NOTES AND COMMENTS

A SIBLING IS AS VALUABLE AS AN OFFSPRING: REPLY TO XIA

Xia (1993) presented a single-locus model to compare the inclusive fitness of individuals helping siblings with the inclusive fitness of those helping offspring. From his model, he argued that helping offspring is more advantageous evolutionarily and that the differential is dependent on both the frequency of helping alleles in the population and the number of offspring per sibship. Unfortunately, Xia erred in his formulation of inclusive fitness and made an error in calculating probabilities of allele sharing. Correcting Xia's errors leaves Hamilton's rule, $RB - C > 0$, intact and accurate.

Xia's first error was in his interpretation of R as the probability of the recipient of helping behavior carrying the same allele as its helper. To calculate fitness differentials caused by helping behavior, one must calculate not the probability that the helper and recipient share alleles but the probability that they share alleles identical by descent from a common ancestor (Hamilton 1964). Therefore, R should be the "coefficient of relationship" between the individuals (0.5 between siblings or between a parent and offspring for autosomal loci in sexually reproducing diploid organisms). The reason that alleles shared, but not identical by descent, are not included in calculations of inclusive fitness is that benefits to individuals sharing an allele independently transmitted through the pedigree will be exactly the same as benefits to individuals carrying the alternative allele. Except in the case of shared alleles identical by descent with those of the helper, alleles conferring helping behavior and those that do not will receive equal benefits from the helping behavior of others: No differential in fitness between the alternative alleles will result. To see that this is the case, one need only consider an allele that causes its bearer to disperse help to others randomly. By Xia's formulation (see his eqq. [9] and [11]), if inclusive fitness is calculated on the basis of the probability of helping an individual sharing the allele, regardless of whether that sharing is due to its being identical by descent, such blindly altruistic alleles would be favored if they were common, as most of the recipients would share the allele. Yet the fact that most help would go to those with the helper allele is irrelevant; what matters is that all individuals, regardless of genotype, would have the same probability of receiving help. All of the terms that contain products of p or q should have been omitted from Xia's equations.

Xia also erred by assuming that the presence of an allele in one individual

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within a sibship would change the probability that the allele was transmitted from the parent to other offspring in the sibship (see his eqq. [5] and [6]). Although the expected frequency in a sibship of an allele carried by a parent is 0.50 (plus the irrelevant contribution due to sharing alleles not by common descent), knowledge that the allele has been transmitted to one offspring does not change the wholly independent probability that the allele was also transmitted to any other offspring. (Flipping a coin once and getting heads does not make it more likely that the next toss will produce tails.) Because Mendelian alleles are transmitted independently, only Xia's equations that assume an infinite number of offspring in the sibship can be correct.

Making both the above corrections to Xia's model yields $W_o = W_s = B/4 + C$ for the increments to the fitness of offspring helpers and sibling helpers, which is identical to Hamilton's rule, as B in Xia's model is the benefit conferred by a homozygous helper or twice the benefit provided per helper allele. Thus, there is no deterministic cost to helping siblings rather than offspring.

Xia also argued for a stochastic cost of helping siblings rather than offspring. However, the stochastic effect in his model is due entirely to his incorrect formulations of inclusive fitness. As Xia points out, the stochastic effect disappears when the number of offspring per sibship approaches infinity: The effect disappears if allele transmission to multiple offspring is viewed properly as a series of independent events and if only shared alleles identical by descent are considered. For either a sibling or an offspring, the probability of sharing an allele identical by descent is 0.50, and, as the allele is either shared once or not at all, the binomial variance in the number of shared copies is $pq = 0.25$.

It is interesting to note the one special case in which there can be a genetic difference between helping siblings and helping offspring, but the advantage goes to those that help siblings. To the extent that helping behavior is due to the genotypic combination at a locus rather than additive effects of alleles, siblings will more commonly share the helping trait than will a parent and offspring, because siblings can share both alleles at a locus identical by descent, with a probability of 0.25. Such dominance interactions are not heritable, however, as genotypes are split up by Mendelian segregation each generation. Thus, the greater phenotypic correlation among full siblings than between parent and offspring is relevant to the evolution of helper alleles only if the helping behavior is at least in part a case of reciprocal altruism in which helpers can expect to accrue benefits to their direct fitness (in addition to increments to inclusive fitness indirectly, through the increased fitness of kin) because genotypically identical individuals receiving help provide help in return.

As an explanation for the evolution of social behaviors through effects on inclusive fitness, Hamilton's rule does not need to be overstretched: The rule is so powerful because it is simple, intuitive, and quantitatively precise.

LITERATURE CITED

Hamilton, W. D. 1964. The genetical theory of social behaviour. I, II. Journal of Theoretical Biology 7:1–52.

Xia, X. 1993. A full sibling is not as valuable as an offspring: on Hamilton's rule. American Naturalist 142:174–185.

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