

# Re: Underestimating 'r'

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- *From:* [name and address supplied@xxxxxxxxxx](mailto:xxxxxxx@xxxxxxxxxx)
  - *Date:* Mon, 24 Oct 2005 01:39:47 -0400 (EDT)
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Catherine Woodgold wrote:

> (name\_and\_address\_supplied@xxxxxxxxxx) writes:  
>>  
>> Let  $Dzbar = \text{"delta z-bar"} = \text{"the change in the mean value of trait z in}$   
>> the population, due to natural selection". Let  $w =$  individual fitness.  
>> Let  $wbar =$  mean fitness of the population. let  $Cov[X,Y]$  be the  
>> covariance between the random variables X and Y. Let  $Reg[X,Y]$  be the  
>> least squares regression of X on Y. Let  $Var[X]$  be the variance in X.  
>>  
>>  $Dzbar = Cov[w/wbar, z]$  (Price's theorem)  
>>  
>>  $Cov[X,Y] = Reg[X,Y]Var[Y]$   
>>  
>>  $\Rightarrow Cov[w/wbar] = Reg[w/wbar, z]Var[z]$   
>>  
>>  $\Rightarrow Dzbar = Reg[w/wbar, z]Var[z]$   
>>  
>> The change in the mean value of a trait in the population, due to  
>> natural selection, is the product of the selection differential  
>>  $Reg[w/wbar, z]$  on that trait and the variation in that trait  $Var[z]$ .  
>> Since  $Var[z] > 0$  if there is any variation, then if we assume there is  
>> some variation in z, the mean value of the trait will be selected to  
>> increase when  
>>  
>>  $Reg[w/wbar, z] > 0$   
>>  
>> Now,  
>>  
>>  $Reg[x,y] = Reg[x, y | y2] + Reg[x, y2 | y] Reg[y2, y]$   
>>  
>> where we allow for another predictor variable y2, and where "|" denotes  
>> "conditional on". Then we have the change in the mean trait value due  
>> to selection is positive when:  
>>  
>>  $Reg[w/wbar, z | Z] + Reg[w/wbar, Z | z] Reg[Z, z] > 0$   
>>  
>> Lets interpret z as the trait value for our focal individual, and Z as  
>> the trait value for her social partners.

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>>  
>>  $\text{Reg}[w/w_{\text{bat}}, z | Z]$  is the impact of our individual's own actions on her  
>> own relative fitness, holding fixed the actions of her social partners.  
>> Lets call this the personal "cost" of the individual's actions,  $-c$ .  
>>  
>>  $\text{Reg}[w/w_{\text{bar}}, Z | z]$  is the impact of the social partners' actions on the  
>> focal individual's relative fitness, holding fixed her actions. Lets  
>> call this the 'benefit',  $b$ .  
>>  
>> And  $\text{Reg}[Z, z]$  tell us how the behaviour of social partners varies with  
>> one's own behaviour. Lets call this  $r$ , for short.  
>>  
>> So, our condition for when our social action will evolve is:  
>>  
>>  $-c + b r > 0$   
>>  
>> That is just about as general a derivation of Hamilton's rule that you  
>> will find, for a simple single class model. It is easily extended to  
>> multiple classes -- see Price 1970 on how to weight the covariance by  
>> class reproductive values -- giving the same result. We find that  $r$  is  
>> fundamentally a regression measure.  
>>  
>> For an explicitly genetical model, we can write the regression in terms  
>> of probabilities of identity in state:  
>>  
>>  $r = ((\text{Prob of picking gene from actor and recipient and them being the}$   
>>  $\text{same}) - (\text{population average})) / ((\text{prob of picking two genes with}$   
>>  $\text{replacement from actor and them being the same}) - (\text{population average}))$   
>>  
>> For a rare gene, this simply the ratio of IBD for actor-recipient and  
>> IBD actor-actor. Since we are typically looking for ESSs, it is the  
>> behaviour of a rare gene that we are ultimately interested in, hence  
>> the focus on IBD.  
>  
> I've looked at this post several times and seem to have  
> gotten a little closer to understanding it, but still  
> not very far. It looks interesting, though.  
>  
> I suppose  $z$  is a real number associated with each  
> individual, such as: height, or amount of pigment in  
> the hair, etc. I suppose  $\bar{dz}$  is the average amount  
> of  $z$  in one generation minus the average amount of  $z$   
> in the previous generation.

Right.

> I've done linear regression in the past, and I just skimmed the  
> Wikipedia article for regression, but I don't know whether  
>  $\text{Reg}[X, Y]$  is a number, or a two-element vector (slope and  
> intercept), or some other mathematical object.

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Read  $\text{Reg}[X,Y]$  as the slope of the least squares linear fit through the data; it is simply a number.

- > If X and Y are expressed as vectors, then I think
- >  $\text{Cov}(X,Y)$  is:
- >
- >  $\frac{\sum(x_i y_i)}{\sqrt{(\sum(x_i^2) \sum(y_i^2))}}$
- >
- > or something like that. The definition for
- > random variables will be something similar.

$$\text{Cov}[X,Y] = E[X Y] - E[X] E[Y]$$

where E is the expectation, or arithmetic average. If X and Y are independent,  $E[XY] = E[X]E[Y]$ , and the covariance is zero. So the covariance is a measure of the departure from statistical independence.

- > Hmm, I think I'm starting to understand. Price's
- > theorem looks as if it may be relatively obvious once
- > I get the definitions clear in my mind.

It's a simple identity, which provides a conceptual aid in partitioning the components of evolutionary change. It is simple and obvious because it says very little. But it provides the generality we need in order to give a general derivation of Hamilton's rule. I believe you noted previously that, although the single locus, two allele, diploid models and associated derivations of HR presented by Joe Felsenstein are helpful, they are not completely satisfactory in that they do not provide a general proof. The above Price's theorem approach is the only way at making such general statements.

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- **Follow-Ups:**

- ◆ **Re: Underestimating 'r'**  
◇ From: Joe Felsenstein

- **References:**

- ◆ **Underestimating 'r'**  
◇ From: Tim Tyler

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