BENEFIT/ COST RATIOS IN THE EVOLUTION OF ALTRUISTIC BEHAVIOR TOWARD PARENTS AND FULL SIBLINGS

D. Kelly McLain
Department of Biology
Emory University
Atlanta, Georgia 30322

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ABSTRACT: When the B/C ratio, benefit to the beneficiary/ cost to the benefactor, of an altruistic act exceeds the number of altruism alleles per offspring of the altruist/ the number of altruism alleles per offspring of the beneficiary, altruistic behavior is favored. Calculated in this fashion, the minimum B/C ratio for altruistic behavior to be favored is smaller than when calculated by $1/r$ where r is the probability that an altruism allele is identical by descent in beneficiary and benefactor. Also, altruistic behavior toward parents is favored for smaller values of B/C than is altruistic behavior toward full siblings. Dominance of the altruism allele and allele frequency contribute to the magnitude of the minimum B/C ratio necessary for selectively favored altruistic behavior.

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INTRODUCTION

The magnitude and direction of selection on an allele determining a particular behavior depends both upon the effect of the behavior on the fitness of the individual performing the behavior and the effect on other individuals which carry replicas of the allele (Hamilton, 1964). Thus, an individual can be selected to behave in a manner which lowers its personal fitness if such behavior increases the fitness of other individuals. Such behavior is defined to be altruistic (West Eberhard, 1975). Hamilton (1964) proposed that altruistic behavior would be favored in outbred populations when $B/C > 1/r$ where B is the gain in fitness to the beneficiary, C is the cost to the benefactor, and r is a coefficient of relationship between the benefactor and beneficiary. The coefficient, r, may be interpreted as the fraction of genes shared identical by descent by beneficiary and benefactor (Michod and Anderson, 1979) or the probability that the beneficiary has a copy of the altruism allele identical by descent with the altruism allele of the benefactor (Charnov, 1977). Since r is based upon pedigree, it is not dependent upon the frequency of the altruism allele. Thus, for interactions between full siblings, altruistic behavior will be favored if $B/C > 2$ since $r=1/2$ for full siblings. For a more distant relationship between beneficiary and benefactor, r is smaller and the B/C ratio necessary for selectively favored altruism is larger. Wade (1978, 1979) and Charnov (1977) have derived "Hamilton's rule", $B/C > 1/r$, from population genetic models of altruistic behavior within families. Other mathematical models have shown some dependency of the B/C ratio on the frequency of the altruism allele (Charlesworth, 1978; Orlove, 1975). Yet, despite various approaches by numerous theorists, most coefficients derived to define the minimum B/C ratio necessary for the spread of an altruism allele are equivalent (Michod and Hamilton, 1980).

However, Scudo and Ghiselin (1975) question the appropriateness of the use of the coefficient of relationship, r, in determining the minimum B/C ratio necessary for the spread of an altruistic allele. They develop a model for selection at the level of the family which differs qualitatively in its predictions from other models of selection on the family (eg. Wade, 1978, 1979). West Eberhard (1975) has also questioned the appropriateness of r. She suggests that r be replaced by "relatedness to the beneficiary's offspring/ benefactor's relatedness to its own offspring". I will refer to this as r' (following Craig, 1979). Use of r' leads to the prediction

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that altruistic behavior toward parents will be more easily selected for than altruistic behavior toward full siblings since this gives $B/C > 1$ in the former instance and $B/C > 2$ in the latter.

In the present analysis, the minimum B/C ratio is derived from a consideration of the actual number of altruism alleles at a single autosomal locus possessed by the beneficiary, benefactor, and their offspring. Thus, there will be some dependency of B/C upon the frequency of the altruism allele. The analysis assumes a monogamous and random system of mating and beneficiaries and benefactors of equal reproductive value.

Thus, altruistic behavior is favored when B/C is greater than the average number of altruism alleles per offspring of the benefactor/ average number of altruism alleles per offspring of the beneficiary. The emphasis on progeny follows the suggestion of West Eberhard (1975) cited above. Cost and benefit should be measured in terms of effects on reproductive success. The larger that B/C must be in order to satisfy the inequality, the more restrictive are the circumstances in which altruistic behavior will favor the altruism allele.

Mealey (personal communication) suggests that determining the minimum B/C ratio from the actual number of altruism alleles per offspring of the beneficiary and benefactor is equivalent to using $1/r'$ plus the inclusion of a parameter for allele frequency, representing the effects of inbreeding if all altruism alleles are identical by descent. Thus, the approach employed here resembles the suggestion by Hamilton (1972) that $B/C > (1+F)/2r$ must obtain if the altruistic behavior is favored by selection, where F is the inbreeding coefficient of the benefactor and r is the coefficient of relationship between benefactor and beneficiary.

