Re: Bet Hedging, Risk Aversion, Sex, and the Unit of Selection

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- *From*: "Perplexed in Peoria" <jimmenegay@xxxxxxxxxxxxx>

- *Date*: Sat, 28 Jan 2006 13:12:03 −0500 (EST)

"William Morse" <wdmorse@xxxxxxxxxxxx> wrote in message
news:drccbo$1ko0$1@xxxxxxxxxxxxxxxxxxxxxx
> "Perplexed in Peoria" <jimmenegay@xxxxxxxxxxxxx> wrote in news:dr1gik$80f
> $1@xxxxxxxxxxxxxxxxxxx:
>
> > A man sits down at a roulette wheel with $100. How should he
> > distribute his bets?
> (snip)
>
> > What does all this have to do with evolutionary biology? Well,
> > some theorists have claimed that the units of natural selection
> > behave as if they were risk averse maximizers of fitness (i.e.
> > reproductive success). For example, Lewontin and Cohen
> > On Population Growth in a Randomly Varying Environment
> > R. C. Lewontin, D. Cohen
> > PNAS Vol 62, No 4, (Apr 15, 1969), 1056−1060
> > used the mathematical theory of "Gambler's Ruin' to argue that
> > in a randomly varying environment, the unit's goal is not
> > the maximization of the expectation of absolute fitness, but
> > rather the maximization of the expectation of the logarithm of
> > absolute fitness. The expectation is taken over the space
> > of environmental variation.
> >
> > ... The idea is that an organism can and
> > should 'hedge its bets' by having some offspring adapted to one
> > environment and other offspring adapted to different environments.
> >
> > But is this even possible? An organism only HAS a few offspring.
>
> That is only true for a small subset of species. An interesting question
> is whether any species could have developed the strategy of only having a
> few offspring if they had not already developed the ability to learn, so
> that they could hedge their bets by plasticity in responding to changes
> in the environment.

A lot depends upon the scale of the environmental variation in time and
space. It is my impression that the difference between species that

produce many unnurtured offspring and those which produce only a few offspring and nurture them well is related to the nature of fine grained variation in the environments experienced by individuals. If most of your seeds will fall on barren ground, and if there is no way to adapt to barren ground, then the best strategy is to produce lots of seeds and cast their fate to the winds. But if the environment is harsh, but uniform, then produce big, well nourished seeds − perhaps seeds with the 'smarts' not to attempt germination unless the moisture and temperature are just right.

If there is a very fine grained environment such that an organism encounters a range of environments in its lifetime, then it makes sense to invest in sensory and behavioral adaptations. The hare doesn't much care about the global density of Lynx. It is more concerned with the local density − like whether there is a high density lynx currently approaching on a ballistic trajectory.

If the environment varies on a time scale of a few generations, then developmental plasticity may be the best approach. Let the embryonic organism 'sense' the environment it is likely to have to live with, and develop appropriated for those conditions.

Bet hedging is something different from the above strategies. It makes sense for environments which vary on large spatial and temporal scales. Say a spatial scale of ten times the ability of the propagules to disperse and a time scale of several generations. Something like the effect of decade−long droughts or rainy spells on an annual plant.

> > The 'stake' cannot be evenly divided among the bets. However
> > risk averse the organism is, its opportunities for bet hedging
> > seem severely limited. Furthermore, bet hedging only makes sense
> > if the bets are NOT independent. An organism with two offspring
> > adapted to two different environments is only hedging if both
> > of those offspring encounter the same environment.
>
> > So much for the background − now it is time for some wild conjectures.
> > 1. Sex exists because it provides a mechanism for bet hedging.
>
> Interesting conjecture − but if that is the only explanation for sex then
> I would think more organisms would have mechanisms for multiple parents
> of different offspring. While a number of species (e.g. domestic cats)
> have evolved such mechanisms, I don't think they are particularly
> numerous.

That would be true if bet hedging were something that were beneficial for individuals to engage in. But I am claiming that it is not.

Once an individual has produced enough offspring to counter the fine−grained harshness of the environment, and once the environment has taken its toll, there are only (one average) two offspring left. Not enough. But bet hedging can be practiced by higher−level units

of selection which can divide the 'stake' into more pieces.

