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KINSHIP, NEED, AND THE DISTRIBUTION OF ALTRUISM

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Ever since Hamilton (1964) showed that altruism could be favored by natural selection as long as it was directed toward relatives, there has been controversy over how altruistic acts should be distributed when different types of kin are potential recipients. It has often been assumed that an altruist should distribute aid in proportion to the degree of relatedness between itself and beneficiaries of its altruism (Bertram 1976; Dawkins 1976; Barash 1977; Kurland 1977; Massey 1977; Kaplan 1978; O'Hara and Blaustein 1981). However, Altmann (1979) has criticized this idea of proportional investment. Altmann astutely pointed out that distributing the stakes (investment in kin) in proportion to the odds (genetic relatedness) is a common gambler's fallacy. He suggested instead, that if the benefits of receiving assistance increase as a linear function of the amount of investment received, the altruist should concentrate all of its resources on its most closely related relative.

In natural populations altruistic acts are dispensed to more than just closest kin. To account for this, Altmann suggested that a number of additional factors shape investment patterns. First, returns on investment rarely increase linearly. Instead, they usually increase, but at an ever decreasing rate. Thus, although an additional unit of investment may help the closest kin and increase the altruist's inclusive fitness, the increase may be less than that which could be derived by transferring that unit to a less closely related individual. Whether or not this is the case would depend on the shape of the investment return curve as well as the coefficients of relationship. Second, other phenotypic attributes may affect disbursement of altruism, and may oppose the pattern dictated purely by kinship considerations. For example, kin of similar relatedness may differ with respect to body size, agility, or ability to care for offspring, all of which may make their reproductive potential substantially different. Alternatively, kin of different relatedness may be of equivalent value to an altruist because of compensating phenotypic differences. This will most likely be the case whenever a closer relative has a substantially lower reproductive value (*sensu* Fisher 1931) than a more distant relative (Hamilton 1964; West-Eberhard 1975; Milinski 1978; Chapais and Schulman 1980; Schulman and Chapais 1980; Charlesworth and Charnov 1981; Rubenstein 1982*a*; Gadgil 1982; Goodman 1982).

It is clear that many factors will affect the way an altruist distributes its resources, but apart from Weigel's (1981) numerical simulations, little work has been done to construct a general model to evaluate how these factors interact to determine the optimal allocation of altruism directed toward kin. If conditions of diminishing returns on investment obtain, Weigel (1981) showed that an altruist's distribution of resources among kin is sensitive to relatedness but does not follow a strictly proportional pattern. Our purpose here is to further explore how the exact distribution of aid depends on (1) the magnitude of the diminishing returns to investment, (2) whether investment augments reproduction or survivorship, (3) relative frequencies of different classes of kin, and (4) differences among kin in their ability to profit from the altruistic acts.

<div align="center">BASIC MODEL</div>

To investigate how altruism should be distributed among potential recipients differing in both phenotype and relatedness to the altruist, we first construct a general framework based on the following assumptions. First, as in Weigel (1981) we make the simplifying assumption that there is only one altruist. Second, we assume the altruist has a finite amount of resources available for investment in kin. Third, we need only consider the kin component (γ) of the altruist's total inclusive fitness. Thus,

$$\gamma = \sum_{i=1}^{n} r_i W_i$$

where r_i is the relatedness between the altruist and individual i and W_i is the fitness of individual i. Fourth, we will only consider four classes of relatives $r = 1/2, 1/4, 1/8, 1/16$. Initially our population will consist of only one recipient of each class. Fifth, returns to altruism are always positive, but each additional contribution has a smaller effect than the previous one. In other words, investment incurs diminishing returns (fitness is a concave function of investment $d\gamma/dx > 0$ while $d^2\gamma/dx^2 < 0$). After Weigel (1981) we use the exponential relationship $W_i = 1 - e^{-ax_i}$, where W_i is the ith individual's fitness, a is a fitness conversion efficiency rate constant determining the rate of change in fitness per unit of investment, and x_i is the proportion of the altruist's investment in the ith individual. Determining the optimal allocation among kin of the altruist's finite amount of resources involves maximizing the expression:

$$\gamma = \max \sum_{i=1}^{n} r_i(1 - e^{-a_i x_i}), \tag{1}$$

subject to the constraints

$$\sum_{i=1}^{n} x_i = 1 \quad \text{and} \quad x_i \geq 0 \quad \text{for all } x_i,$$

where n is the number of potential kin recipients of ego's aid, and r_i is the coefficient of relatedness between ego and individual i. The fitness conversion

efficiency constant a_i is the ith individual's fitness conversion efficiency. Different fitness conversion efficiencies would be characteristic of different phenotypes. Organisms most able to convert investment into fitness, for reasons related to superior genotypes or bodily condition, might possess higher a_i values. Alternatively, individuals who suffered some permanent injury or deprivation during ontogeny and whose fitness could never be augmented regardless of how much aid it received, might have low values of a_i.

