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Reply to Dan Wilson

I really appreciated Dan Wilson taking up the issue of genetic variation and frequency dependent selection (FDS) in the January ASCAP. It is good to get some dialogue going, rather than have one's contribution disappear into nothingness like a splashless pebble into a pond.

We are not really interested in positive FDS (when the fitness of a phenotype increases with its frequency) because this just reduces variation. But we are very interested in negative FDS (when the fitness of a phenotype is inversely proportional to its frequency), because this can cause variation and even bimodality in a trait. So, I will use the term FDS, meaning negative FDS.

We might try making a list of instances of FDS, one could always give up if it got too long. And subdivided according to whether the instance might be relevant to ASCAP. Among the irrelevant instances, priority would probably go to those concerned with predator avoidance, such as mimetic morphs in butterflies; lizards who "break" up or down a rock when a bird swoops; I expect that book on predator-avoiding strategies called Protean Behaviour gives lots of examples. What about fish which turn left when the rest of the shoal turns right? That would probably depend on whether the predator fish was geared to eating a single fish or a whole school.

Thinking of relevant possibilities, what about habitat selection? Is it more advantageous to select a fringe habitat when everyone else is crowding into the fertile valley; or a mountain habitat, when everyone else is in the plain? Is this sort of thing maintaining the variation along John Birtchnell's closeness/distance dimension (or along the introversion/extraversion dimension, whose basis is thought to be highly genetic)? And would it pay to be attracted to fishing when everyone else is mad on hunting? The same would apply to food preferences.

As you know I think the most relevant examples to psychiatry are the alternative competitive strategies, basically Maynard Smith's Hawk and Dove, which translate into escalating and de-escalating strategies or even into high self-esteem and low self-esteem strategies (both temporary as in mood change and lifelong as in personality variants along the "vertical dimension").

Then there are alternative strategies for dealing with adverse climate. Consider species in which a proportion of the population migrates or hibernates, while the remainder of the population stays at home or above ground. It must be the case that the larger the proportion which migrates or hibernates, the more it pays any one individual to try to battle through the winter fully awake on its original territory (and, of course, vice versa).

What about mating strategies? Does it pay more to be monogamous when everyone else is promiscuous? Does it pay to fancy redheads when the crowd prefers blondes (this would be the opposite of Fisher's runaway sexual selection)?

These examples can be seen against a background of those probably more numerous cases in which it pays to do the same as everybody else. I am sure we as human beings have a tendency to check all the time to make sure we are going along with everyone else, and not only in clothes. I can remember a patient who worked in a factory and lived about an average distance from it. Every morning he would walk or cycle to work "with the throng". Then he retired and got a morning job in the opposite direction to the factory. He had to go to work every morning "against the throng". He found this very stressful, it made him feel out of step with his community. I am not saying that is why he got depressed, but it can't have helped.

In these cases, the payoff is maximal in the middle, and gets less as you approach the extremes; the result is reduced variation unless the variation is "fixed" by heterozygote advantage. If for any reason, it pays to be nearer one extreme, you get normal directional selection; if it pays to be nearer either extreme, regardless of which, you get an increase in variation until you get bimodality and can then speak of alternative strategies and FDS.

I was amazed recently to read about alternative mammalian mothering strategies (1). Apparently some rabbit mothers keep their litter in a separate nest, which they only visit once every 24 hours. And tree-shrews are even more extreme, only visiting their young once in 48 hours. Are they good or bad mothers? Certainly, John Bowlby might raise an eyebrow at them. And what about captive rabbits who are forced to share a cage with their litter - is this stressful for them? Do they get raised HPA activity?

The function of this apparent neglect is thought to be the avoidance of predators, in that the predator finds it easier to locate the young when the mother is in the nest, or when the mother is going to or from the nest. I am not absolutely sure whether this variation in mothering occurs within species or only between species. Russ, what sort of gene, or protein, could keep a mother from her offspring for forty eight hours at a stretch? (I imagine the genetic basis of the variation has not been worked out, if it occurs within species, or the authors would have said; it could be a single gene, or polygenic with a threshold).

The nest-with/nest-apart variation does not seem to be so obviously frequency dependent as the migration/stay-at-home options. It is difficult to see how predators could become skilled in detecting nests with or without mothers preferentially. It seems more likely that just directional selection has been occurring for this mothering behaviour, and that is why the variation has not been retained within species, if in fact that is the case.

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Regarding the distinction made recently in ASCAP between those who look at woods, trees and leaves, I am a leaf man myself. I would like to have discovered chlorophyll, or the fact that some leaves fall off in winter when others don't. Likewise with diagnoses. I would rather get the MRI people to examine a population of soloists after receiving standing ovations, and compare them with a population who have received cat-calls, and get to grips with the physiology of receiving boosting signals (anathesis, but I have rather given up trying to get people to use this terminology) and putting-down (catathetic) signals. It already seems likely from Michael McGuire's work that the applauded soloists would have high platelet 5HT, and from a lot of studies that the booed ones would have high blood cortisol (assuming hedonic anathetic signals evolved from agonic anathetic signals [submissive signals] and the same for the hedonic catathetic signal of booing). What and where is going on in the brain? I think the biggest difference would be found in Roman generals having a triumph through the streets of Rome, but even in Roman times that (e.g., the venepuncture) might have been hard to set up.

What was the physiological status of that tribal elder (reported somewhere in the anthropological literature) who farted during a solemn ceremony, got up and went and committed suicide by impaling himself through the anus onto the top of a pointed tree? He did not even receive catathesis, he only anticipated it (or got it from an internalised other). Back to trees, you see, it pays to stick to the point.

A final thought. We know there are two major dimensions of variation in human behaviour: extraversion/introversion and neuroticism/stability. How is this variation maintained? The two main possibilities are heterozygote advantage (at one or many gene loci) and frequency dependent selection (also at one or many loci). How can we tell the difference between them? I think for this problem we need a mathematical expert like Lindon Eaves, who when I was working in genetics was trying to detect directional selection for extraversion, and his equations were something else. I think it is true to say that heterosis predicts unimodality whereas frequency dependent selection predicts bimodality of the distribution of some underlying trait. People think you only get bimodality with single genes, but you also get it with FDS, even when the genetic basis is polygenic. The possibility of FDS makes it worth looking for bimodality even in a trait which seems sure to be polygenic.

It is sometimes said that the nineteenth century novelists were the first psychologists, forerunners of Wundt, and able to deal with more fundamental issues than Wundt was able to in his laboratory. Thackeray gave an interesting adumbration of Maynard Smith's Hawk and Dove strategies in The History of Henry Esmond (1852, Penguin, 1970, p 435):

> 'Tis nature hath fashioned some for ambition and dominion, as it hath formed others for obedience and gentle submission. The leopard follows his nature as the lamb does, and acts after leopard law; she can neither help her beauty, nor her courage, nor her cruelty; not a single spot on her shining coat; nor the conquering spirit which impels her; nor the shot which brings her down.
> (Re Beatrix Esmond's proud reaction to the Duke of Hamilton's death just before their wedding.)

A similar view was expressed by Henry Kissinger in The Necessity for Choice:

> The real distinction is between those who adapt their purposes to reality and those who seek to mould reality in the light of their purposes.

I have a similar quote by Philip Roth on my file in England. These quotations and the theoretical work of Maynard Smith and his colleagues give us a challenge to look for bimodality in the "vertical dimension".

Manning, A. and Dawkins, M.S. (1992) Animal Behaviour 4th Edition. Cambridge: Cambridge University Press.