Re: Hamilton's rule

Source: http://sci.tech−archive.net/Archive/sci.bio.evolution/2005−11/msg00274.html

- *From*: Guy Hoelzer <hoelzer@xxxxxxx>
- *Date*: Fri, 18 Nov 2005 13:25:34 −0500 (EST)

in article dliqtbohd1@xxxxxxxxxxxxxxxxxxx, Perplexed in Peoria at
jimmenegay@xxxxxxxxxxxxx wrote on 11/17/05 12:58 PM:

> "Guy Hoelzer" <hoelzer@xxxxxxx> wrote in message
> news:dlh6sj$274$1@xxxxxxxxxxxxxxxxxxxxxx
>> in article dlft8t$2fog$1@xxxxxxxxxxxxxxxxxxx, Perplexed in Peoria at
>> jimmenegay@xxxxxxxxxxxxx wrote on 11/16/05 10:20 AM:
>>
>>> "Guy Hoelzer" <hoelzer@xxxxxxx> wrote in message
>>> news:dldgfc$1drk$1@xxxxxxxxxxxxxxxxxxxxxx
>>>> in article dl58qa$p8l$1@xxxxxxxxxxxxxxxxxxx, Catherine Woodgold at
>>>> an588@xxxxxxxxxxxxxxxxxxx wrote on 11/12/05 9:29 AM:
>>>>
>>>>> Guy Hoelzer (hoelzer@xxxxxxx) writes:
>>>>>> My confusion is rearing its ugly head again. If the axes of the graph
>>>>>> are "frequency in focal individual (Y axis) vs frequency in population (X
>>>>>> axis)", then I don't see how dominance/recessiveness can influence the
>>>>>> lines at all. What am I missing?
>>>>>
>>>>> One of the lines is labelled "donor". The only individuals
>>>>> who act out the "donor" phenotype are the ones which have
>>>>> the set of genes that code for altruism. If altruism is
>>>>> a recessive trait, then all of the "donors" must have
>>>>> two copies of the altruism gene. Therefore the frequency
>>>>> in the "donor" focal individual is always 1 if altruism
>>>>> is a recessive trait.
>>>>>
>>>>> But if the altruism gene
>>>>> is dominant, then the set of "donors" includes some
>>>>> individuals with one copy of the gene and some individuals
>>>>> with two copies of the gene. If an individual is
>>>>> observed to carry out an altruistic act, or if it
>>>>> finds itself experiencing an overwhelming urge to
>>>>> carry out an altruistic act, then an observer
>>>>> (or the organism itself) can conclude that the
>>>>> individual has one or two copies of the altruism gene.
>>>>> The expected frequency in this individual can thus be
>>>>> predicted to lie between 0.5 and 1 (closer to 1 if
>>>>> the altruism gene is very common in the population).

>>>>
>>>> Maybe I should have said more. All of this was apparent to me. In the
>>>> artificially restricted world of modeling perfect dominance/recessiveness
>>>> the starting point of the donor line would be 0.5 (pure recessiveness) or
>>>> 1.0 (pure dominance). In either case, however, there is a simple linear
>>>> relationship on the frequency/frequency graph that converges on the point
>>>> (1,1). The comment you quoted above came from a discussion where I thought
>>>> it was implied that the shape of the relationship (e.g., linearity) was
>>>> said to depend on dominance/recessiveness. I may have been reading too
>>>> much into Jim's comments, which I still think reached way outside the scope
>>>> of the simple frequency/frequency graph.
>>>
>>> Reached way outside how? My claims are fairly simple:
>>> − If the (single) altruism locus is purely recessive, the graph of allele
>>> frequency in donors is a constant 1.0. (Obviously).
>>> − If the altruism locus is purely dominant, the graph of allele frequency
>>> in donors rises linearly from 0.5 to 1.0 as the allele frequency in the
>>> population rises from 0.0 to 1.0. I am uninterested in a 'glitch' in
>>> this curve at allele frequency exactly 0.0 − there technically are no
>>> donors at exactly this frequency.
>>
>> I'm with you so far.
>>
>>> − Given other assumptions about gene expression besides pure dominance or
>>> recessiveness, it is possible that the donor line may be something other
>>> than linear. That doesn't matter as long as the donor D line never drops
>>> below the 45 degree population P line. Regardless of how the line runs,
>>> or of how many loci are involved, it remains the case that the recipient
>>> R line lies a fraction 'r' of the way up from the P line to the D line.
>>> This fact is a consequence of the definition of IBD 'r' and the assumption
>>> of random mating.
>>
>> Ooooooh. I got lost in semantics here. Let me try to put some words in
>> your mouth and you tell me how they taste. The R line does not represent
>> the frequency of the allele among actual recipients.
>
> Well, it represents individuals related to the donor(s) by r. That pretty
> much means the same thing as 'recipients' to me.

I see how "it represents individuals related to the donor(s) by r." However
your second sentence introduces a problem in my mind, and I think this leap
diverges significantly from Hamilton's paradigm.

>> Instead, it represents the tipping point of HR. If the recipients of
>> altruism fall above the R line relative to their donors, then HR predicts
>> that kin selection will favor the altruism allele.
>
> No! The lines have been drawn without reference to the values of b and c.

Good point. Thanks. I'm afraid I am not as close to understanding the point
of your graph as I thought.

>> It would be optimal, from the viewpoint of the
>> allele, if actual recipients had the maximum number of altruism alleles
>> possible (2).
>
> Yes, but if we are going to use Hamilton's rule, the expected number of
> copies of the allele will be (P + (D−P)r); that is, the expected number
> of copies in the recipient will be R.