Using Lagrangean multipliers (Chiang 1974), an analytical solution to the constrained optimization problem of equation (1) can be obtained. Rewriting equation (1) as a Lagrangean function incorporating the first constraint yields:

$$\gamma = \max \sum_{i=1}^{n} r_i(1 - e^{-a_i x_i}) + \lambda(1 - \sum_{i=1}^{n} x_i) \qquad (2)$$

where λ is an undetermined multiplier. Differentiating γ with respect to each x_i and λ and then solving the system of $n + 1$ equations when set to zero yields optimum values of x_i and λ.

$$\frac{\partial \gamma}{\partial x_1} = a_1 x_1 + \ln(\lambda) - \ln(r_1 a_1) = 0$$

$$\frac{\partial \gamma}{\partial x_2} = a_2 x_2 + \ln(\lambda) - \ln(r_2 a_2) = 0$$

$$\vdots \qquad \vdots \qquad \vdots$$

$$\frac{\partial \gamma}{\partial x_n} = a_n x_n + \ln(\lambda) - \ln(r_n a_n) = 0$$

$$\frac{\partial \gamma}{\partial \lambda} = 1 - \sum_{i=1}^{n} x_i = 0.$$

RESULTS

Altruism Augments Fecundity of Recipients

When the benefits of altruism lie primarily in the enhanced fecundity of recipients, the distribution of altruism among kin is affected by the fitness conversion rate a_i. From the solutions of the systems of linear equations described above, utilizing different values of a_i, various optimal altruistic investment distributions were obtained (tables 1–9). For the situation involving four kin related to the altruist by 1/2, 1/4, 1/8, 1/16, optimal investment by the altruist becomes more evenly distributed as fitness conversion efficiencies increase (table 1). In the extreme case where conversion efficiency is uniformly low for all kin ($a_i = .6$), the rate of return on the altruist's investments is nearly linear and as a result, it should concentrate its investment on the most closely related kin. Conversely, when conversion efficiency is exceedingly high ($a_i = 500$), even small amounts of investment increase the recipient's fitness to near maximum. Consequently, the

TABLE 1

OPTIMAL INVESTMENT IN KIN OF DIFFERENT RELATEDNESS AND UNIFORM FITNESS
CONVERSION EFFICIENCIES

FITNESS CONVERSION EFFICIENCY (a_i)	RELATEDNESS (r_i)			
	1/2	1/4	1/8	1/16
.6 ...	1.0	0	0	0
.8 ...	.933	.067	0	0
1	.847	.153	0	0
2.75 ..	.585	.333	.081	0
10	.354	.285	.215	.146
100	.260	.253	.247	.248
500	.252	.251	.249	.248

TABLE 2

OPTIMAL INVESTMENT IN FOUR FULL SIBS WHEN ONE SIB (*) IS LESS EFFICIENT
(For efficient sibs $a_i = 2.75$)

CONVERSION EFFICIENCY OF INEFFICIENT RECIPIENT	RELATEDNESS (r_i)			
	1/2	1/2	1/2	1/2
	.250	.250	.250	.250
2.5	.240*	.253	.253	.253
2.0	.205*	.265	.265	.265
1.5	.128*	.291	.291	.291
1.0	0*	.333	.333	.333

altruist spreads its resources equally among all kin irrespective of their degree of relatedness.

In natural populations, individuals differ not only in their reproductive abilities, but also in their abilities to utilize assistance to enhance their reproductive potential. These differences have dramatic consequences for the optimal distribution of altruism (table 2). When all potential recipients are equally related to the altruist and all possess identical conversion efficiencies, then the altruist distributes its resources equally among them. However, when one of the recipients has a lower conversion efficiency, the altruist withdraws some support from the inefficient individual and divides it equally among the other kin. The amount withdrawn depends upon the relative differences in conversion efficiencies. The situation becomes more complex when recipients differ both in degree of relatedness and conversion efficiencies. Table 3 shows the altruist's proportional investment in kin when all have similar conversion efficiencies, as well as when one relative possesses a lower conversion efficiency. From the altruist's perspective, there is no general rule governing how its investment strategy changes should a recipient's conversion efficiency decline. When a distant relative ($r = 1/8$) undergoes a decline in efficiency (row 3 in tables 3A and 3B) the altruist shifts

