

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

Source: <http://sci.tech--archive.net/Archive/sci.bio.evolution/2006-02/msg00019.html>

- *From:* William Morse <wdmorse@xxxxxxxxxxxxx>
 - *Date:* Wed, 1 Feb 2006 22:16:58 -0500 (EST)
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"Perplexed in Peoria" <jimmenegay@xxxxxxxxxxxxx> wrote in [news:dri0kv\\$1adb\\$1@xxxxxxxxxxxxx](mailto:news:dri0kv$1adb$1@xxxxxxxxxxxxx):

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>
> "Perplexed in Peoria" <jimmenegay@xxxxxxxxxxxxx> wrote in message
> news:drqc5j\$896\$1@xxxxxxxxxxxxx
>>
>> "William Morse" <wdmorse@xxxxxxxxxxxxx> wrote in message
>> news:drccbo\$1ko0\$1@xxxxxxxxxxxxx
>> > "Perplexed in Peoria" <jimmenegay@xxxxxxxxxxxxx> wrote in
>> > news:drlqik\$80f\$1@xxxxxxxxxxxxx:
>> > > 2. [Bet hedging] 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:
> [thinking snipped again]
>
> In my other response (to myself ;-) I recommend a paper by Alan
> Grafen with the disclaimer that I don't really understand it.
>
> NOW I UNDERSTAND! Some of it, anyways...
>
> The situation with hedging of bets given a stochastic environment is
> exactly analogous to the more familiar situation of maintaining a
> balanced sex ratio. Individuals don't do it. Populations do it,
> by providing an incentive structure leading individuals to intervene
> if necessary.
>
> When the sex ratio is already balanced, an individual doesn't have to
> balance its own production of males and females. It gains equal
> amounts of fitness regardless of which it produces - therefore it
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> can produce all males, all females, or a mix, at its own 'discretion'.
> However, if the sex ratio were to somehow become unbalanced, then
> the individual has an incentive to correct the imbalance by personally
> creating a countervailing imbalance in the sex ratio of its own
> progeny.
>
> Similarly, the population hedges its bets by providing a mix of
> individuals adapted to the various environments which might be
> encountered. If the population has hedged correctly, the individual
> can balance or place all its eggs in one basket, at its own
> 'discretion'. The individual is NOT risk averse - it does a
> straightforward maximization of expected Fisher fitness; it doesn't
> worry about the variance. However, if the population happens to be
> hedging badly, then the individual is given the incentive to correct
> the imbalance by producing offspring that are adapted to those
> environments which are underrepresented in the population's hedging
> distribution.
>
> Grafen argues that bet hedging is not a useful concept at all -
> everything can be understood as simple maximization of individual
> fitness (though you have to pick the right definition of fitness).
> But ISTM that an alternative viewpoint at some deme or population
> level might also be useful. And entities at this level DO hedge their
> bets, and ARE risk averse. And it is possible that entities at this
> level have 'chosen' sexual reproduction as the way to have their
> constituent individuals reproduce BECAUSE it provides a mechanism
> which lets the population hedge its bets.
>
>
>

I would agree with you and disagree with Grafen. Bet hedging results in polymorphism - but individuals choosing to be polymorphic would I think be counterproductive in the case of environmental change. Individual choice could maintain four alleles per locus. If I am Aa I can choose a mate who has neither A nor a and who is also heterozygous. But in that case none of my children will be like me, and presumably I have survived the environmental crisis precisely because of my particular genetic makeup.

Now this is probably dependent on the time scale of the environmental challenge versus the time scale of the organism lifetime. If the challenge is likely to change within the organisms lifetime, then disassortative mating should be favored, since the organisms offspring will not be likely to face the same environment as the organism, and the fact of the organism's survival will provide little information as to the relevance of the organism's genotype on the likelihood of offspring survival.

If the challenge changes in jerks and on a time scale of several lifetimes, then assortative mating should be favored, although polymorphism would still be expected. In this case the fact of the organism's surviving the jerky change will make it likely that its offspring will also survive if they share its genome.

Yours,

Bill Morse

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