been explored thoroughly only for biased sex ratios, which, under some circumstances, qualify as altruistic traits. For this specific adaptation, group selection can exert a strong effect even when ten generations are spent within groups between dispersal episodes (Wilson and Colwell, 1981; Bulmer and Taylor, 1980; Charnov, 1982). The altruistic allele is continuously selected against within groups, but the differential productivity of groups also increases. Thus, the opposing forces of group and individual selection both intensify, and the equilibrium is only slightly altered.

The results for sex ratios suggest that Maynard Smith's general conclusions may be seriously in error. In this paper, I reanalyze the haystack model, using the additive fitness functions employed by most kin-selection models. The results confirm that, as with sex ratio, altruistic behaviors can evolve among individuals that are unrelated in terms of immediate parents but closely related through an initial colonist.

The Model

Evolution within Single Groups.—Consider a single locus with an allele (A) that codes for altruism and an alternate allele (a) that codes for selfishness. Let C = the clutch size of each female in the absence of altruistic behavior. Altruists increase the fitness of a single recipient chosen at random from their group, with a decrement to their own fitness. Let b = benefit to recipient of AA genotype's behavior, c = cost to AA genotype, hb = benefit to the recipient of Aa genotype's behavior, hc = cost to Aa genotype ($0 < h < 1$), N = size of a single group, p = frequency of the A allele in the group, and t, u, v = frequencies of the AA, Aa, and aa genotypes in the group, respectively. Absolute fitnesses can then be specified as follows:

$$W_{AA} = C - c + \frac{b(Nt - 1) + hb(Nu)}{N - 1} \quad (1)$$

$$W_{Aa} = C - hc + \frac{b(Nt) + hb(Nu - 1)}{N - 1} \quad (2)$$

$$W_{aa} = C + \frac{b(Nt) + hb(Nu)}{N - 1}. \quad (3)$$

Each altruist suffers the cost of its behavior (c for AA and hc for Aa genotypes). In addition, each altruist is a potential recipient for the other altruists, who distribute benefits among $N - 1$ group members (excluding themselves). By contrast, nonaltruists have the dual advantage of no cost and a slightly higher expectation of receiving benefits, since they serve as recipients to all altruists in the group. The dual advantage of selfishness is rarely stressed in the literature, but it is important in what follows.

When b and c are positive, the fitnesses of the genotypes are ranked $W_{aa} > W_{Aa} > W_{AA}$. The altruistic behavior always declines in frequency within single groups. On the other hand, the altruistic behavior increases the size of the group (and therefore the fitness of the average individual within the group) whenever $b > c$.

Equations (1–3) are the standard additive fitness functions for modelling altruistic behavior; they are used here to facilitate comparison with the well known criterion for the evolution of altruism among siblings. When applied over several generations, however, they cause the groups to grow ex-

ponentially. To explore the evolution of altruism in groups that reach a carrying capacity, one version of the model employs the following fitness functions.

$$W_{AA} = \left[1 + I\left(1 - \frac{N}{K(1 + xp)}\right)\right](1 - 2s) \quad (4)$$

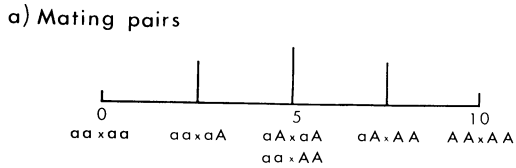
$$W_{Aa} = \left[1 + I\left(1 - \frac{N}{K(1 + xp)}\right)\right](1 - s) \quad (5)$$

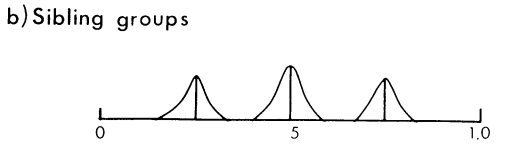
$$W_{aa} = \left[1 + I\left(1 - \frac{N}{K(1 + xp)}\right)\right]. \quad (6)$$

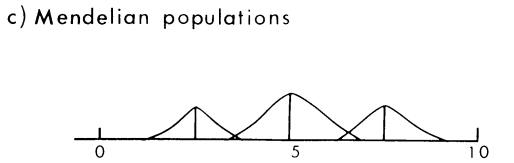
Here, I is the rate of increase in the absence of density dependence, and K is the carrying capacity in the absence of altruistic behavior. The altruistic allele increases the size of the group at equilibrium by a factor $(1 + xp)$, but is nevertheless selected against by the factor $(1 - s)$ in heterozygotes and $(1 - 2s)$ in homozygotes. These fitness functions are close to those used by Maynard Smith (1964) and Wright (1945).

Population Structure.—The formation of groups was modelled by Monte Carlo simulation and is represented pictorially in Figure 1. An initial global allele frequency (P) is first specified ($P = 0.5$ for this example), from which global genotype frequencies are calculated. Genotypes can be thought of as groups of two alleles with $p = 0$, 0.5, or 1. At Hardy-Weinberg equilibrium the groups are randomly drawn from a large gamete pool.