DIPLOIDY

Altruism allele recessive.

If the altruism allele is recessive then each altruist will possess 2 alleles. The number of altruism alleles per full sibling is:

$$\{1(2pq)^2 + 1.5(2q^2 \cdot 2pq) + 2(q^2)^2\}/\{(2pq)^2 + (2q^2 \cdot 2pq) + (q^2)^2\}$$

where p is the frequency of the dominant allele, q is the frequency of the recessive altruism allele, the bracketed terms are the proportions of each mating pair which will give an altruist among the offspring, while the terms outside the brackets are the average number of altruism alleles in progeny from each mating pair. This fraction reduces to: $2/(2-q)$.

The average number of altruism alleles per progeny of an altruist, assuming outbreeding and random mating with regard to the locus involved in the altruistic behavior is:

$$1(p^2) + 1.5(2pq) + 2(q^2) = 1 + q$$

where the bracketed terms are the frequency of the genotypes of mates of the altruist and the numbers outside the brackets are the average number of altruism alleles per progeny should the altruist mate an individual of the genotype indicated in the brackets.

Therefore, the B/C ratio for selectively favored altruistic behavior toward a parent must be greater than $(1+q)/\{2/(2-q)\}$ where the numerator is the number of altruism alleles per progeny of the benefactor and the denominator is the average number of altruism alleles per progeny of the beneficiary. The fraction varies from 1 when q is 1 to a maximum value of 1.125 when $q=0.5$ (Fig. 1, curve d). Thus, the calculated minimum value is much smaller than the value of greater than 2 calculated with r and only slightly larger than that calculated by r'. In fact, the reproductive value of the altruist is probably lower than the reproductive value of its parents when it is very young and the parents are not old. If this were taken into account, the calculated minimum value for B/C would be even smaller (Charlesworth and Charnov, 1981). In conclusion, aid toward parents may be selected for very easily.

Altruistic behavior toward a full sibling will be favored when B/C is greater than the number of altruism alleles per progeny of the altruist/ the number of altruism alleles per niece or nephew. The number of altruism alleles per niece or nephew of the altruist is:

$$\{1/(2-q) + 0\}p^2 + \{1/(2-q) + 0.5\}2pq + \{1/(2-q) + 1\}q^2 = \{1/(2-q)\} + q$$

where on the left side of the equation the terms outside the brackets are the frequency of genotypes of potential mates of the altruist's full sibling and inside the brackets the second term is the average number of altruism alleles contributed by the sibling's mate to the progeny and 1/(2-q) is the number of altruism alleles contributed by the altruists full sibling to its own progeny. Thus, for altruism toward a full sibling to be favored the following condition must be met:

$$B/C > (1+q)/\{1/(2-q) + q\}$$

Here, B/C varies from approximately 2 when q is close to 0 to 1 when q is 1 (Fig.1, curve a).

Altruism allele dominant.

If the altruism allele is dominant, then the altruist may be homozygous or heterozygous with respect to the locus where the altruism allele is located. Thus, the average number of altruism alleles per altruist is:

$$\{1(2pq) + 2(q^2)\}/\{2pq + q^2\}$$

where the bracketed terms are the proportions of altruists which are heterozygous or homozygous and the numbers outside the inner brackets are the numbers of altruism alleles per altruist. This fraction reduces to: 2/(2-q). The average number of altruism alleles per progeny of the altruist is:

$$1/(2-q) + q = (1 + 2q - q^2)/(2-q)$$

where on the left side of the equation 1/(2-q) is the average number of altruism alleles contributed by the altruist and q is the number contributed by the altruist's mate.

The average number of altruism alleles per full sibling is:

$$\frac{2(q^4) + 1.5(4q^3p) + 1(4p^2q^2) + 0.5(4qp^3) + 1(2p^2q^2)}{q^4 + 4q^3p + 4p^2q^2 + 4qp^3 + 2p^2q^2}$$

where q is the frequency of the altruism allele and p is the frequency of the alternate allele, the bracketed terms are the proportions of each mating pair which will give an altruist among the progeny, while the terms outside the brackets in the numerator are the average number of altruism alleles in offspring from each mating combination. The fraction reduces to:

$$2/(4 - 6q + 4q^2 - q^3).$$

Therefore, altruistic aid to parents will be favored if:

$$B/C > \{(1 + 2q - q^2)/(2-q)\}/\{2/(4 - 6q + 4q^2 - q^3)\}$$

This ratio equals 1 when q=1 but is slightly smaller than the corresponding values for the recessive case when q < 1 (Fig. 1, curve c).