> > 2. But this only makes sense if the unit of selection is seen
> > as the gene−clone, as in a gene's eye view justification
> > of Hamilton's rule. A gene clone can spread its bets
> > evenly among the alternatives − it has a 'stake' that is
> > divisible. Organisms, for the most part, do not.
>
> You will need to explain this further for me to understand your argument.
> I would have thought that bet hedging only makes sense if the unit of
> selection is the organism, or better yet the species. The organism
> "tries" different combinations of genes to see which ones will work out.
> The species maintains polymorphism so that it can respond to
> environmental changes, even though this sacrifices some individual
> fitness − The Selfish Gene Pool.

I agree that the species level might be the best viewpoint, and disagree
that it makes sense at the individual level. But here is the thinking
behind my claim that it also makes sense at the gene clone level:

Consider a sexual species with several loci with alleles A and a at one,
B and b at another, etc. Consider NS from the viewpoint of our focal
allele A, which is engaged in a long term struggle for world domination
(well, at least domination of the species) with its enemy, the allele a.
Any individual gene (DNA molecule segment) in any organismic individual
is merely a foot soldier in this epic struggle. The antagonists are
the entire A clone and the entire a clone − each distributed among
many individuals.

For simplicity, we will assume that the species undergoes selection
in haploid form. Now neither A nor a care much about the environment.
But alleles B and b DO care about the environment − in fact, each is
adapted to a different environment. The question is, should our protagonist
A prefer to have its 'troops' billeted with B or b. My claim is that
if bet hedging makes sense in this situation, then A should want to have
a mix of AB and Ab individual organisms.

How does A accomplish this laudable goal? Well, it does what it can.
It firmly opposes any conspiracy at other loci to switch individual
reproduction from sexual to asexual. And, it attempts to locate itself
on a different chromosome than the B locus.

The situation is more interesting if there are epistatic interactions
between the two loci. Now it may be the case that it makes sense for
A to try to be linked with the B locus on the same chromosome. It
may be that the AB combination is fitter than Ab. If so, selection will
lead to a deviation from multi−locus HW equilibrium. And that deviation
must be viewed as a good thing from the standpoint of a non−hedging
optimizer who is only interested in maximizing ln(E(W)). But it may
not be a completely good thing from the standpoint of a bet hedging
optimizer who is interested in maximizing E(ln W). Hence recombination

(which reshuffles genes in a way that LOWERS average individual fitness).
Hence sex is useful only if the optimizer is a bet hedger.

> > 3. As suggested in the paper by Bergstrom and Lachmann
> > The Fitness Value of Information
> > Carl Bergstrom and Michael Lachmann
> > http://arxiv.org/PS_cache/q−bio/pdf/0510/0510007.pdf
> > the process of natural selection can be given an information
> > theoretic interpretation in which there is an identity between
> > fitness (Fisher's r) and information acquired about the actual
> > distribution of environments.
> >
> > My rudimentary grasp of probability and statistics doesn't allow
> > me to express this stuff in a rigorous model yet. The difficulty
> > lies in separating the environmental variation into temporal variation
> > (affecting all organisms the same) and spatial variation (affecting
> > organisms differently). The interplay between these two kinds of
> > variation seems crucial.
>
> The interplay may well be crucial, and I question your trying to make the
> distinction, at least without some additional classification. As I
> understand you, you are trying to differentiate between variations that
> occur throughout the geographic range of a population based on time (e.g.
> the Little Ice Age in Europe), and other variations that are severe but
> occur only in limited portions of the geographic range of a population
> (e.g. the eruption of Mt. St. Helens). I think the problem you will find
> is that these effects are not uniform across species.

Oh, I'm quite sure that they are not uniform across species. As I have suggested, the dividing line between temporal variation leading to hedging and temporal variation leading to developmental or behavioral plasticity is at a time scale of a few generations. And generation time varies between species.

Thank you for a thought provoking response.

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- ***Follow−Ups***:
  - ♦ ***Re: Bet Hedging, Risk Aversion, Sex, and the Unit of Selection***
    - ◊ *From:* Perplexed in Peoria
  - ♦ ***Re: Bet Hedging, Risk Aversion, Sex, and the Unit of Selection***
    - ◊ *From:* Perplexed in Peoria

- ***References***:
  - ♦ ***Bet Hedging, Risk Aversion, Sex, and the Unit of Selection***
    - ◊ *From:* Perplexed in Peoria
  - ♦ ***Re: Bet Hedging, Risk Aversion, Sex, and the Unit of Selection***

◊ *From:* William Morse

- Prev by Date: ***Paper: Comparative analysis of chimpanzee and human Y chromosomes unveils complex evolutionary pathway***
- Next by Date: ***Some junk ain't junk***
- Previous by thread: ***Re: Bet Hedging, Risk Aversion, Sex, and the Unit of Selection***
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