Individuals throughout the global population mate randomly to form six pair types ($AA \times AA$, $AA \times Aa$, $AA \times aa$, $Aa \times Aa$, $Aa \times aa$, and $aa \times aa$) in easily calculated proportions. These may be thought of as groups of four alleles with $p = 0$, 0.25, 0.50, 0.75, and 1, as shown in Figure 1a. Each female then has a clutch of C offspring, who interact only among themselves. Sibling groups from $AA \times AA$, $AA \times aa$, and $aa \times aa$ matings have only one genotype and, therefore, only one allele frequency. The others contain a mix of genotypes, randomly drawn from large gamete pools. For example, $Aa \times aa$ matings produce sibling groups with an average of $t = 0$, $u = 0.5$, $v = 0.5$, and a variance in the frequency of altruists of $\sigma_u^2 = 0.25/C$. Sampling error therefore causes three bell-shaped curves to develop, as shown in Figure 1b.







d) Selection

Group	1	2	3	4	5
p	0	.25	.50	.75	1.0
p′	0	.196	.459	.736	1.0
Δp	0	-.054	-.041	-.014	0
N	1000	1000	1000	1000	1000
N′	2000	2306	2525	2656	2700
ΔN	1000	1306	1525	1656	1700

FIG. 1. Graphical representation of the haystack model. The x axis is the frequency of the A allele in a local population (p), and the y axis is the proportion of local populations that exist at a given value of p. a) The distribution of mated pairs, which can be regarded as groups of four alleles; b) the distribution of sibling groups derived from the mated pairs; c) the distribution of Mendelian populations derived from the sibling groups; d) calculation of changes in frequency (p) and density (N) for five local groups.

If selection acts within each group at this point, followed by dispersal back into the global pool, then the simulation is identical to the family-structured models of kin selection reviewed by Michod (1982). Alternatively, the sibling groups can persist to grow into Mendelian populations, which has two effects in the absence of selection. First, genotype frequencies reach Hardy-Weinberg equilibrium within each group. Second, since reproduction involves sampling from a large gamete pool, the variance in p among groups increases with every generation, although the effect becomes small at large group sizes. The greater variance

among groups caused by reproduction is represented in Figure 1c.

Selection within groups is modelled in two ways; 1) altruism expressed every generation and 2) altruism expressed once, after the sibling groups have grown into Mendelian populations. The latter case is biologically plausible for altruistic responses to high density, for example. A single round of selection for five representative groups is shown in Figure 1d. Equations (1–3) are used as fitness functions with $C = 2$, $c = 0.5$, $b = 1.2$, $N = 1{,}000$, and genotypes in Hardy-Weinberg equilibrium. The altruistic allele is selected against in all polymorphic groups (Δp negative), but the density of groups after selection correlates positively with p (compare ΔN with p).

All individuals disperse after the last round of selection. To calculate global allele frequencies, the frequency within each group must be weighted by the size of the group. When this calculation is made for the five groups in Figure 1d, the global allele frequency after selection is $P = 0.514$. Group selection overwhelms individual selection.

Most versions of the model were run with $T = 50{,}000$ groups and initial P values of 0.05 to 0.95 in increments of 0.05. Change in P was then calculated for a single cycle of group formation, growth, selection, and dispersal. The range of initial P values allowed internal equilibria to be discerned. For example, if ΔP is negative for $P = 0.05$ to 0.20, positive for $P = 0.25$ to 0.80, and negative for $P = 0.85$ to 0.95, there is an unstable equilibrium between 0.20 and 0.25, and there is a stable equilibrium between 0.80 and 0.85. Version 6 of the model (see below) explores a population structure that requires several cycles of group formation and dispersal to establish itself. This version was run with $T = 5{,}000$ groups and initial global P values of 0.05, 0.5, and 0.95. Change in P was then followed for 50 successive dispersal episodes.

Because group and individual selection are influenced by numerous factors in the haystack model, the simulation results are presented in a stepwise fashion. Kin selection with interactions among siblings (version 1) serves as the baseline against which other versions will be compared. The other versions are 2) sib groups grow into Mendelian populations prior to dispersal, 3) genetic drift after the formation of sib groups, 4) selection acting every generation, 5) local population regulation, 6) mating within groups prior to dispersal and buildup of variance occurring over several cycles of group formation, and 7) interactions among siblings within local groups. It is important to emphasize that a given version is designed to explore the effect of a single factor and, therefore, may ignore other factors that operate in any real-world structured population. For example, one effect of the haystack model is to increase the frequency of homozygotes in the global population, but this factor is not included until version 6.

It is clear from Figure 1 that group selection is enhanced by any process that increases the variance in allele frequency among groups. Kin selection is itself such a process; groups of size C vary more when initiated by two individuals than when initiated by C individuals arriving independently. Another process is assortative mating; groups of size C vary more when initiated by two individuals of the same genotype than when the pair is chosen at random. As we shall see, these sources of variation persist when the sibling groups grow into Mendelian populations, and a variety of additional sources come into play.