I accept this as a population level model in which each parameter represents a mean field approximation that is faithful to Hamilton's original model. Ironically, Hamilton's break through was to stop treating recipients as a unified mean field and distinguish among them with regard to 'r'. Are you incorporating these distinctions by positing that the position of the R line differs among pairs of individuals based on their 'r' values? If so, are you also taking into account that the realized mean and distribution of R values in the population with regard to altruistic interactions can vary?

> But sometimes the donor will be
> lucky and find 2 copies in the recipient. But sometimes he will be unlucky
> and find none. Actually the donor doesn't care that much. The recipient
> will have a similar excess of ALL of the donors genes, not just the
> altruism allele. The donor is not trying to spread the altruism allele
> per se. He is 'trying' to spread ALL of his genes.

Teleology aside, I appreciate this point.

>>> This fact is all that is needed to establish Hamilton's rule.
>>
>> I'm going to have to apologize again for being dense, but I don't see how
>> your graph justifies HR at all.
>
> Well, the graph doesn't exactly justify HR. The relationship R = P +(D_P)r
> plus some simple reasoning justifies HR.
>
>> It would be a nice graphical representation of the HR claim,
>
> No it wouldn't. The graph says nothing about 'b' and 'c'.

You're right.

>> but how would it lead to the conclusion that the R line
>> ought to lie "a fraction 'r' of the way up from the P line to the D line."
>> This is essentially the claim of HR, ...
>
> You are apparently working under the 'tipping point' misunderstanding
> that you tried to put into my mouth above. You are incorrect.

Yup.

>> but it seems to be something that you have assumed here.

>
> Yes, I assumed it in drawing the graph. The graph reflects this assumption.
> But the assumption is easy to prove.

OK. I think I see your logic on this point now. Let me try another taste test, assuming that you agreed with my claim that the position of the R line can vary and its mean position is a function of the distribution of 'r' values from realized altruistic interactions in the population. To tie this discussion more closely to HR, I am also going to invoke 'b' and 'c'. I think you are saying that if 'b' is marginally larger than 'c', then 'r' must only be marginally greater than the average relatedness among individuals in the population for kin selection to favor an increase in frequency of the altruism allele.

I hope I got it right this time, because I think it is an interesting clarification of HR. A huge advantage to this point of view is that the difference between 'r' and average relatedness in the population can potentially be estimated without bias, which is not true of 'r' in isolation.

>> As you said, "this fact is a consequence of the
>> definition of IBD 'r' and the assumption of random mating." Because it
>> relies so fundamentally on the definition of IBD 'r', how can it justify the
>> use of IBD 'r'?
>
> You are beginning to sound like McGinn. The logic is that the definition
> of 'r' (IBD) and the assumption of random mating leads to the relationship
> $R = P + (D-P)r$. That relationship, leads (by a different line of reasoning)
> to Hamilton's rule. We use the IBD definition of 'r' because it leads
> to a nice (and correct) rule.

OK. While I agree that it works with the IBD definition of 'r' in principle, I don't think it lends itself well to the empirical estimation of 'r' in practice. However, as I optimistically suggested above, your approach may be able to bypass the direct estimation of 'r' itself, say through the limited study of family pedigrees.

>>> The rule does not depend on linearity. The frequency
>>> independence of the rule does not depend upon frequency.
>>
>> OK.
>
> You have just said OK to a typo. I meant to write that the frequency
> independence of the rule does not depend upon the linearity of the D line
> and the R line.

That's even better.

>>> − What MAY depend on frequency is how fast the altruism allele spreads.
>>> That will depend upon just how separated the lines are, and the count
>>> of altruists (or of acts of altruism, depending on what b and c measure).

>>> It will also depend on the size of b and c. I offered my straight lines
>>> as an argument against YOUR claim that the impetus toward the spread of
>>> the altruism alleles pretty much peters out at gene frequencies of 30−40%.
>>
>> Under your graphical model, which I accept as a representation of Hamilton's
>> model, the strength of kin selection diminishes monotonically with the
>> frequency of the allele.
>
> Well, if you mean that the difference between the inclusive fitness of an
> altruist and the inclusive fitness of a member of the general population
> decreases monotonically, then yes.

That's right. Selection is generated by fitness differences, and the strength (effectiveness) of selection is determined by the extent of fitness differences.

>> I guess you have swayed me to the position that
>> under Hamilton's model, as opposed to a more realistic version of the same
>> model, there is not a frequency threshold where kin selection becomes
>> irrelevant. Instead, it becomes irrelevant monotonically.
>
> In the same way that any beneficial trait becomes irrelevant as more and
> more of the population has that trait.

Well, you have been arguing that it happens in a different 'way' because the strength of selection changes in a sigmoid fashion relative to frequency for 'ordinary' beneficial traits. A simple way to see this is to use Joe's freeware program called PopG, which simulates changes in allele frequencies under specified models of evolution. If you start a simulation with a beneficial allele in low frequency, you will see the sigmoid trajectory of its frequency by tracing the 'infinite population size' line that eliminates the noise of drift. While some aspects of the trajectory's shape will depend on dominance/recessiveness of the allele, it is always sigmoidal.

> But perhaps a better way to look at it is to compare the possessor of the
> trait to (not the population average, rather to) an individual without the
> trait. If you compare in this way, then I don't agree that the 'strength of
> kin selection' decreases monotonically. Once the allele becomes fixed in the
> population, there is still strong selection AGAINST mutations that change the
> altruism allele to selfishness (i.e. ineffectiveness).

Here I think you have contradicted yourself. While you have been convincing me of the validity of your argument along the way, that same argument persuades me that your last point is false. A largely altruistic population would be quite vulnerable to invasion and persistence of low frequencies of alleles for selfish behavior. If what you meant was that the largely altruistic population is unlikely to be replaced by a regime of selfishness, then I would agree.

Guy

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    - *From:* Catherine Woodgold
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