



Revisiting Hamilton's Rule

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REVISITING HAMILTON'S RULE

In an earlier note (Xia 1993) I compared the fitness gains of helping offspring with the gains of helping full siblings. I concluded that there is a deterministic cost to sibling-helping individuals relative to offspring-helping individuals because R , defined as the probability of the recipient carrying the allele of its helper, is smaller for sibling-helping individuals than for offspring-helping individuals with a finite litter size. I also concluded that there is a stochastic cost to sibling-helping individuals relative to offspring-helping individuals in a finite population because the variance of fitness gain for sibling helping is greater than that for offspring helping. These together imply that genes responsible for offspring helping have an evolutionary advantage over genes responsible for sibling helping.

These conclusions differ from commonly accepted kin-selection theory, and questions have been raised concerning their validity (Lacy 1995). Three major concerns have been expressed. First, I might have misinterpreted R in Hamilton's rule. Second, the difference in R between sibling helping and offspring helping might be attributable to incorrect calculations. Third, the stochastic cost in my note might be an artifact due to my incorrect formulation of inclusive fitness.

I believe that these three concerns are representative because I have also heard of similar concerns from S. Krackow, A. Bourke, and S. P. Otto (personal communications) and from an anonymous reviewer for *American Naturalist*. In this note I will attempt a straightforward explanation to validate the two conclusions in my earlier note (Xia 1993).

In the first section, I will show that I did not misinterpret Hamilton's rule in my previous note (Xia 1993) and that it is correct and convenient to use R as the probability of the recipient carrying the allele of its helper when there are an offspring-helping allele and a sibling-helping allele (O and S, respectively, in Xia 1993) at the same locus. Using R in this way, I have treated not only the benefit to the O allele from offspring helping and the benefit to the S allele from sibling helping but also included the benefit to the O allele from sibling helping and the benefit to the S allele from offspring helping.

Second, I will show that R is indeed smaller for sibling-helping individuals than for offspring-helping individuals when litter size is finite. In doing so, I have set the litter size at two for simplicity. This section is crucial for establishing the deterministic cost of sibling helping because, if R is not smaller for sibling helping than for offspring helping, there is no deterministic cost to sibling helping no matter which way one prefers to write down Hamilton's rule. I will also show that, when the cost of helping is negligible, R does not differ between sibling helping and offspring helping, and the deterministic cost disappears.

In the third section, I will show the greater stochastic cost of sibling helping

relative to that of offspring helping, by again setting the litter size at two. I will also show that this stochastic cost is independent of the deterministic cost. I hope that these explanations involving a simpler situation will help to clarify the confusion arising from my earlier note (Xia 1993).

A. R IN HAMILTON'S RULE

Lacy (1995) thinks that I erred in interpreting R in Hamilton's rule as the probability of the recipient of helping behavior carrying the same allele as its helper. To illustrate that my interpretation of R is not an error, I will first derive Hamilton's rule for sibling helping by calculating marginal allele fitnesses and then show why, when dealing with an offspring-helping allele and a sibling-helping allele at the same locus, it is both correct and convenient to use R as the probability of the recipient carrying the allele of its helper.

Let A be the gene that causes its carrier to help its full sibling, and let a be the alternative allele that does not confer help. An AA , Aa , or aa individual will offer two doses, one dose, or no help, respectively, to its sibling. Each dose of help will have a benefit, B , to the sibling and a cost, C , to the helper. Let p and q be the allelic frequencies of A and a , respectively, in the population with random mating and a large population size. For simplicity, I assume that each individual will have just one sibling of the same age to receive help. Without receiving or giving help, an individual has a fitness of one.

The probability that an AA individual has an AA sibling is

$$P_{AA-AA\text{ sib}} = \frac{1 + 2p + p^2}{4}, \quad (1)$$

and its probability of having an Aa sibling is

$$P_{AA-Aa\text{ sib}} = \frac{q + pq}{2}. \quad (2)$$

Its fitness, W , is therefore

$$\begin{aligned} W_{AA} &= 1 - 2C + P_{AA-Aa\text{ sib}}B + P_{AA-AA\text{ sib}}2B \\ &= 1 + B(1 + p) - 2C. \end{aligned} \quad (3)$$