Results

Version 1: Kin Selection.—Interaction among siblings followed by dispersal serves as a baseline against which other versions of the model can be compared. At P near zero, virtually all altruists exist in sibling groups derived from $Aa \times aa$ matings, for which $p = 0.25$, $t = 0$, $u = 0.5$, $v = 0.5$, and the variance in the frequency of altruists among groups is $0.25/C$. Momentarily assume that C is very large; the variance term can then be ignored, as can the effect of altruists removing themselves in the calculation of benefits. Approximations of Equations (2) and (3) then become

$$W_{Aa} = C - hc + hbu \quad (7)$$

$$W_{aa} = C + hbu. \quad (8)$$

Altruists always have a lower fitness than nonaltruists from the same group; however, at P near zero, virtually all nonaltruists exist in sibling groups derived from $aa \times aa$ mat-

ings, for which $t = u = 0$ and $W_{aa} = C$. Thus, the A allele increases in frequency throughout the global population when $C - hc + 0.5hb > C$, which works out to $b/c > 2$. The recipient's gain must be greater than twice the altruist's cost. This is identical to Hamilton's (1963, 1964*a*) celebrated result, which he obtained with his inclusive-fitness approach. The same result holds for P near 1. Thus, the evolution of altruism appears to be independent both of global allele frequency and the degree of dominance (Michod, 1982).

Small clutch sizes (C) have two opposing effects on the evolution of altruism. Since altruists cannot serve as recipients for their own behavior, the effect of subtracting a single altruist in the calculation of benefits for the AA and Aa genotypes can be significant for small C [see Equations (1) and (2), with $N = C$). Thus, small clutch sizes intensify selection against altruists within groups. On the other hand, small clutch sizes increase the variance in allele frequency among groups at the stage depicted in Figure 1b, thus promoting the evolution of altruism. The opposing effects of group and individual selection for P near zero can be compared using the subjective frequency approach outlined in Wilson (1977, 1980). Even though the average frequency of altruists in sib groups derived from $Aa \times aa$ matings is $u = 0.5$, the average altruist experiences a frequency of $0.5 + \sigma_u^2/0.5$ (including itself). Inserting this "subjective frequency" into Equation (2) with $\sigma_u^2 = 0.25/C$ and $N = C$, we obtain:

$$W_{Aa} = C - hc + hb\left[\frac{C\left(0.5 + \frac{0.5}{C}\right) - 1}{C - 1}\right] = C + h(0.5b - c). \quad (9)$$

Altruists have a higher fitness than selfish individuals from $aa \times aa$ matings whenever $b/c > 2$. Thus, Hamilton's result is independent of sibling-group size, but only because C has two effects on the evolution of altruism that exactly cancel.

Version 2: Multiple Generations within Groups, Altruism Expressed Once, No Sampling Error after the Formation of Sibling Groups.—Now suppose that the sibling groups grow into large Mendelian populations, after which the altruistic behavior is expressed once, followed by dispersal. Momentarily ignore the stage shown in Figure 1c by assuming that no sampling error occurs after the formation of sibling groups; the allele frequency of a large population before selection is identical to the allele frequency of the sibling group from which it was derived.

As for version 1, at P near zero we must calculate the fitness of A alleles from populations derived from $Aa \times aa$ matings. Unlike sibling groups, however, the populations are in Hardy-Weinberg equilibrium with all three genotypes present. Again assume that initial clutch size (C) is very large, so that all populations derived from $Aa \times aa$ matings have allele frequencies of $p = 0.25$. The fitnesses of AA and Aa genotypes are then approximately

$$W_{AA} = C - c + b(0.0625 + 0.375h) \quad (10)$$

$$W_{Aa} = C - hc + b(0.0625 + 0.375h). \quad (11)$$

Twenty-five percent of the A alleles exist as homozygotes, and the rest are heterozygotes. Weighting Equations (10) and (11) accordingly and comparing them with the fitness of a alleles derived from $aa \times aa$ matings, we obtain the following conditions for the initial spread of the altruistic behavior.

$$\frac{b}{c} > \frac{0.25 - 0.75h}{0.6255 + 0.375h}. \quad (12)$$

In sibling groups derived from $Aa \times aa$ matings, half the individuals are phenotypically altruistic despite the fact that $p = 0.25$. In Mendelian populations derived from the sibling groups, the phenotypic expression of altruism depends on the degree of dominance (h). When $h = 1$, altruistic phenotypes exist at a frequency of $p^2 + 2pq = 0.4375$, and the behavior evolves when $b/c > 2.29$. The frequency of altruists is slightly lower than for sibling groups, and the evolution of altruism requires a slightly higher ratio of benefit to cost. When $h = 0$, only $p^2 = 0.0625$ of the phenotypes are altruistic, and the behavior evolves only when $b/c > 4.00$. Dominance becomes a critical variable for the evolution of altruism.

