

Re: Hamilton's rule

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- *From:* Guy Hoelzer <hoelzer@xxxxxxx>
 - *Date:* Wed, 19 Oct 2005 19:14:06 -0400 (EDT)
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in article [dj603t\\$kb4\\$1@xxxxxxxxxxxxxxxxxxxxxx](#), Catherine Woodgold at [an588@xxxxxxxxxxxxxxxxxxxxxx](#) wrote on 10/19/05 10:34 AM:

> Guy Hoelzer (hoelzer@xxxxxxx) writes:

>> in article [dj1v9g\\$1p6k\\$1@xxxxxxxxxxxxxxxxxxxxxx](#), Perplexed in Peoria at

>> [jimmenegay@xxxxxxxxxxxxxxxxxxxxxx](#) wrote on 10/17/05 9:56 PM:

>> As we know from Ohta's Nearly

>> Neutral Theory, very weak selection pressure is virtually the same as no

>> selection pressure at all, leaving alternative alleles free to drift.

>

> (A)

> Only if it's really extremely weak. Suppose it's so weak that

> in the time it would normally take for genetic drift to wipe out

> a gene that started as being in half of a large population, the

> weak selection pressure only increases the number of individuals

> with the gene by 1. Well! The gene has just greatly increased

> its chance of survival, then, hasn't it? Instead of being

> completely wiped out, there's still this one individual with

> it. It would then have something like a 50% chance of

> soon getting completely lost, and a 50% chance of continuing,

> with perhaps about as much chance of taking over the whole

> population by genetic drift as of being wiped out later.

>

> I consider weak selection pressure to be a very important

> factor in evolution. To put it another way: you can neglect

> it if you choose to, but I find it quite interesting.

You might find Ohta's work on Nearly Neutral Theory interesting reading. Her theory predicts that selection will have virtually no influence when:

$$s \leq 1/2N_e$$

for diploid populations (s = selection coefficient; N_e = effective population size). You may consider this degree of selection to be large or small, but the question is really how often does selection reach this degree of intensity for traits with a reasonable amount of heritable variation. In any case, this equation captures the point I was making.

>> My

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>> contention is that the extent of kin selection pressure (the strength of kin selection) becomes very weak as the altruism allele becomes common.

>

> (B)

> I disagree. Even if 99.99% of the population has the altruism gene, the individuals who do not have it face a quite significant probability that their siblings and close relatives don't have it either: something on the order of 0.5, 0.25 etc., not 0.0001. > This lack of the gene in their siblings can then provide quite a considerable impact on the fitness of those individuals > without the gene, causing considerable selection pressure against > individuals without the gene.

I think we have pretty different expectations of the strength of selection generated by altruism. In a mature social system, cooperation and altruism may have become critical for successful participation in the society. At this stage it could indeed be very damaging to one's fitness if they forego social amenities. This is not the situation addressed by Hamilton's model, however. He asked how altruistic behavior could get started in an essentially asocial system. IMHO the fitness effects of receiving altruism would typically be quite modest in this situation. Similarly, failing to receive altruism in a nearly asocial system would not effect fitness much either. We often imagine large effects to help us understand the model, and I think this is very useful. My skeptical view of the role of kin selection in nature, on the other hand, comes from the next phase of model processing where you narrow the realm of the model to realistic parameter values. We may disagree on that range, but that is a purely empirical question.

It is interesting that you flip the coin this way to consider the disadvantage of being in a family without the altruism allele, rather than focusing on the advantage of being in a family with the altruism allele. It is a good way to make your point. On the other hand, relatedness (r) becomes a poor criterion for discriminating those likely to carry the allele from those unlikely to carry the allele once the allele reaches intermediate frequencies. At that point, an altruist would do just about as well by the altruism allele to distribute its generous behaviors randomly, and that might avoid costs of kin discrimination. At that point the altruist would do even better by the altruism allele to play the tit-for-tat game, than it would through kin discrimination. Another factor that diminishes the strength of kin selection at intermediate frequencies of the altruism allele in my view is that the effectiveness of kin selection would be optimized by being twice as altruistic toward homozygotes compared with heterozygotes. To the extent that heterozygotes benefit by receiving altruism, they increase the frequency of the less common allele. When the altruism allele exceeds a frequency of 50%, altruism toward heterozygotes has the net effect of favoring the non-altruistic allele. Of course, altruism toward heterozygotes is a key to the effectiveness of kin selection when the altruism allele is very rare.

>> In

>> fact, I think it would typically become negligible even at intermediate

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>> frequencies of the altruism allele (say above 20 or 30%).

>

> I completely disagree (see two arguments above).

Consider my counter arguments.

>> To be clear, the validity of the kin selection model is NOT dependent on

>> allele frequencies, however the influence of kin selection over the

>> evolutionary process IS dependent on allele frequencies. I am not arguing

>> that kin selection is an example of a frequency dependent selection model.

>

> To be honest, I don't understand the above paragraph at all.

I'm not sure how to say it more clearly, or rather how to say it in a way that would work for you. Try this. The distinction I am making is analogous to the distinction between statistical significance and biological significance. The former is utterly unimportant in the absence of the latter. Regarding kin selection, I am arguing that the logic of the model is equally valid for all frequencies of the allele, hence the validity of your coin flipping perspective above, but that the evolutionary force generated by kin selection becomes so weak when the altruism allele is no longer rare that it loses its relevance to the evolutionary process.

>>> Or are you saying that 'rb>c' remains valid in determining the direction

>>> of the evolutionary force, regardless of frequency, but that the

>>> magnitude of the force depends upon frequency? If that is your position

>>> then I apologize unconditionally.

>>

>> Oops. I should have read this first. This is indeed my position.

>>

>> Guy Hoelzer

>

> I would need a quantifiable definition of "evolutionary force"

> before I could decide whether I agree with the above.

> I suspect I disagree with it (see my argument labelled "(B)" above).

I am tempted to bring up the issue of response to selection, but that is called "R", which has been co-opted in this discussion for a different meaning. This wouldn't be directly responsive to your request anyway.

One standard way to quantify the force of selection is with the selection coefficient. [Jim McGinn – Please don't jump all over me for using the term "force" improperly. I am admittedly using it in a metaphorical sense as applies universally in discussions of evolutionary "forces."] The selection coefficient is the difference in relative fitness between the best-adapted phenotype (or genotype in Pop Gen models) and that of some other, less well-adapted phenotype (or genotype). Selection is generated by fitness differences and the selection coefficient aims to measure the extent of those differences. Under standard population genetic models of natural selection (assuming infinite population size to eliminate drift), the strength of selection can be measured directly as the rate of change in

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allele frequencies in a population, and it can be nicely estimated by considering the fitness difference between pairs of individuals selected at random in the population.

Guy

• *Follow-Ups:*

◆ **Re: Hamilton's rule**

◇ *From:* Perplexed in Peoria

• *References:*

◆ **Re: Hamilton's rule**

◇ *From:* John Edser

◆ **Re: Hamilton's rule**

◇ *From:* Catherine Woodgold

• Prev by Date: **Re: Hamilton's Rule is Xeno's Paradox (was Re: Underestimating 'r')**

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