Similarly, the fitnesses of Aa (W_{Aa}) and aa (W_{aa}) individuals are

$$W_{Aa} = 1 + B\left(\frac{1}{2} + p\right) - C \quad (4)$$

and

$$W_{aa} = 1 + Bp, \quad (5)$$

respectively. Note that $B \times p$ is a benefit to the population due to helping by A -carrying individuals. Assuming weak selection (to satisfy the Hardy-Weinberg equilibrium), we get the fitnesses of alleles A and a as

$$W_A = \frac{p^2 W_{AA} + pq W_{Aa}}{p^2 + pq} = 1 + \frac{3Bp}{2} + \frac{B}{2} - C - pC \quad (6)$$

and

$$W_a = \frac{q^2 W_{aa} + pq W_{Aa}}{q^2 + pq} = 1 + \frac{3Bp}{2} - pC. \quad (7)$$

For allele A to spread, W_A must be greater than W_a . This gives

$$\frac{B}{2} - C > 0, \quad (8)$$

which is the conventional (Hamilton's) rule for sibling helping. We will get exactly the same result if sibling helping is replaced with parents helping offspring.

The fitness increment, ΔW , for an A allele through the helping behavior of an AA genotype can be shown to be identical to what one would get on the basis of my interpretation of R . From equation (3), the fitness increment due to a single copy of allele A through helping behavior of an AA individual is

$$\Delta W_A = \frac{W_{AA} - 1}{2} = B \left(\frac{1}{2} + \frac{p}{2} \right) - C = BR - C, \quad (9)$$

where $R = 1/2 + p/2$, which is exactly the allelic frequency of A in full siblings of an AA individual. However, equation (5) shows a fitness increment of $B \times p$ to aa individuals accrued from sibling helping by A-carrying individuals. If W_{aa} is set to one, then $W_{AA} - W_{aa}$ would be equal to $B - 2 \times C$. This leads to $\Delta W_A = B/2 - C$, which corresponds exactly to Hamilton's $R \times B - C$, where $R = 1/2$ is the coefficient of relationship for full siblings. We would have known this had we just compared equations (6) and (7).

Given this, why should I deviate from the convention and use R as the probability of the recipient of helping behavior carrying the same allele as its helper, as I did in the previous note (Xia 1993)? The answer, which I hope is already obvious, is that in that note (Xia 1993) both O and S alleles are helping. If we want to write down the fitness increment to the O allele due to offspring helping only (relative to an allele that codes for no help), then the fitness increment is equal to $B/2 - C$ according to Hamilton's rule. But there is also a benefit to the O allele from sibling helping, and this benefit, as is specified in equation (5) of the present note, equals $p \times B/2$. Thus, the total fitness increment to the O allele due to offspring helping and sibling-helping is

$$\Delta W_O = \frac{B}{2} - C + \frac{Bp}{2} = \left(\frac{1}{2} + \frac{p}{2} \right) B - C = RB - C, \quad (10)$$

and the total fitness increment to the S allele due to sibling helping and offspring helping is identical in form. It is equation (10) that prompted me to use R as the probability of the recipient of helping behavior carrying the same allele as its helper in my earlier note (Xia 1993). Using it in this way maintains the form of

Hamilton's rule in the situation in which O and S, both helping, are alternative alleles at the same locus.

Now the total benefit to the O allele from offspring helping and sibling helping is $\Delta W_O = R_{OO\text{-off}} B - C$, where $R_{OO\text{-off}}$ is the allelic frequency of O in offspring of an OO individual. The equivalent for the S allele is $\Delta W_S = R_{SS\text{-sib}} B - C$, where $R_{SS\text{-sib}}$ is the allelic frequency of A in full siblings of an AA individual. Thus, to demonstrate a deterministic cost of sibling helping relative to offspring helping, one needs only to prove that $R_{SS\text{-sib}}$ is smaller than $R_{OO\text{-off}}$. To demonstrate a stochastic cost of sibling helping relative to offspring helping, one needs only to show that $R_{SS\text{-sib}}$ is more variable than $R_{OO\text{-off}}$. In the last section of this note, I will show that $R_{SS\text{-sib}}$ is more variable than $R_{OO\text{-off}}$ even when $R_{SS\text{-sib}}$ and $R_{OO\text{-off}}$ have a mean value identical to each other.

It is true that I did not make a clear statement about why I used R in my own way in the earlier note (Xia 1993), assuming that the reader would notice the difference between a model of sibling helping and nonhelping and a model of sibling helping and offspring helping. This assumption now seems unwarranted, and I apologize to everyone suffering from the resulting confusion.

B. THE DIFFERENCE IN R BETWEEN OFFSPRING HELPING AND SIBLING HELPING

Lacy writes (1995) that I erred in assuming that the presence of an allele in one individual in a sibship would change the probability that the allele was transmitted from the parent to other offspring in the sibship. In fact, I did not make this assumption. What I did state (Xia 1993) is that, given a finite litter size, R for the sibling-helping genotype should be smaller than R for the offspring-helping genotype. I will now elaborate this point for the special case in which the litter size equals two.