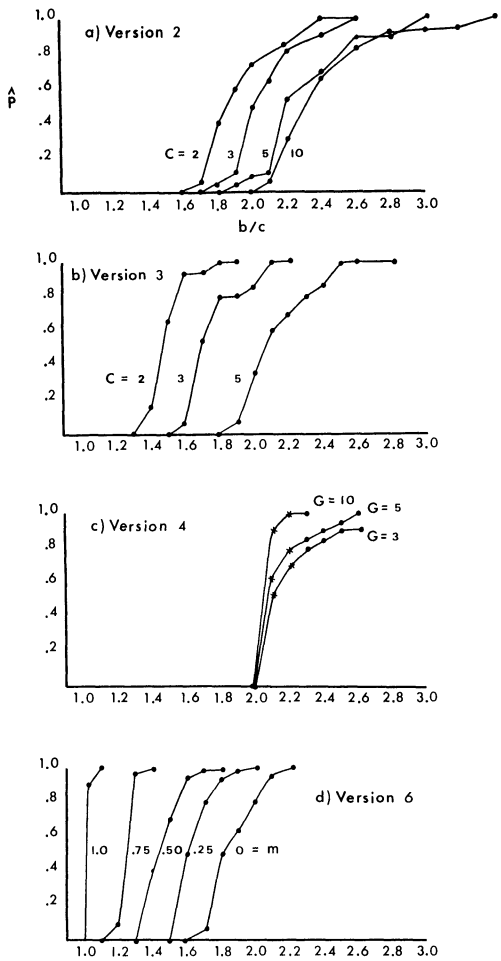


FIG. 2. Results of Monte Carlo simulations. The x axis (b/c) is the ratio of recipient's benefit to donor's cost. The y axis ($\hat{P}$) is the frequency of the altruistic allele at equilibrium in the global population. Asterisks indicate the presence of unstable equilibria (not shown), in addition to the stable equilibria that are shown. C = clutch size, G = number of generations spent within the group, m = the proportion of within-group mating prior to dispersal.

At P near 1 the a allele exists as aa and Aa genotypes in populations derived from $AA \times Aa$ matings, which must be compared with the fitness of A alleles in populations derived from $AA \times AA$ matings. The altrustic behavior spreads to fixation when

$$\frac{b}{c} > \frac{1 - 0.75h}{0.4375 + 0.375h}. \qquad (13)$$

When $h = 1$ the selfish a allele enjoys a frequency of $p^2 + 2pq = 0.9375$ altruistic phenotypes and can invade, unless $b/c > 4.00$. When $h = 0$ the a allele still enjoys a frequency of $p^2 = 0.5625$ altruists and can invade, unless $b/c > 2.29$. In both cases, the frequency of altruists is higher than for sibling groups derived from $AA \times Aa$ matings, and conditions for the fixation of altruism are correspondingly more stringent. Notice that for $h = 1$, altruistic behaviors that fall within the range of $b/c = 2.29$ to 4.00 will be maintained as protected polymorphisms in the population. The evolution of altruism has become frequency dependent.

The effect of clutch size is difficult to treat analytically, but the qualitative trends are straightforward. Small clutch sizes increase the variance in p among sib groups (σ_p^2). For $P = 0.5$, $\sigma_p^2 = 0.0936$ when $C = 2$ and 0.0691 when $C = 10$. This effect persists as the sib groups grow into Mendelian populations. Small clutch sizes also cause selfish siblings to receive a disproportionate share of the benefits, as previously mentioned. This effect diminishes as the sib groups grow into Mendelian populations, because the effect of subtracting a single altruist in the calculation of benefits becomes negligible for large values of N. Thus, group selection is unopposed by individual selection, and we expect small clutch sizes to favor the evolution of altruism. This expectation is confirmed by the Monte Carlo simulations, as shown in Figure 2a for $h = 1$ and $N = 1{,}000$. For small values of C and P, large populations are actually more favorable for the evolution of altruism than are the sibling groups from which they were derived.

To summarize, version 2 differs from version 1 in only two respects: $N \gg C$ and the genotypes are in Hardy-Weinberg equilibrium. These two differences are profound, however, and cause the evolution of altruism to be influenced by global allele frequency (P), the size of the initial sibling group (C), and the degree of dominance (h). Conditions for the evolution of altruism are usually more stringent than in the case of sibling groups, but for certain parameter values they are less so.

Version 3: Genetic Drift after the Formation of Sibling Groups.—Sampling error occurs whenever a sample is drawn from a larger population. This can occur at repro-

TABLE 1. Group and individual selection in three groups, with altruism [modelled by Equations (1–3)] expressed every generation. The groups are derived from $AA \times Aa$, $Aa \times Aa$, and $Aa \times aa$ matings respectively. Allele frequency (p) and density (N) for each group is shown for nine generations. The last two columns show changes in allele frequency for all three groups combined. See text for explanation.

	$AA \times Aa$		$Aa \times Aa$		$Aa \times aa$			
Generation	p	N	p	N	p	N	P	ΔP
0	0.750	5	0.500	5	0.250	5	0.500	—
1	0.750	20	0.466	18	0.212	16	0.496	−0.004
2	0.743	78	0.443	65	0.185	50	0.497	−0.003
3	0.736	305	0.422	229	0.162	150	0.505	+0.005
5	0.727	4,618	0.381	2,771	0.124	1,278	0.527	+0.027
9	0.692	1,041,306	0.293	353,699	0.066	76,978	0.563	+0.063

duction (when progeny are "drawn" from a large gamete pool) or as the result of mortality (when the survivors are "drawn" from a larger initial population). Every round of sampling error increases the variance in allele frequency among groups, thus improving conditions for the evolution of altruism.