The average number of altruism alleles per niece or nephew of an altruist is:

$$\{1/(4 - 6q + 4q^2 - q^3)\} + q.$$

For aid to full siblings to be selectively favored the following condition must hold:

$$B/C > \{(1 + 2q - q^2)/(2-q)\}/\{1/(4 - 6q + 4q^2 - q^3) + q\}.$$

Again, the ratio varies from approximately 2 when q is very small to 1 when q=1 (Fig. 1, curve b). The calculated minimum B/C ratio for intermediate values of q is

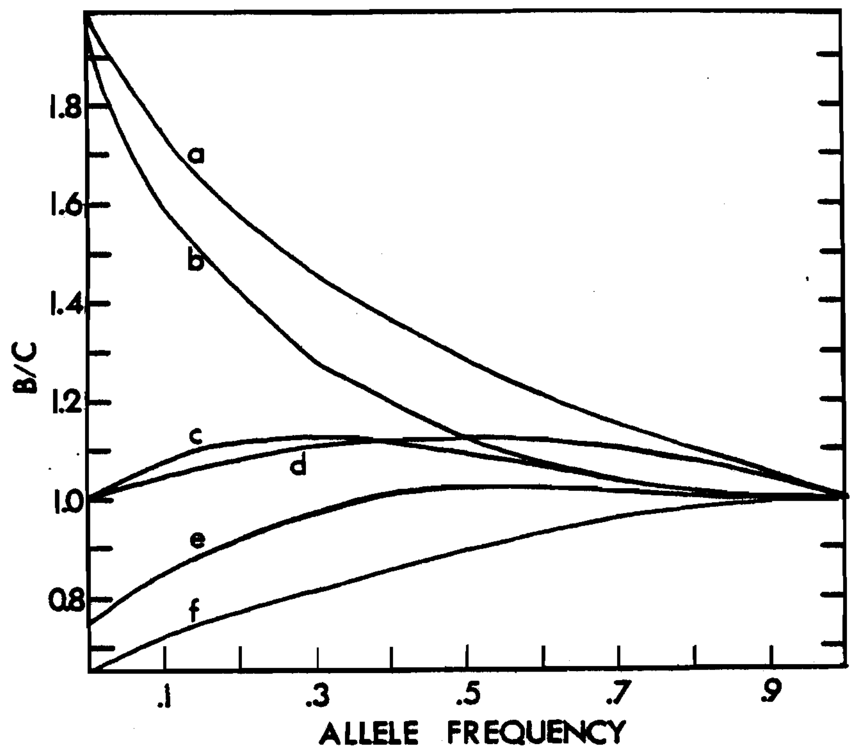

Figure 1. Value of B/C which must be exceeded for selectively favored altruistic behavior as a function of the frequency of the altruism allele in diploid(a-d) and haplo-diploid (e,f) inheritance. a) Aid to full siblings, altruism allele recessive, b) aid to full siblings, altruism allele dominant, c) aid to parents, altruism allele dominant, d) aid to parents, altruism allele recessive, e) aid to parents, altruism allele dominant, and f) aid to parents, altruism allele recessive.

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slightly smaller when the inheritance of the altruism allele is dominant rather than recessive.

HAPLO-DIPLOIDY

Altruism allele recessive.

If the altruism allele is recessive, each female altruist carries 2 altruism alleles and the average number of altruism alleles per female full sibling of the altruist is:

$$1 + \{0.5(2pq) + 1(q^2)\}/\{2pq + q^2\} = (3-q)/(2-q)$$

where on the left side of the equation, 1 represents the number of altruism alleles contributed by the altruist's father to each of his daughters, while the fraction is the average number of altruism alleles contributed by the mother of the altruist with the bracketed terms in the numerator being the frequency of the maternal genotypes capable of producing an altruistic daughter and numbers outside the brackets are the average number of altruism alleles contributed to the daughters.

The average number of alleles per female offspring of an altruistic female is:

$$1(p) + 2(q) = 1 + q$$

where p and q are, respectively, the frequencies of males without and with the altruism allele. Altruism toward parents will be favored when:

$$B/C > (1+q)/\{(3-q)/(2-q)\}.$$

This is less than 1 for $q<1$ (Fig. 1, curve f), suggesting that altruistic behavior will be relatively easily favored by selection. For small values of q, the B/C ratio calculated is similar to that calculated by $1/r'$ where $B/C>2/3$ is expected to favor altruistic behavior.

