

## Re: Felsenstein and reproductive excess

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- *From:* [joe@xx](mailto:joe@xx) (Joe Felsenstein)
  - *Date:* Thu, 2 Jun 2005 17:10:58 -0400 (EDT)
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In article <d7m79s\$2t5s\$1@xx>, Perplexed in Peoria <jimmenegay@xxxxxxxxxxxxxxxx> wrote:  
>The phrase "environmental deterioration" is somewhat ambiguous. In  
>discussions of Fisher's Fundamental Theorem and the riddle this creates  
>with its picture of fitnesses increasing over time without bounds, one  
>occasionally sees the claim that the increase in the fitness of your  
>conspecifics constitutes a deterioration in the environment for you.  
>Van Valen makes the same point with his Red Queen hypothesis. So, I  
>have to ask, when you talk about "environmental deterioration", are you  
>limiting this to the physical environment? Is ReMine so limiting it? And  
>most importantly, did Haldane intend to limit it in this way?

Neither I nor Haldane (ReMine can speak for himself) limited the source of environmental deterioration to physical, abiotic factors (see <http://www.blackwellpublishing.com/ridley/classic texts/haldane2.asp> where you can actually read Haldane's paper on-line, for free).

>I cannot claim to know Haldane's intentions, but ISTM that he was trying  
>to come up with a mathematically tractable, but biologically realistic,  
>model which would allow fitness to "increase" over time without population  
>counts (unrealistically) increasing (and accelerating!) to match. That is,  
>he needed some population-limiting assumption to counteract the population-  
>expanding continual increase in "fitness".

I do not see this intention in his paper. Where in that PDF do you see that?

>The question that Haldane sought to address is difficult to handle under  
>the usual methods of population genetics. Pop gen, when it computes the  
>increase in the fitness of a population (i.e. the increase in the average  
>of the fitnesses of individuals) does not usually project the consequences  
>of this increase forward over evolutionary or geological time.

Most population genetic arguments use relative, not absolute fitnesses. They thus do not actually address the absolute fitness of the population. By using relative fitnesses they make their argument work either with or without population density regulation, provided only that any mortality or lowered fecundity that is caused by density-dependence falls equally on all genotypes, lowering absolute fitnesses by multiplying them by some factor.

## Re: Felsenstein and reproductive excess

>ISTM that

>Haldane avoided this problem (correctly) by adding the assumption that  
>the fitness increases are exactly matched by deterioration of the environment,  
>and hence that population densities do not increase.

Where do you see this in the PDF of his paper?

>But I think that he

>intended to include in this deterioration the increasingly effective  
>competition of conspecifics.

He is pretty explicit that he includes biotic as well as abiotic environmental changes, but he does talk about the deteriorations of environment having an effect when the density of the population is low. See page 513 in the on-line PDF.

[me:]

>> The condition needed is the reproductive excess needed to allow the population  
>> to grow when its density is low. That is the very situation when density-  
>> dependence is not relevant.

>

[Perplexed:]

>I understand and agree, IF the environmental deterioration is understood to  
>take place independently of population density. However, I am not sure that  
>this is either realistic or what Haldane intended.

I think he was not treating the case where the deterioration only affects the species at high density. See page 513.

[me:]

>> Second, we have to distinguish between mutations that make an individual  
>> lower its conspecifics' survival or reproduction, and those that instead  
>> more effectively resist competition. Here is the standard Beverton-Holt  
>> discrete-generations density-dependent growth equation:

[... snip details]

>> The class of mutations you posit may not actually fit into this  
>> equation. Does it decrease everyone's K? Or just the K's of those who  
>> do not have the mutation?

[Perplexed:]

>But I also doubt that directly answering your question "Does it decrease  
>everyone's K?" is the right approach either. Consider a mutation which  
>transforms a population of small bushes into a population of large trees  
>with spreading canopies. I suppose you could say that it decreases everyone's  
>K. But it also probably is constrained to defer the age of reproductive  
>maturity, so it negatively affects r as well.

A mutation could increase K and reduce r at the same time. That fits into the Beverton-Holt equation framework. In the Beverton-Holt population dynamics the equilibrium population size achieved is a function of both.

Re: Felsenstein and reproductive excess

>Perhaps the simplest model would be one in which each organism (indexed by  $i$ )  
>has a competitive ability  $C_{sub_i}$ . The organism achieves a fraction  
>  $C_{sub_i} / \text{Summ}(C_{sub_i})$   
>of the available resources. But, as an independent trait, each organism  
>also has a resource requirement or need  $N_{sub_i}$ . The effective growth rate  
>of a type (positive or negative) can be taken to depend linearly upon the  
>ratio between resources needed and resources achieved. ISTM that one still  
>comes up with a two parameter model, like the rK one, but it doesn't have  
>the objectional (to me) property that K mutations are ineffective at low  
>densities and r mutations are ineffective at high densities.

OK, interesting model. Let's take a look. If we have two genotypes with numbers  $n_1$  and  $n_2$  (I use the LaTeX notation of underscore for subscripts rather than your "\_sub\_") and a total amount  $A$  of available resources, and if competitive abilities per individual are then  $C_1$  and  $C_2$  for these two genotypes, and if their "needs" are  $N_1$  and  $N_2$  and growth rate is the ratio (upside down from your statement because I think you misspoke) of resources achieved to  $N_1$  or  $N_2$ , type 1 achieves resources

$$A n_1 C_1 / (n_1 C_1 + n_2 C_2)$$

so in a discrete-time model the next generations numbers of type 1 are

$$n_1' = A n_1 C_1 / (N_1 (n_1 C_1 + n_2 C_2))$$

$$n_2' = A n_2 C_2 / (N_2 (n_1 C_1 + n_2 C_2))$$

The ratio  $n_1/n_2$  has  $A$  and the second part of the denominator cancel out. So interestingly,  $n_1/n_2$  is multiplied each generation by  $(C_1/N_1)/(C_2/N_2)$  and this means the genotype with highest  $C/N$  wins. In this model when only one genotype is present (erase the  $_2$  terms in the first equation above) the population immediately equilibrates at  $n_1' = A / N_1$ . That only happens in the Beverton-Holt equations when their  $R$  (the growth rate at low density) is infinitely large.

In your model a change of environment can change  $N$ 's or  $C$ 's or both. If it changes  $N$ , raising the "needs", it lowers everyone's population sizes. No one goes extinct but their population densities get lower. If it changes everyone's  $C$ 's proportionately, it does not change their growth rates or equilibrium density.

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Joe Felsenstein joe@xxx  
Department of Genome Sciences and Department of Biology,  
University of Washington, Box 357730, Seattle, WA 98195-7730 USA

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Re: Felsenstein and reproductive excess

- *Follow-Ups:*
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