The simulation studies of version 2 consisted of two rounds of sampling error: drawing mated pairs from the global population and drawing offspring from their gamete pools. Sampling error beyond this point was (unrealistically) ignored by assuming that the p value of each Mendelian population was identical to the p value of the sibling group from which it was derived. Version 3 adds one additional round of sampling error, by allowing the second generation of size $C^2/2$ individuals to be randomly drawn from the gamete pool of the siblings. As with version 2, subsequent population growth to large values of N is assumed to occur without changes in p. Figure 2b shows that conditions for the evolution of altruism are substantially improved for small clutch size but become negligible when $C = 10$.

Additional rounds of sampling error have not been explicitly modelled, but it is easy to envision their effect. If the groups grow exponentially to large numbers, then sampling error can be ignored after the first one or two generations. If the groups spend a number of generations at low densities before increasing, however, or are periodically reduced to low densities, then variance in allele frequency among groups is further increased, and conditions for the evolution of altruism improved. In the extreme case, all groups become fixed for one allele or the other, and altruism is selected whenever $b/c > 1$.

Version 4: Selection Acting Every Generation.—In this version, altruism is first expressed among the siblings, with corresponding changes in allele frequencies and group size. The siblings then mate amongst themselves (producing a population in Hardy-Weinberg equilibrium but without genetic drift, as in version 2), and altruism is again expressed among their offspring, with corresponding changes in allele frequencies and group size. This process is repeated for G generations, after which the groups disperse back into the global pool.

Repeated selection intensifies both group and individual selection, as shown in Table 1 for three representative groups. Changes in density and allele frequency within each group were calculated by applying the fitness functions (1–3) every generation, with $C = 5$, $h = 1$, $c = -0.5$, and $b = 2.0$. The groups start as sib groups (generation 0), but thereafter are in Hardy-Weinberg equilibrium. Within each group the A allele declines in frequency every generation and would go extinct in all groups if they remained isolated for a long enough period of time. However, the differential productivity of groups also increases with every generation. From Table 1, the ratio of the most productive to the least productive group is only 1.25 after one generation and 13.53 after nine generations. The net effect on global allele frequencies is shown in the last two columns of Table 1. The balance shifts slightly in favor of group selection, at least over the first nine generations.

Figure 2c shows the results of the Monte Carlo simulations for three sets of runs, in

TABLE 2. Group and individual selection in three groups, with altruism expressed every generation, as in Table 1, but with fitness functions (4–6) used instead of (1–3). See text for explanation.

	AA × *Aa*		*Aa* × *Aa*		*Aa* × *aa*			
Generation	*p*	*N*	*p*	*N*	*p*	*N*	*P*	ΔP
0	0.750	5	0.500	5	0.250	5	0.5	0
5	0.732	345	0.475	311	0.233	267	0.5006	+0.006
10	0.711	336	0.449	282	0.215	236	0.487	−0.123

which $C = 5$ and $G = 3$, 5, and 10. The asterisks designate the existence of saddle points. For example, when $G = 5$ and $b/c = 2.2$, there is a stable equilibrium at $P = 0.80$ (shown in the figure) and a saddle point at $P = 0.10$ (not shown in the figure). Altruistic behaviors with a b/c ratio of 2.2 will be selected against until they reach a global frequency of $P > 0.10$, after which they will be selected for to a value of $P = 0.8$. Saddle points probably exist in this version because the fitness functions (1–3) no longer are additive when compounded over several generations. Figure 2c confirms the result of Table 1; at least over the first ten generations, the evolution of altruism is favored by increasing the number of generations spent within groups.

Version 5: Imposing Carrying Capacities on the Groups.—When the fitness functions (1–3) are applied over many generations, the groups grow exponentially as shown in Table 1. Exponential growth followed by dispersal accurately describes the population dynamics of many species. For many other species, however, a variety of density-dependent factors can be expected to impose a carrying capacity (K) on group size. Two scenarios are of interest.

a) K is independent of p. In this scenario, groups with many altruists initially grow faster than groups with few altruists (as in Table 1), but all groups ultimately attain the same carrying capacity. At this point, group selection ceases to exist. Variance in p among groups means nothing unless linked with differential productivity.
b) K is a function of p. Here, altruists increase the carrying capacity of the group, even while declining in frequency within the group. Fitness functions (4–6) are intended to model this situation. Table 2 shows three representative groups for which $I = 1.8$, $K = 200$, $x = 1$, and $s = 0.02$. Groups composed entirely of altruists ($p = 1$) have twice the carrying capacity as groups without any altruists ($p = 0$), but altruists are selected against in all groups with coefficients of selection of 0.02 for heterozygotes and 0.04 for homozygotes. The groups approach their carrying capacities in roughly five generations. At this point, group selection is slightly stronger than individual selection, and the global frequency of the A allele (P) increases. With ensuing generations, however, the balance shifts in favor of individual selection. The differential productivity of groups remains roughly constant from generations 5–10, while selection continues to operate within groups.