TABLE 3

OPTIMAL INVESTMENT IN KIN (Inefficient recipients are underscored)

A. EFFICIENT (a = 2.75), INEFFICIENT (a = 1.0)			
1/2	1/4	1/8	1/16
.585	.333	.081	0
.585	.333	.081	0
.626	.374	0	0
.676	.153	.171	0
.591	.331	.079	0
B. SUPEREFFICIENT (a = 10.0), INEFFICIENT (a = 1.0)			
1/2	1/4	1/8	1/16
.354	.285	.215	.146
.403	.333	.264	0
.382	.313	.131	.174
.334	.345	.195	.126
.558	.217	.147	.078

more aid to closer kin. When the closer kin are inefficient recipients, the pattern is less clear cut; half sibs (r = 1/4) lose resources when they are somewhat inefficient relative to the others (table 3A, row 4), but actually receive additional resources when they are much less efficient than the others. Furthermore, full sibs (r = 1/2) always appear to receive additional resources whenever they are relatively inefficient. These complex patterns arise because the inefficient individual converts resources to fitness along a shallower but more linear curve than the others. Thus more aid can be converted to fitness before diminishing returns becomes a consideration and therefore, at least for close kin, the additional aid contributes significantly to the altruist's fitness.

   Seemingly paradoxical allocation patterns can result when differences in efficiency vary inversely with degree of relatedness. For example, if the most distant relative (r = 1/16) has a conversion efficiency of 2.75 while closer kin (r = 1/2, 1/4, 1/8) all have relatively low efficiencies of .091, we find that the optimal distribution of altruism results in an equal investment in the closest and most distant kin (r = 1/2, 1/16) with no investment in intermediate kin (r = 1/4, 1/8). Thus the altruist's inclusive fitness balances high relatedness with low efficiency, and vice versa.

   The demographic structure of the population also influences the distribution of an altruist's investments. In the previous analyses, the population consisted of four relatives each occupying a different relatedness class. If the pool of potential recipients is increased to eight relatives with two in each relatedness class, the pattern of kin-directed altruism changes. Although each class still contains only 25% of the recipient pool, more of the altruist's resources will be concentrated in the more closely related classes than they were when the population was half as large (cf. tables 1 and 4). Since the individuals in each class receive an equal

TABLE 4

Optimal Distribution of Investment in Eight Kin

Fitness Conversion Efficiency (a_i)	Relatedness (r_i)							
	1/2	1/2	1/4	1/4	1/8	1/8	1/16	1/16
2.75 ...	.38	.38	.12	.12	0	0	0	0
10	.23	.23	.16	.16	.09	.09	.02	.02

amount of the altruist's resources going to that relatedness class, each individual actually received fewer resources than it would have, had it been the only kin of that degree of relatedness. Thus how an altruist dispenses its resources depends on the distribution of kin in the population. For altruists with many close relatives, distant ones will rarely receive aid. For altruists with many distant relatives and few close ones, investment is concentrated in fewer individuals but distributed among more relatedness classes (table 5).

Altruism Increases Survivorship of Recipients

Although altruism may enhance reproductive output of recipients, it need not be the only effect. Additional resources may increase one relative's survival prospects over another's. To examine how changes in survival prospects of relatives affect the altruist's distribution of resources, the basic model was modified by incorporating a function by which a recipient's survivorship (s) is increased in proportion to both the amount of altruism received (x_i) and the extent to which survivorship can be augmented $(1-s)$. Such a function is incorporated in equation (3) which is a modified version of equation (1):

$$\gamma_{II} = \max \sum_{i=1}^{n} r_i(1 - e^{-a_i x_i})[s + x_i(1 - s)] \tag{3}$$

subject to the constraints:

$$\sum_{i=1}^{n} x_i = 1 \quad \text{and} \quad x_i \geq 0 \quad \text{for all } x_i.$$

Particular solutions to equation (3) can be obtained iteratively (Carnahan et al. 1969) when (s), the probability of surviving to the next breeding period is set equal to 1, equation (3) reduces to equation (1).

