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NEWS AND COMMENTARY

Evolutionary genetics

Sexually selected mutation rates

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A long-standing problem in evolutionary biology is whether females derive genetic benefits from mating with well-ornamented males. Male sexual ornaments are believed to be informative signals of male genetic quality as they exhibit condition-dependent expression, with condition being influenced by many loci in a male's genome. But persistent selection on ornaments and condition should cause genetic variation in male fitness to be depleted rapidly, thereby eliminating any advantage to female mate preference – a problem known as the 'lek paradox'. Recently, Petrie and Roberts (2006) proposed that female mate choice indirectly selects for elevated rates of mutation, and claim this increases the amount of available genetic variation faster than sexual selection can erode it. Their solution provides an intriguing resolution to the lek paradox, but can it really account for the maintenance of genetic variation in fitness associated with sexual ornaments?

Most mutations are either neutral or deleterious, so minimal mutation rates are expected to evolve in constant environments. Nonetheless, mutations may occasionally confer benefits, and a number of theoretical analyses have shown that selection favours mutator alleles when a population is subject to environmental fluctuations (e.g. Taddei *et al*., 1997). Mutators spread by genetically hitchhiking with the rare beneficial alleles they generate, especially when the recombination rate is low. Laboratory studies of bacteria have shown that higher mutation rates can evolve in populations undergoing adaptive change (e.g. Sniegowski *et al*., 1997), and these rates correspond to those seen at low frequency in natural isolates (Matic *et al*., 1997).

These conclusions have not been thought to carry over to populations that reproduce sexually, as recombination reduces linkage between the mutator and beneficial alleles, thereby severely limiting indirect selection for mutators (Johnson, 1999). However, Petrie and Roberts (2006) show that sexual selection makes a difference. They consider evolution of the mutation rate in a sexual population in which females pick the best (i.e. fittest) of n males ($n = 2$–10), and compare this to random mating ($n = 1$). They find that hitchhiking of mutators is more prevalent under sexual selection, resulting in an increasing mutation rate with n. The model assumes that females assess males through condition-dependent sexual ornaments that accurately reflect the number of beneficial and deleterious mutations. So sexual selection amplifies the benefit of beneficial mutations, as these now confer both a viability advantage and a mating advantage. Conversely, sexual selection more strongly disfavours individuals with deleterious alleles. Overall, to favour mutator alleles, sexual selection must cause a disproportionate effect on beneficial mutants. This is perhaps most easily seen when thinking about extreme forms of mate choice when females pick the best male from a large sample. In this case, males with beneficial mutations gain most of the matings, whereas other males lose out irrespective of the number of deleterious alleles they carry. This leads to a net selective advantage for linked mutator genes (Petrie and Roberts (2006) only consider tightly linked modifiers of the mutation rate).

Petrie and Roberts (2006) suggest that female preference, mutator alleles and condition-dependent male ornaments interact in such a way that sexual selection generates self-sustaining variability. Mate preference indirectly causes mutators to be favoured and these increase variance in genetic quality and hence increase the selective benefit on preference itself. This is potentially a novel solution to the paradox of why genetic variance in fitness exists in the face of strong selection (although this solution is more similar to other explanations than Petrie and Roberts (2006) admit – see Pomiankowski and Møller, 1995; Rowe and Houle, 1996). However, their results do not fully support this conclusion. Variance in the number of beneficial and deleterious mutations is reported for random mating and strong (best-of-10) female choice (see Figure 3, Petrie and Roberts, 2006). For both types of mutation, variance is lower with female choice. In spite of the evolution of higher rates of mutation with female choice, sexual selection is effective at causing more rapid fixation of beneficial mutants and purging of deleterious mutants. So the standing genetic variance decreases with female choice, and the lek paradox remains. Outcomes with other parameter values are not reported and might be different.

Another problem is that there can be no certainty of sexual selection increasing the mutation rate. To be effective, sexual selection must overcome natural selection, as the latter is expected to favour minimal mutation rates. The relative strength of these two forces depends on a number of biological parameters which are not well known; for instance, the distribution of mutational effects on fitness, the accuracy of male ornaments in reflecting underlying genetic quality, the strength of female preference, and the rate of recombination between mutation modifiers and fitness genes. Petrie and Roberts (2006) make a first stab at assessing some of these (e.g. they show that recombination rates must be very low <0.05), but testable quantitative predictions remain to be developed.

At the modelling level there are several matters that need attention. In particular, mate preference was modelled as a non-evolving static strategy. It is therefore not possible to examine the evolutionary dynamics of female mate preference. It would be interesting to know the degree to which mutators drive the evolution of female preference for condition-dependent male ornaments, and *vice versa*. In addition, the distribution of mutational effects was assumed to be constant in time and independent of any previous adaptive change. This seems an inappropriate model for adaptive change in many types of novel environment. For instance, assuming a static adaptive peak, the potential gain in fitness decreases with each beneficial mutant fixed (Orr, 2005), except if the adaptive landscape changes very rapidly.

Finally, these theoretical findings need to be tested empirically. Petrie and Roberts' (2006) cite recent evidence for a positive correlation between mutation rate and the intensity of sexual selection in avian species (Møller and Cuervo, 2003). However, this evidence is at best inconclusive for Petrie and Roberts (2006) argument, as it is unclear whether sexual selection caused the increased mutation rates, or whether the greater levels of genetic variation engendered stronger sexual selection.

One possible avenue of research would be to use a model organism such as *Drosophila* to monitor the dynamics of mutator alleles under an experimental evolution regime with sexual selection *versus* that from a regime in which sexual selection is experimentally prohibited. Such experiments have been carried out before for other reasons (e.g. Holland and Rice, 1999), but have not been investigated for changes in mutation rate. Petrie and Roberts' (2006) study points at the scarcity of relevant empirical estimates and the need for further theoretical investigation of how selection causes evolutionary change in genetic variation.

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