The variance in p for the three groups in Table 2 is less than for the Monte Carlo simulations, which include groups for which $p = 0$ and $p = 1$. When the same values for I, K, x, and s are used in the simulations, group selection prevails for values of $G = 5$ and 10 but not for $G = 15$. If the coefficient of selection is reduced to $s = 0.01$ for heterozygotes and 0.02 for homozygotes, group selection prevails when $G = 15$. Thus, increasing the duration of the group can decrease conditions for the evolution of altruism, but some degree of altruism still can evolve when several generations are spent within groups.

Version 6: Buildup of Variance over Several Cycles of Group Formation, and Mating within Groups Prior to Dispersal.—All of the preceding versions assume that groups are initiated by colonists drawn from a global population in Hardy-Weinberg equilibrium. After reproduction has occurred within

groups, however, the proportions of genotypes totalled over all groups departs from Hardy-Weinberg equilibrium, even in the absence of selection (Falconer, 1981). For example, version 2 assumes that at P near zero, A alleles exist primarily in groups derived from $Aa \times aa$ matings, with a local allele frequency of $p = 0.25$. These groups produce an appreciable number of AA homozygotes, which ultimately disperse back into the global pool. Specifically, during the next round of group formation, 0.25 of the altruistic A alleles exist as AA homozygotes that form $AA \times aa$ matings (the A allele still is very rare globally, so $AA \times AA$ and $AA \times Aa$ matings can be ignored). Mendelian populations derived from these matings produce an even greater frequency of AA homozygotes, and after several iterations of this process, fully a third of the A alleles exist in groups derived from $AA \times aa$ matings, with a local frequency of $p = 0.50$. Following the same procedure that led to Equation (11), altruism can be shown to spread when P is near zero if $b/c > 1.846$ for $h = 1$ and if $b/c > 2.67$ for $h = 0$. Thus, by ignoring the buildup of variance in p that occurs over several cycles of group formation and dispersal, the previous versions underestimate the degree of altruism that can evolve in Mendelian populations derived from sibling groups.

Even more extreme levels of altruism can evolve when genotypes mate within local groups prior to dispersal. Obviously, when P is near zero an appreciable number of $Aa \times Aa$, $AA \times Aa$, and $AA \times AA$ matings occur within local groups of $p = 0.25$ and $p = 0.50$ that do not occur when the genotypes first disperse and then mate. Simulation runs that include both buildup of variance and mating prior to dispersal are shown in Figure 2d. The term m defines the proportion of matings that occur within groups. The other parameter values are the same as for version 2, with $C = 5$ and $h = 1$ (see Fig. 2a). Even moderate values of m enable altruistic behaviors to evolve even though these would be strongly selected against by simple kin selection.

Version 7: Sibling Interactions within Local Groups.—So far, the local groups have been treated as simple Mendelian populations. Not only does mating occur at random (producing genotype frequencies in Hardy-Weinberg equilibrium), but interactions also occur at random, allowing fitnesses to be calculated from genotype frequencies. It is likely, however, that the local Mendelian populations themselves might be subdivided into smaller trait groups (Wilson, 1975, 1977) within which the interactions occur. In particular, it is interesting to examine the case of sibling interactions within local groups. Clearly, when P is near zero, Mendelian populations derived from $Aa \times aa$ matings will themselves create sibling groups derived from $Aa \times Aa$, $AA \times Aa$, and $AA \times AA$ matings, increasing the degree of altruism that can evolve. The Monte Carlo simulations show that b/c values as low as 1.50 can spread to fixation, even when the buildup of variance discussed in version 6 is ignored.

Discussion

The major difference between the haystack model and simple kin selection (with interactions among siblings) concerns the number of generations spent within groups. With kin selection, siblings interact and disperse into the global population. In the haystack model, the sib groups grow into Mendelian populations that remain isolated for several generations before dispersing into the global pool. Maynard Smith (1964) concluded that altruism cannot plausibly evolve under these circumstances. His conclusion, however, appears to be almost entirely an artifact of a simplifying assumption that the altruistic allele survives only in groups founded by AA females fertilized by AA males.

In subsequent discussions of group selection, Maynard Smith (1976, 1982) presented an even more abbreviated model that makes the same simplifying assumption. Groups exist in only three states: 1) uncolonized, 2) $p = 1$ (altruists only), and 3) $p = 0$ (selfish types only). The selfish allele is assumed to spread to fixation so quickly that polymorphic groups are "too transient to matter" (Grafen, 1984). This assumption clearly cannot be justified biologically, for, even with strong individual selection, many generations are required to drive an allele extinct.

When the same fitness functions are used

to compare the haystack model with simple kin selection, a complex pattern emerges. The evolution of altruism depends on global allele frequency (P), clutch size (C), the degree of dominance (h), mating within groups (m), and the number of times the altruistic behavior is expressed. All of these variables, however, are important only insofar as they relate to the fundamental processes of group and individual selection—the creation of genetic variation among groups, the differential productivity of groups, and the selection within groups.

In general, highly altruistic behaviors can evolve in Mendelian populations derived from sibling groups, often surpassing the b/c ratio of 2.0 that marks the limit for the sibling groups themselves. At least in retrospect, this result should not be surprising. Sampling error is a ratchet-like process that increases the variation among groups for as long as they remain isolated from each other. The formation of sib groups is only the first turn of the ratchet. Subsequent turns can only improve conditions for the evolution of altruism. Individual selection against altruism does intensify with the duration of the group, but often it is matched, and sometimes even exceeded, by intensifying group selection for altruism.