When altruistic investment is dynamically coupled with recipient survivorship, the consequences for the optimal allocation of resources are very different from when investment only affects fecundity. This can be seen most clearly in the case when the altruist must distribute altruism among four kin of identical relatedness and conversion efficiency (table 6). In favorable environments, or those where the intensity of predation is low and survivorship is ordinarily high, the optimal

TABLE 5

OPTIMAL DISTRIBUTION OF INVESTMENT WITH UNIFORM CONVERSION EFFICIENCY

	A. Many close kin with few distant kin RELATEDNESS (r_i)					
a_i	1/2	1/2	1/2	1/2	1/4	1/16
.50	.25	.25	.25	.25	0	0
2.75	.25	.25	.25	.25	0	0
10.00	.213	.213	.213	.213	.144	.005

	B. Many distant kin with few close kin					
a_i	1/2	1/4	1/16	1/16	1/16	1/16
.5	1.0	0	0	0	0	0
2.75	.626	.374	0	0	0	0
10.00	.317	.248	.109	.109	.109	.109

TABLE 6

OPTIMAL INVESTMENT IN FOUR FULL SIBS WITH EQUAL FITNESS CONVERSION EFFICIENCIES ($a_i = 2.75$) WHEN ALTRUISM IS DYNAMICALLY COUPLED WITH SURVIVORSHIP (Distributions are given for several extrinsic survivorship conditions.)

EXTRINSIC SURVIVORSHIP (s)	RELATEDNESS (r_i)			
	1/2	1/2	1/2	1/2
1	.25	.25	.25	.25
.4	.25	.25	.25	.25
.37	.328	.328	.328	.016
.35	.479	.479	.042	0
.30	1	0	0	0
.10	1	0	0	0

pattern is an equal allocation of resources among the four kin. However, as survivorship declines because of extrinsic factors, it becomes advantageous for the altruist to increasingly concentrate its resources in a smaller number of kin despite the fact that they are equally related to the altruist and possess similar abilities to convert investment into fitness. At some critical point it becomes optimal for the altruist to arbitrarily select one of the otherwise identical potential recipients and bestow on it all surplus resources available for altruistic investment (table 6). Apparently, as conditions become harsher, spreading resources among many kin is less likely to increase the altruist's inclusive fitness than concentrating its resources in one individual.

The altruist's investment strategy is complicated when equally related kin recipients differ in their abilities to utilize resources (table 7). In these examples, the altruist must distribute aid among four full sibs, two of whom have marginally better phenotypes than the other two. As long as extrinsic survivorship is high, the optimal policy is essentially an equal distribution. However, as survivorship

TABLE 7

OPTIMAL INVESTMENT IN FOUR FULL SIBS WHEN TWO HAVE MARGINALLY POORER EFFICIENCIES AND WHEN SURVIVORSHIP AND ALTRUISM ARE DYNAMICALLY COUPLED

	RELATEDNESS			
	---	---	---	---
	1/2	1/2	1/2	1/2
		EFFICIENCY		
EXTRINSIC SURVIVORSHIP	2.65	2.65	2.75	2.75
1	.248	.248	.252	.252
.9	.247	.247	.253	.253
.5	.241	.241	.259	.259
.4	.229	.229	.271	.271
.35	0	0	.5	.5
.3	0	0	1	0
.1	0	0	1	0

TABLE 8

OPTIMAL INVESTMENT IN KIN OF DIFFERENT RELATEDNESS AND UNIFORM CONVERSION EFFICIENCY ($a_i =$ 2.75) WHEN ALTRUISM AND SURVIVORSHIP ARE DYNAMICALLY COUPLED (Results are illustrated under several different intrinsic survivorship conditions.)

EXTRINSIC SURVIVORSHIP (s)	RELATEDNESS (r_i)			
	1/2	1/4	1/8	1/16
1	.585	.335	.080	0
.9	.629	.326	.045	0
.8	.687	.313	0	0
.5	.949	.051	0	0
.4	1	0	0	0

declines, a skewed distribution favoring recipients with higher conversion efficiencies becomes optimal. As in table 6, as survivorship reaches a critical level it becomes worthwhile to arbitrarily target one individual with the higher efficiency for concentrated investment even though other potential recipients may have identical phenotypic attributes.

Table 8 shows the effect of declining survivorship on investment strategy when potential recipients differ in relatedness to the altruist but have similar conversion efficiencies. When survivorship is 1.0, the results are identical to those when the investment affected only fecundity. However, as survivorship declines, it becomes increasingly worthwhile for the altruist to concentrate investment in the most closely related individual(s).