Table 1 shows a mating table with the resulting distribution of offspring pairs. This table can be used to obtain allelic frequencies among siblings of an AA individual. We already know that, when defining p as the frequency of the A allele in the population, the frequency of the A allele among offspring of an AA helper is $1/2 + p/2$. We now consider whether the frequency of the A allele among siblings of an AA helper is equal to, or smaller than, $1/2 + p/2$.

I will consider two extreme cases. First, assume the cost of helping to be so great that the AA sibling helper would die a Haldanian death for its siblings or would, like a bee, die of stinging an invading enemy for its siblings. This implies that, in AA-AA offspring pairs (table 1), only one AA individual can perform this heroic act, while the potential of help in the other AA individual is wasted. In other words, the AA individual that has performed the helping act is dead forever and can no longer receive help from its sibling to boost its fitness. This is what I meant in my earlier note (Xia 1993, p. 176) by "excluding this SS individual," where S is the allele for sibling helping. Given this, the frequency of an A allele in siblings of an AA individual is

$$p_{AA\text{-sib}} = \frac{\frac{\text{SUM1}}{2} + \frac{\text{SUM2}}{4}}{\frac{\text{SUM1}}{2} + \frac{\text{SUM2}}{2} + \frac{\text{SUM4}}{2}} = \frac{3 + 2p - p^2}{7 - 2p - p^2}, \quad (11)$$

TABLE I
MATING TABLE AND THE RESULTING DISTRIBUTION OF OFFSPRING PAIRS

PARENTS	ALLELE FREQUENCY	OFFSPRING					
		AA-AA	Aa-AA	Aa-Aa	AA-aa	Aa-aa	aa-aa
AA × AA	$P_1 = p^4$	1	0	0	0	0	0
Aa × AA	$P_2 = 4p^3q$	1/4	1/2	1/4	0	0	0
Aa × Aa	$P_3 = 4p^2q^2$	1/16	1/4	1/4	1/8	1/4	1/16
AA × aa	$P_4 = 2p^2q^2$	0	0	1	0	0	0
Aa × aa	$P_5 = 4pq^2$	0	0	1/4	0	1/2	1/4
aa × aa	$P_6 = q^4$	0	0	0	0	0	1
SUM		$SUM1 = p^2(1 + p)^2/4$	$SUM2 = p^2q(1 + p)$	$SUM3 = pq(1 + pq)$	$SUM4 = p^2q^2/2$	$SUM5 = pq^2(1 + q)$	$SUM6 = [q^2(1 + q)^2]/4$

NOTE.—Alleles A and a are at the same locus. Data were compiled by S. P. Otto.

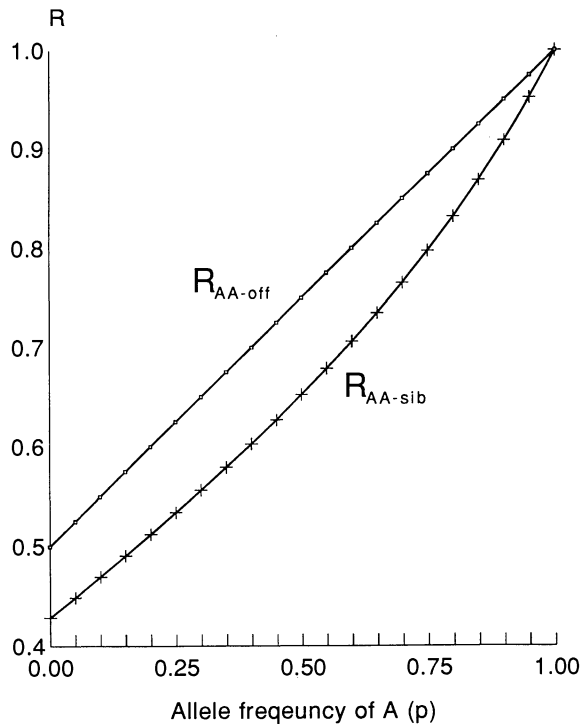


FIG. 1.—The probability of the recipient of helping behavior carrying the same allele as its helper (R) as a function of allele frequency. The probability R is smaller for an AA individual helping its full siblings than for an AA mother helping its offspring when the cost of helping is extreme (i.e., death). R_{AA-sib} , R for the AA individual helping its siblings; R_{AA-off} , R for the AA mother helping its offspring. Probabilities R_{AA-sib} and R_{AA-off} become identical when the cost of helping is negligible. Litter size is two.

which is clearly smaller than $1/2 + p/2$ for all values of p , except when $p = 1$ (fig. 1; SUM1, . . . , SUM6 are defined in table 1.)