Two implications of the revised haystack model merit discussion; one concerns the relationship between kin selection and group selection, while the other concerns the existence of altruistic behaviors in nature.

The Relationship between Kin and Group Selection.—Many aspects of evolution are influenced by population structure, which therefore has received careful attention from population geneticists. Two approaches have been taken; one explicitly follows the divergence of isolated local groups, while the other represents the divergence of local groups with an inbreeding coefficient (F), or the closely related coefficients of kinship (f) and relationship (r) (Falconer's [1981] terminology used), which measure the probability that interacting alleles are identical by descent. Falconer (1981 Ch. 3, 4) is especially careful to stress that these are different ways of looking at a single process. F, f, and r measure the degree to which isolated lines have diverged from each other, and from the base population from which they were derived, by repeated sampling error. The base population can be spatially subdivided into groups or behaviorally subdivided by breeding/interaction preferences among the genotypes.

In contrast to general treatments of population structure, the group/kin selection literature is remarkable for treating the two approaches as separate processes that can operate independently of each other (Wilson, 1983). Thus, kin selection, which relies upon high coefficients of relationship among interacting individuals, is thought to be a plausible mechanism for the evolution of altruism. Inbreeding increases the coefficient of relationship, often (but not always) allowing even more highly altruistic behaviors to evolve (Michod, 1979, 1980, 1982; Michod and Hamilton, 1980; Uyenoyama, 1984; Wade and Breden, 1981). At the same time, group selection, which requires the genetic divergence of isolated groups, is rejected as a mechanism for the evolution of altruism.

Although the artificiality of this distinction is now widely recognized (see references cited in Introduction), many authors still feel the need to assert it, widely citing Maynard Smith (1964, 1976) as support. As one example, in his review of group and kin selection, Grafen first describes Maynard Smith's (1976) model, concluding that the conditions for the altruistic allele to spread are "too stringent to be realistic" (Grafen, 1984 p. 77). He then redescribes the same process in terms of kinship and relatedness, with a very different conclusion: "It is vital to remember, of course, that when the population is grouped there may be unsuspected kin links; and that in groups that last for a number of generations, relatedness builds up as the generations proceed" (Grafen, 1984 p. 84).

I hope that my reanalysis of the haystack model will help to demonstrate the fundamental similarities between kin and group selection, and the advantages of studying the evolution of altruism with a levels-of-selection approach. Coefficients of relationship can accurately represent simple population structures, such as sibling interactions when the parents are unrelated, but become difficult to calculate and interpret for the complex population structures de-

scribed here. Furthermore, the genetic variation among groups expressed by the coefficient of relationship means nothing unless it is linked with differential productivity. For additive fitness functions [such as Equations (1–3)], the benefit to the recipient can be multiplied by r, providing a simple and elegant solution. For more complex fitness functions, such as Equations (4–6) or Equations (1–3) applied over several generations, the solution is not nearly as simple and usually is not even attempted. In short, approaches using the coefficient of relationship are well suited for simple population structures and simple fitness functions, but they provide less insight for more complex situations.

In addition to reanalyzing the haystack model, it also is interesting to reexamine Maynard Smith's verbal distinction between group and kin selection:

> The distinction between kin selection and group selection as here defined is that for kin selection the division of the population into partially isolated breeding groups is a favourable but not an essential condition, whereas it is an essential condition for group selection, *which depends on the spread of a characteristic to all members of a group by genetic drift* (Maynard Smith, 1964 p. 1145; italics mine).

Maynard Smith placed great emphasis on the idea that kin selection does not involve any "improbable events," while group selection requires the altruistic allele to spread to fixation within groups by genetic drift, against the current of individual selection. This was a common idea at the time, and it is indeed a necessary feature of interdemic group-selection models, in which the groups persist indefinitely until driven extinct by the selfish allele (reviewed by Wade [1978] and Wilson [1983]). However, the haystack model departs from interdemic models by assuming that all groups periodically dissolve when their members disperse into the global pool, to be replaced by a new set of groups. The variance among groups generated by sampling error during colonization and reproduction is not only probable, but inevitable, given large numbers of local groups. Nothing more is needed for the differential productivity of groups to oppose individual selection, as described by the various Monte Carlo simulations. Thus, group selection does not require "improbable events" in the haystack model any more than does kin selection. The essential condition for both group and kin selection is the division of the population into partially isolated interaction groups (trait groups), within which fitness is determined. The breeding structure of the population is important only as it affects the interaction structure.

The Existence of Altruism in Nature.— Most sociobiologists expect to find altruism expressed primarily among close relatives—parents and offspring, siblings, cousins, and so on. Inbreeding is thought to enhance the evolution of altruism, but it is usually treated in the narrow sense of mating pedigrees involving close relatives.