The interaction of extrinsic levels of survivorship, kinship, and conversion efficiency, is complex and often produces counterintuitive optimal investment patterns (table 9). For example, when extrinsic survivorship is held at .5 and the four potential recipients all have identical conversion efficiency but are differently

TABLE 9

OPTIMAL INVESTMENT IN KIN OF DIFFERENT RELATEDNESS AND DIFFERENT EFFICIENCIES WHEN
SURVIVORSHIP AND ALTRUISM ARE DYNAMICALLY COUPLED (Extrinsic survivorship
is held constant at .5.)

	RELATEDNESS (r_i)			
	1/2	1/4	1/8	1/16
Efficiency (a_i)	2.75	2.75	2.75	2.75
Investment (x_i)	.949	.051	0	0
Efficiency (a_i)	2.00	2.75	2.75	2.75
Investment (x_i)	1	0	0	0
Efficiency (a_i)	2.75	2.00	2.75	2.75
Investment (x_i)	1	0	0	0
Efficiency (a_i)	2.00	2.00	2.75	2.75
Investment (x_i)	1	0	0	0

related to the altruist (r = 1/2, 1/4, 1/8, 1/16), the optimal strategy is for the altruist
to allocate about 95% of its resources toward the most closely related individual
and direct the remaining 5% toward the next closest kin. However, if the closest
kin, or the second closest kin, or both have lower efficiencies, then it becomes
optimal in all three cases for the altruist to concentrate 100% of its investment in
the most closely related individual!

DISCUSSION

Perhaps the issue most central to sociobiology concerns altruism and its distri-
bution. The results of this study show that the distribution of altruism among kin
can take on many forms. As Weigel (1981) has shown previously, the presence of
diminishing returns on the altruist's investment is one of the most important
factors governing the final disbursement of resources. Only as a coincidence will
the distribution be proportional to the degree of relatedness between the altruist
and potential recipients. Furthermore, only if the returns to scale remain linear for
large investments will all resources be concentrated on the closest kin.

Even the conventional rule of thumb that close kin should receive more aid than
distant ones breaks down when individual differences in conversion efficiency are
accounted for. Distantly related kin with high conversion efficiencies can augment
an altruist's inclusive fitness as much as close kin of lower efficiency.

Most studies of altruism in the field rarely take into account the demographic
structure of the population. Different altruists may have different perspectives
since the pool of potential recipients may be distributed among kin classes differ-
ently. As we have shown, the consequences of such differences can be profound.

How altruistic acts affect the recipient's fitness helps shape the altruist's invest-
ment strategy. The optimal distribution of altruism may be quite different depend-
ing on whether altruism primarily enhances the recipient's survivorship or fecun-

dity. Other things being equal, the altruist should tend to favor closer relatives to a greater extent when altruism affects survivorship than when it primarily affects fecundity (tables 1 and 8). In addition, when survivorship and altruism are dynamically coupled, small changes in parameters may have large threshold effects. This is clearly manifest in table 6 when a small reduction in extrinsic survivorship from .35 to .30 contracts the optimal distribution from three of four kin to a total concentration of investment in the one closest kin.

The major implication for empirically oriented sociobiologists is that knowledge of genetic relatedness alone will be insufficient evidence with which to support or reject a kin selection interpretation of observed behavior. Merely demonstrating that the frequency of social interactions corresponds in a loose way with genetic relatedness does not demonstrate that kin selection is operating. However, strong predictions are possible if the degree of relatedness between the altruist and potential recipients can be ascertained and if the shape of the diminishing returns curve can be approximated for different recipients. It is obvious, therefore, that field workers must know more details about the individuals making up the study population, their abilities to benefit from aid, their genealogical position, etc. More attention will need to be directed toward developing adequate techniques for gauging the shape of fitness mapping functions for different individuals. For populations for which long-term demographic data are available, calculation of reproductive value will account for some of the variability (between age-class variability) in the value of different recipients in terms of their investment potential. Applications in studies of equid and primate social behavior can be found in Rubenstein (1982a) and Chapais and Schulman (1980). Charlesworth and Charnov (1981) present a more general discussion of the use of reproductive value in kin-selection models. Because reproductive value is an age-class attribute, however, it is incapable of accounting for other important differences among recipients rendering them more or less desirable as targets for altruistic investment. Factors such as disease, permanent injuries, nest site, or territory quality could produce large within age-class variability.

