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SHORT PAPER

Hitch-hiking effect – counter reply

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Haigh & Maynard Smith (1976) have dealt with two distinct situations in replying to our criticism (Ohta & Kimura, 1975) on their analyses of hitch-hiking effect (Maynard-Smith & Haigh, 1974); (i) a new mutant is neutral while a linked selected locus is segregating, (ii) a new mutant is advantageous while a linked neutral locus is segregating, and have emphasised the importance of the latter. They then assumed that the selective advantage exists from the moment of the occurrence of the mutant and consider only those mutations which are destined to be fixed in the population. If the majority of gene substitutions by natural selection are of this type with a large initial selective advantage and a rate limited only by the consequent substitutional load, then it is possible that hitch-hiking has a real effect in reducing heterozygosity at neutral loci. But it seems to us that such assumptions are unrealistic for the following reasons. If the population size is very large (this may be contested) such that the product of population size and mutation rate is large, numerous rare alleles (either neutral or deleterious) will be present in the population at each locus and a stable mutation-selection balance reached for deleterious alleles. Then it is likely that the 'new' advantageous allele will be chosen, in response to environmental changes, from the pre-existing alleles rather than occurring by mutation. Those alleles which have been kept for a long period in the population by recurrent mutations, should be more or less in the state of linkage equilibrium, even if their frequencies are small. Note that the 'alleles' here are not meant to be unique at the level of amino acid sequences since there should be many alternatives at the molecular level that respond to the environmental change.

In concluding that the aggregate effect of hitch-hiking will be important in explaining the observed rough uniformity of heterozygosity over many species, Maynard Smith & Haigh (1974) in their original paper assume that there is a constant flow of new advantageous mutants with fairly large selection coefficients through the population. In particular, they seem to suppose that the rate of advantageous gene substitution is independent of environmental changes, population size or even the rate of occurrence of advantageous mutations. Otherwise it would not be possible to explain the uniformity of heterozygosity over many species, since the hitch-hiking effect would be as variable as the 'effective' population size of the actual species.

Finally, Maynard Smith & Haigh (1974) consider a modification of case (ii) in which segregation at the second locus is actively maintained but with selective forces less than those at the first and show that the effect of hitch-hiking is now much reduced. Thus selectively maintained polymorphisms will protect neutral loci tightly linked to them from the hitch-hiking effects due to loci under directional selection.

From the above considerations, we think that hitch-hiking is generally not so important for reducing heterozygosity as Maynard Smith & Haigh conclude.

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