Inbreeding in the broad sense represents all forms of population structure, so presumably all of the results presented here could be restated in terms of coefficients such as F, f, and r. This would not be very useful operationally, however, nor would it represent the intuition of sociobiologists. Consider the dilemma of a sociobiologist studying a species whose population structure approximates version 6 of the Monte Carlo simulations. Unless there is some foreknowledge of long-term colonization and dispersal events, the sociobiologist may well begin by studying a single large Mendelian population. Within this population there is no inbreeding and no preferential interactions among relatives—unlikely conditions indeed for the evolution of altruistic behaviors. Yet the creatures are extremely altruistic, with b/c ratios less than 2.0. The species is indeed "inbred," and the interactions are indeed "preferential," but only in reference to the global population and through colonization events occurring several generations ago, which are unknown to the investigator.

Thus, the sociobiological focus on immediate ancestry misses the long-term and large-scale aspects of population structure embodied by the haystack model. To the extent that these aspects are important, altruistic behaviors will exist where sociobiologists do not expect them.

This does not mean that extreme altruism among seemingly unrelated individuals

should be commonly observed in nature, or that Wynne Edwards's original claims are now justified. In fact, probably very few species have a population structure that exactly approximates the haystack model. Groups usually are initiated by more than one individual, and migration between groups takes place prior to global dispersal. These events decrease the variance in allele frequency among groups, thereby decreasing conditions for the evolution of altruism. Synchronized colonization, growth, and dispersal obviously are stylizations, and dispersal is rarely truly global. No firm statement can be made about more common population structures until they are explicitly modelled (see Fix [1985] for an interesting example). One of the beauties of the levels-of-selection approach, however, is its focus on a property of population structure that can be measured apart from the complex of events that created it—the variation in allele frequency among local groups. Such variation is frequently observed in natural populations, and, to the extent that it is caused by isolation and drift, large-scale and long-term aspects of population structure may well play a role in the evolution of altruistic and other group-advantageous behaviors.

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Literature Cited

Bulmer, M. G., and P. D. Taylor. 1980. Sex ratio under the haystack model. J. Theoret. Biol. 86:83–89.

Charnov, E. L. 1982. The Theory of Sex Allocation. Princeton Univ. Press, Princeton, NJ.

Falconer, D. S. 1981. Introduction to Quantitative Genetics, 2nd Ed. Longman, London, U.K.

Fix, A. G. 1985. Evolution of altruism in kin-structured and random subdivided populations. Evolution 39:928–939.

Grafen, A. 1984. Natural selection, kin selection and group selection, pp. 62–84. *In* J. R. Krebs and N. B. Davies (eds.), Behavioral Ecology: An Evolutionary Approach, 2nd Ed. Blackwell, Oxford, U.K.

Hamilton, W. D. 1963. The evolution of altruistic behavior. Amer. Natur. 97:354–356.

———. 1964*a*. The genetical evolution of social behavior I. J. Theoret. Biol. 7:1–16.

———. 1964*b*. The genetical evolution of social behavior II. J. Theoret. Biol. 7:17–52.

Maynard Smith, J. 1964. Group selection and kin selection. Nature 201:1145–1147.

———. 1976. Group selection. Quart. Rev. Biol. 51: 277–283.

———. 1982. The evolution of social behavior—A classification of models, pp. 29–45. *In* Kings College Sociobiology Group (eds.), Current Problems in Sociobiology. Cambridge Univ. Press, Cambridge, U.K.

Michod, R. E. 1979. Genetical aspects of kin selection: Effects of inbreeding. J. Theoret. Biol. 81:223–233.

———. 1980. Evolution of interactions in family structured populations: Mixed mating models. Genetics 96:275–296.

———. 1982. The theory of kin selection. Ann. Rev. Ecol. Syst. 13:23–56.

Michod, R. E., and W. D. Hamilton. 1980. Coefficients of relatedness in sociobiology. Nature 288: 694–697.

Uyenoyama, M. K. 1984. Inbreeding and the evolution of altruism under kin selection: Effects on relatedness and group structure. Evolution 38:778–795.

Uyenoyama, M., and M. W. Feldman. 1980. Theories of kin and group selection: A population genetics perspective. Theoret. Popul. Biol. 17:380–414.

Wade, M. J. 1978. A critical review of the models of group selection. Quart. Rev. Biol. 53:101–114.

———. 1979. The evolution of social interactions by family selection. Amer. Natur. 113:399–417.

———. 1980. Kin selection: Its components. Science 210:665–667.

Wade, M. J., and F. Breden. 1981. Effect of inbreeding on the evolution of altruistic behavior by kin selection. Evolution 35:844–858.

Wilson, D. S. 1975. A theory of group selection. Proc. Nat. Acad. Sci. USA 72:143–146.

———. 1977. Structured demes and the evolution of group-advantageous traits. Amer. Natur. 111:157–185.

———. 1980. The Natural Selection of Populations and Communities. Benjamin-Cummings, Menlo Park, CA.

———. 1983. The group selection controversy: History and current status. Ann. Rev. Ecol. Syst. 14: 159–187.

Wilson, D. S., and R. K. Colwell. 1981. Evolution of sex ratio in structured demes. Evolution 35:882–897.

Wright, S. 1945. Tempo and mode in evolution: A critical review. Ecology 26:415–419.

Wynne-Edwards, V. C. 1962. Animal Dispersion in Relation to Social Behavior. Oliver & Boyd, Edinburgh, U.K.

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