However, the average number of altruism alleles per female sibling of an altruistic male is:

$$\{0.5(2pq\cdot p) + 1(q^2\cdot p) + 1.5(2pq\cdot q) + 2(q^2\cdot q)\}/\{2pq + q^2\}$$

where the bracketed terms in the numerator are the frequency of the mating genotypes and numbers outside the brackets are the number of altruism alleles per female progeny of such matings. The fraction reduces to:

$$(1 + 2q - q^2)/(2 - q).$$

The average number of altruism alleles per female offspring of an altruistic male is:

$$1(p^2) + 1.5(2pq) + 2(q^2) = 1 + q.$$

Thus, altruistic behavior by males will be favored if:

$$B/C > \{1 + q\}/\{(1 + 2q - q^2)/(2 - q)\} = (2 + q - q^2)/(1 + 2q - q^2),$$

which is greater than for $q<1$. Thus, selection can not so readily select for altruistic behavior in males as in females.

Altruism allele dominant.

If the altruism allele is dominant, then the average number of altruism alleles per sister of an altruist is:

$$\frac{2(q^3) + 1.5(2q^2p) + 1(qp^2) + 1(q^2p) + 0.5(2qp^2)}{(q^2\cdot q) + (2pq\cdot q) + (q\cdot p^2) + (q^2\cdot p) + (2pq\cdot p)} = \frac{2}{(q^2 - 3q + 3)}.$$

The average number of altruism alleles per female progeny of an altruist is dependent upon whether the altruist is homozygous or heterozygous. The probability that the altruist is homozygous is:

$$\frac{1(q^3) \;+\; 0 \;+ 0.5(2q^2p) + \;0\; + \;0}{1(q\cdot q^2) + 0.5(2q\cdot p^2) + 1(2q^2\cdot p) + 1(p\cdot q^2) + 1(p^2\cdot q)} = \frac{q}{2 - q},$$

where on the left side of the equation, the bracketed terms in the denominator are the mating frequencies for genotypes giving an altruistic female and the numbers outside the brackets are the proportion of altruistic progeny from such matings, while in the numerator, bracketed terms are the frequencies of mating genotypes giving homozygous altruists and the terms outside the brackets are the proportion of altruists which are homozygous. The proportion of heterozygous altruists is:

$$(2-2q)/(2-q).$$

Therefore, the average number of altruism alleles per female offspring of the female altruist is:

$$\{(2-2q)/(2-q)\}\{1.5(q) + 0.5(p)\} + \{q/(2-q)\}\{2(q) + 1(p)\} = (1 + 2q - q^2)/(2-q).$$

For altruistic behavior toward parents to be selectively favored the following condition must be satisfied:

$$B/C > \{(1 + 2q - q^2)/(2-q)\}/\{2/(q^2 - 3q + 3)\}.$$

This ratio varies from 1 when $q=1$ to a minimum value of 0.75 when q is close to 0 with values greater than 1 for intermediate values of q (Fig. 1, curve e). These results suggest that with haplo-diploid inheritance, altruistic behavior toward parents which augments the parental production of sisters at the expense of female offspring will be more easily selected for when the altruism allele is recessive. The same result was obtained from a computer simulation of the evolution of altruism in an idealized wasp (Craig, 1979).

CONCLUSION

In the case of diploidy, the formulae developed indicate that the constraints on the expression of altruistic behavior are less severe than expected when the B/C ratio is calculated by 1/r (Mealey, 1980). Also, the minimum B/C ratio necessary for selectively favored altruism depends upon the dominance of the altruism allele both for diploid and haplo-diploid inheritance. Michod (1979) also found the degree of dominance to influence the ease with which an altruism allele could invade an inbred population experiencing weak selection at the locus.

Calculation of the B/C ratio using the number of alleles for altruistic behavior per altruist and recipient does not suggest that aid to non-relatives will be favored under any but the most extreme circumstances (very high B/C) except when the frequency of the altruism allele is high. For example, the average number of altruism alleles in an individual selected at random from a diploid population is 2q where q is the frequency of the recessive allele causing altruistic behavior. Altruistic behavior to non-relatives is favored only when $B/C > (1+q)/2q$ which is very large when q is small. Thus, altruistic behavior is expected to be restricted to interactions between close relations.

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