Determining the convexity of the fitness mapping function is important for other reasons as well. If in fact most animals encounter diminishing returns on their investments, then it can be demonstrated, other things being equal, that the more conservative investment strategy (with small payoff variance) yields a higher expected fitness (Rubenstein 1982b). However, if the fitness mapping function for some behaviors could be shown to be upwardly convex (implying increasing returns) then for strategies requiring identical investments, the strategy with the larger variance in payoff will result in a greater expectation of fitness.

The helping behavior of older sibs in some monogamous canids (Moehlman 1977) would be a good example of the kind of altruism being modeled here in which one altruist distributes resources among several recipients. A more general model, however, must view each individual as a potential altruist and recipient. Hence, the value of potential recipients will be determined in part by the amount of investment they are receiving from other altruists.

Brood reduction (O'Connor 1978; Howe 1976; Trivers 1974) via preferential feeding of offspring is another good example of the class of behaviors for which

this model might be appropriate. If all nestlings are phenotypically similar and equally related to the parent, then during a breeding season characterized by resources scarcity it may be worthwhile (vis-à-vis number of offspring fledged) for the parent to arbitrarily select a subset of the brood and concentrate investment in them while starving other offspring. Furthermore, differences in egg size, asynchronous hatching, and other sources of variability may result in real differences in conversion efficiencies further skewing the optimal distribution of investment and increasing the value of brood reduction.

Some of the primate populations which have been the subject of long-term study and observation may provide nearly ideal opportunities to test the ideas set forth here. Different individuals from the same social group may have quite different perspectives concerning the investment potential of other group members. These differences are quantifiable. Some individuals come from large genealogies and may have a larger pool of potential recipients than others. Different positions within genealogies will also entail different relatedness perspectives for altruists belonging to the same genealogy. One aspect of fitness conversion efficiency, reproductive value, is readily calculable for some populations. Published field studies like Kaplan's (1977, 1978) studies of flight intervention behavior in macaques could profit from reanalysis in light of the issues raised here.

EXTENSIONS AND SPECULATIONS

It is interesting to consider relaxing or eliminating the non-negativity constraint on investment. Brood reduction accomplished via selective starvation of offspring may be viewed as reduced or eliminated posthatching investment. However, it is not inconceivable that examples of negative investment (not merely zero investment) may exist. An example of negative investment might consist of an individual stealing cached food items from one individual (negative investment) and redistributing them in a cache belonging to another individual (positive investment) perhaps because the latter is more closely related or has a higher fitness conversion efficiency. Aspects of the communal cache defense behavior of acorn woodpeckers (MacRoberts 1970; MacRoberts and MacRoberts 1976) suggest this possibility.

Underlying our treatment, and indeed, all kin-selection models is the notion that the optimal strategy is the one which results in the greatest expectation of the number of gene replicates in subsequent generations. Slobodkin and Rapoport (1974) have suggested that highest expected payoff is not necessarily the best optimization criterion in evolutionary models. When assuming the perspective of the establishment of a new allele in a small population, a strategy entailing a lower expected payoff may stand a better chance of becoming established and going to fixation if it bears a lower variance than an alternative strategy with a higher expected payoff. Consider mutant strategy A which results in an equiprobable payoff of either 0 or 10 offspring equivalents (West-Eberhard 1975) pitted against mutant strategy B which results in either two or four surviving offspring equivalents. While strategy A has a higher expected value, $E(A) = 5$, than strategy B, $E(B) = 3$, strategy A has a .5 probability of producing 0 offspring equivalents yet

strategy *B* is guaranteed to produce at least two offspring equivalents. Consequently a trade-off between reducing risk and maximizing expected fitness may be the more appropriate optimum (Rubenstein 1982*b*). A strategy of concentrating investment in one or a few kin will be more suboptimal as investment and survivorship become more independent. Thus, the more important is risk reduction, the less valid will be results from the basic model. The true optimum in this case will lead to a spreading of risk by not laying all eggs in one basket.

SUMMARY

The optimal distribution of investment in kin cannot be determined solely on the basis of knowledge of genetic relatedness. The distribution will be affected by the fact that altruists are likely to encounter diminishing returns on their investments in kin. Furthermore, returns to altruism will vary because of phenotypic variation among recipients. Differences in fitness conversion efficiencies may outweigh relatedness considerations so that a distant relative may be more valuable than a close relative. Or else, if all kin are superefficient at converting investment into fitness, an even distribution of investment among kin may be optimal irrespective of differences in relatedness. It is necessary to ascertain whether the principal consequence of investment results in increased fecundity or increased survivorship of recipients because the optimal distribution of investment may differ considerably in each case.

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