

The Mathematics of Altruism

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ABSTRACT: The mathematical criterion for the evolution of altruism is more strict than commonly claimed. Specifically, a total loss of individual fitness requires a more than tripling of a sibling's fitness under one-sided risk conditions.

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In Chapter 5 of his book *Sociobiology: The New Synthesis*,¹ E. O. Wilson states that "a genetically based act of altruism...will evolve if the average inclusive fitness of individuals...displaying it is greater than the inclusive fitness of individuals...that do not display it." Then, paraphrasing W. D. Hamilton² he continues "In general, K , the ratio of gain in fitness (of the benefactor) to loss in fitness (of the altruist) must exceed the reciprocal of the average coefficient of relationship (r)". Thus, for altruism to evolve, the gain:loss ratio measured in surviving offspring must be greater than the reciprocal of the degree of relatedness between the altruist and the benefactor.

Although the mathematics is correct, Wilson and others have misapplied it by failing to define "gain" and "loss" comparably. In Wilson's example (pg. 118) when the loss to the altruist is complete (1.0), he states that "the brother's fitness must be more than doubled" for the inclusive fitness of the altruist to be increased. But if we would complete the equation for this example, we would find that the gain:loss ratio equals 1.0 which is less than the inverse of relatedness (2.0). Actually, only a tripling of the brother's fitness would give us a gain:loss ratio equal to 2.0.

The problem lies in semantics and the determination of the value of K . Let us look at four theoretical cases: "A", "B", "C", and "D". "A" represents the ideal case where individual P and his brother Q are both able to reproduce successfully, leaving X offspring each. Each offspring has a coefficient of relationship of $\frac{1}{2}$ with its parent and of $\frac{1}{4}$ with its uncle. The second generation then consists of $2X$ offspring, X of which are $\frac{1}{2}$ related to P and X of which are $\frac{1}{4}$ related to P. P's genetic representation in the next generation is $\frac{1}{2}X + \frac{1}{4}X = \frac{3}{4}X$.

In case "B", P has survived to produce X offspring, but Q has died prematurely leaving no offspring. In case "B" there are X offspring each related $\frac{1}{2}$ to P; therefore P's genetic representation in the second generation is $\frac{1}{2}X$.

Case "C" is the first example involving altruism. P has surrendered his fitness in order to prevent his brother's premature death; Q has survived but P has died leaving no offspring. P's widowed mate now moves in with Q and his mate, helping them to raise more than $2X$ offspring. Since each of Q's offspring are $\frac{1}{4}$ related to their late uncle, P's genetic representation in the next generation is more than $\frac{1}{2}X$, more than if he had not acted altruistically, as in case "B".

In the fourth case, "D", Q's fitness is not in danger, but P manages by sacrificing his own fitness, to increase Q's fitness to more than $3X$. P's genetic representation in the second generation of "D" is thus more than $\frac{3}{4}X$, greater than the ideal case, "A". Only if P can increase his brother's fitness by more than threefold is it in his interest to behave altruistically when his brother's fitness is not in danger.

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Notice at this point that P's inclusive genetic fitness is greatest in case "D" (more than $\frac{3}{4}$), then "A" ($\frac{3}{4}$), then "C" (more than $\frac{1}{2}$), and lastly "B" ($\frac{1}{2}$). While it is to P's advantage for "C" to occur instead of "B", it is not to his advantage if "C" occurs instead of "A". If P were to give up his fitness solely to double his brother's fitness when in fact his brother's fitness was not in danger, he would actually be losing genetic representation in the next generation. As we shall see, Wilson has erroneously defined "gain" in terms of a factor (doubling), but "loss" as absolute.

Mathematically, if we compare case "C", with case "A", we find that the genetic gain to Q was equal to the genetic loss to P; Q's offspring increased from X to 2X while P's decreased from X to zero. The true gain:loss ratio is 1.0, not 2.0 as Wilson implies, and substituting for K and $1/r$, 1 is less than $1/\frac{1}{2}$. Comparing "D" to "A", we find that Q's net gain is more than twice P's loss since his fitness is increased threefold from X to more than 3X. It is here that K becomes more than 2.0 and therefore more than $1/r$. Lastly, in case "C" as compared to case "B", Q receives a gain of more than 2X from zero, whereas in "C" as compared to "A" it is only 1X. Thus, defining both "gain" and "loss" in terms of absolute increase or decrease, the equation shows us that "C" is preferable to "B" (more than 2X is more than $1/\frac{1}{2}$), but not to "A" (1X is less than $1/\frac{1}{2}$).

The same argument can be applied for any degree of relatedness between altruist and benefactor. In examples where the fitness of the benefactor is actually at risk, the minimum absolute gain can be realized by increasing the benefactor's normal number of offspring by the factor $1/r$, or for multiple benefactors of relation r , by $1/br$ where b equals the number of benefactors. But when the only potential loss is that of the altruist, minimum absolute gain must be added to the original number of offspring, giving $X+X(1/r)$, or $X+X(1/br)$ for multiple benefactors.

In finishing, it is interesting to note that when ranking cases "A"-"D" in terms of their ability to evolve altruism, we rank the "D" over "A" over "C" over "B", but in terms of the total number of offspring they produce, they rank "D" over "C" over "A" over "B". In the case where the altruist gives up his fitness for more than a doubling but less than a tripling of his brother's fitness, he will be increasing the total number of their combined offspring yet decreasing the evolution of altruism. Knowing that the increase in gain of fitness from case "C" to case "D" is again as large as the number of offspring in the "ideal" state, it is even more impressive that altruism has evolved at all.

¹ Edward O. Wilson, Sociobiology: The New Synthesis, Belknap Press, Harvard University, Cambridge, Massachusetts, 1975.

² W. D. Hamilton, The Genetical Evolution of Social Behavior. I., J. Theor. Biol. (1964) 7, 1-16.