The effect of litter size on p_{AA-sib} should be intuitively obvious. For example, if the litter size is four, then all three AA individuals in an AA-AA-AA-AA sibship will have help recipients with the frequency of A equal to one, and only one of the four will lose its chance of helping. That is, only one-fourth, rather than one-half, of AA individuals in an all-AA sibship are excluded from the calculation. The effect of this lost chance of helping for the last AA sibling is therefore less than that when the litter size is two. At this point I can see that equations (5) and (6) in my earlier note (Xia 1993), because of faulty reasoning, exaggerated the difference in R between sibling helping and offspring helping, especially when the litter size is small or when the sibling-helping gene is of low frequency. However, the equations do make correct qualitative predictions concerning the effect of litter size on R .

Now assume that the cost of helping is so small that its effect on the fitness of

the helping individual is entirely negligible. This implies that the help between two AA individuals in an AA-AA sibship will be fully reciprocal, so that both AA individuals in an AA-AA sibship will have a help recipient with the frequency of the A allele equal to one. Therefore,

$$p_{AA-sib} = \frac{SUM1 + \frac{SUM2}{4}}{SUM1 + \frac{SUM2}{2} + \frac{SUM4}{2}} = \frac{1}{2} + \frac{p}{2}, \quad (12)$$

which equals exactly the allelic frequency of A among offspring of an AA mother.

Most helping behavior should lie between the two extremes shown in equations (11) and (12). If the helping cost is great (e.g., a Haldanian death), then a large litter size is required; if the helping cost is small so that helping is fully reciprocal (e.g., two male lions helping each other to defend a territory), then a large litter size is not required. Given the small litter size in human populations, the Haldanian death should be a very rare event.

In the earlier note (Xia 1993) I specifically distinguished two kinds of sibling helping at the very beginning of my argument, one being helping siblings directly and the other being helping parents to raise more offspring. In the latter case, the indirect beneficiary (i.e., the future siblings) should have an allelic frequency independent of those that have already been born because the gametic pool in most cases approximates an infinite population. However, in the former case, when the homozygote is helping siblings directly at substantial cost to the helper itself (e.g., death), the allelic frequency of the beneficiary (which I assumed to be of limited number) is not the same as the allelic frequency of the sibship taken as a whole, including the homozygous helper. I stated explicitly that it was this former case that I would consider in my note, and I hope that this point has been made clearer in the present note.

C. THE STOCHASTIC COST

Lacy (1995) thinks that the stochastic cost in my earlier note is an artifact and that it would disappear had I interpreted R in $R \times B - C$ as the coefficient of relationship. To prove that this is not the case, I will now use r as the coefficient of relationship and show how the stochastic cost would arise.

According to Wright's (1922) original definition, the coefficient of relationship is written as

$$r_{II} = \frac{2f_{II}}{\sqrt{(1 + f_I)(1 + f_J)}}. \quad (13)$$

In my previous note (Xia 1993), a randomly mating population was assumed so that f_I and f_J (in Wright's terms) are both zero. The coefficients of relationship

between full sibs (r_{sib}) and between parents and offspring ($r_{\text{p-o}}$) are therefore $2 \times f_{\text{sib}}$ and $2 \times f_{\text{p-o}}$, respectively. Because both f_{sib} and $f_{\text{p-o}}$ are expected to be one-fourth, it is natural for one to think that r_{sib} and $r_{\text{p-o}}$ are identical.

But r_{sib} and $r_{\text{p-o}}$ are not identical. The latter has zero variance because any random pair of parent-offspring would have a genetic relatedness of one-half. The former (r_{sib}), however, is variable. For example, if paternal genotype and maternal genotype are $A_{1f}A_{2f}$ and $A_{1m}A_{2m}$, respectively, for one particular locus, then two offspring could both be $A_{1f}A_{1m}$ (here the two offspring have a genetic relatedness of one), or one offspring could be $A_{1f}A_{1m}$ and the other $A_{2f}A_{2m}$ (here the two offspring have a genetic relatedness of zero). This gives r_{sib} an expected mean of 0.5 and a variance of

$$\text{Var} = \frac{2\left(\frac{1}{2} - \frac{1}{2}\right)^2 + \left(1 - \frac{1}{2}\right)^2 + \left(0 - \frac{1}{2}\right)^2}{4} = \frac{1}{8}. \quad (14)$$

Note that, in the above fictitious example, no maternal allele is carried by the father. So the allelic frequency of the maternal genes is assumed to be effectively zero in the population.

This variance associated with r_{sib} is the source of the stochastic cost discussed in my previous note (Xia 1993). When a mother helps her offspring, she always gains a fitness increment of $B/2 - C$ in our fictitious population. When an individual helps his full siblings, his fitness gain is uncertain and will fluctuate around $B/2 - C$. As a result of Gillespie's works (1972, 1973a, 1973b, 1974, 1975, 1977), most of us now know that this uncertainty has a fitness cost.

Table 1 allows the derivation of a more general equation than equation (14). To show that the stochastic cost is present even when the helping is fully reciprocal, I will use mean $R = 1/2 + p/2$ for both offspring helpers and sibling helpers. The variance of R for an AA sibling helper is

$$\begin{aligned} \text{Var}_{\text{AA-sib}} &= \frac{\text{SUM1}(1 - R)^2 + \frac{\text{SUM2}}{2} \left(\frac{1}{2} - R\right)^2}{p^2} \\ &+ \frac{\frac{\text{SUM4}}{2} (0 - R)^2}{p^2} = \frac{1}{8} - \frac{p^2}{8}. \end{aligned} \quad (15)$$

Equation (15) makes intuitive sense. We know that the parents of an AA individual must be $A?$ and $A?$, where $?$ is unknown but has a probability, p , of being A and a probability, $1 - p$, of being a , the alternative allele. If $p = 1$, then the parents must both be AA . So the variance is zero. When $p = 0$, then the parents must both be Aa and Aa . So the variance reaches the maximum of one-eighth, which is what we have derived in equation (14).

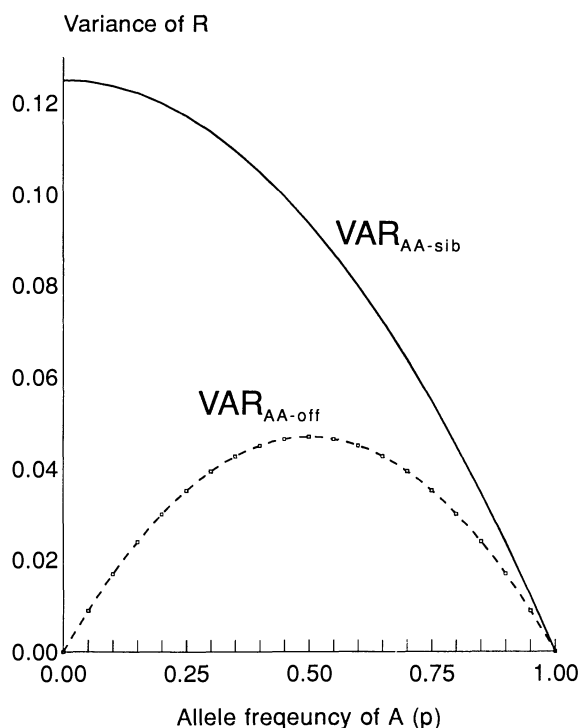


FIG. 2.—The variance of R , the probability of the recipient of helping behavior carrying the same allele as its helper, as a function of allele frequency. The variance is greater for an AA individual helping its siblings than for an AA individual helping its offspring. R_{AA-sib} , variance of R for the AA individual helping its siblings; R_{AA-off} , variance of R for the AA mother helping its offspring. Litter size is two.

The variance of R for an offspring-helping mother is

$$\begin{aligned} \text{Var}_{AA-off} &= \frac{P1(1 - R)^2 + \frac{P4}{2} \left(\frac{1}{2} - R\right)^2}{p^2} \\ &+ \frac{\frac{P2}{2} \left[\frac{1}{4} (1 - R)^2 + \frac{1}{2} \left(\frac{3}{4} - R\right)^2 + \frac{1}{4} \left(\frac{1}{2} - R\right)^2 \right]}{p^2} \quad (16) \\ &= \frac{3}{16} pq. \end{aligned}$$

Equation (16) also makes intuitive sense. If $p = 0$, then the mating partner of the AA individual is aa. So all offspring will be identical, and the variance will equal zero. If $p = 1$, then the mating partner is AA. Again, all offspring will be identical. The greatest variance is achieved when $p = q = 0.5$. Evidently, the variance of R for offspring helping is smaller than that for sibling helping (fig. 2).

It is important to realize that R in Hamilton's $R \times B - C$ is not a constant but a variable with its mean and variance. The variance of R is greater for sibling helping than for offspring helping, which gives rise to the stochastic cost to sibling helping relative to offspring helping. Any factor that increases the variance of R will increase the stochastic cost and vice versa.

In summary, there is a deterministic and a stochastic cost associated with sibling helping relative to offspring helping. The conclusions reached in my earlier note (Xia 1993) are generally valid.

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