LETTERS TO THE EDITORS

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GENETIC EQUILIBRIUM WHEN MORE THAN ONE ECOLOGICAL NICHE IS AVAILABLE

In recent years the attention of experimental evolutionists has been increasingly directed toward polymorphism as furnishing desirable plasticity to a species. In particular, attention has been directed toward polymorphism with a known genetic basis. The best studied case is that of two alleles showing balanced polymorphism: that is, the heterozygote has a higher adaptive value in a certain environment or range of environments than either homozygote. Such balanced polymorphism is the only way a pair of alleles can remain in equilibrium within a single environment (or ecological niche), if we ignore mutation pressure and migration from the outside. On the other hand, it would seem that the existence of several ecological niches, with one allele favored in one niche and the other allele favored in another, might increase the possibilities for attainment of equilibrium with both alleles present in substantial proportions. Recently the question arose of whether it was in fact possible to have equilibrium without the heterozygote being superior to both homozygotes in any single niche. It is shown below that under certain assumptions the answer is yes.

The model here proposed is as follows: Let there be alleles A and A' with gene frequencies of q and $1-q$ respectively, and let mating be at random over the whole population, so that the initial zygotic frequencies are q^2AA, $2q(1-q)AA'$, and $(1-q)^2A'A'$. After fertilization the zygotes settle down at random in large numbers into each of the niches, and are thereafter immobile. There is then differential mortality ending with a fixed number of individuals in each niche. After selection the relative frequencies of AA, AA', and $A'A'$ will be $W_1q^2 : 2q(1-q) : V_1(1-q)^2$ in niche 1, $W_2q^2 : 2q(1-q) : V_2(1-q)^2$ in the second niche, etc., where W_i and V_i are the adaptive values of AA and $A'A'$ individuals relative to AA' in the i-th niche. We need consider only intra-niche comparisons and not the absolute viabilities in the different niches. If we disregard drift and consider only the force of selection, the absolute number of survivors in the different niches is also irrelevant and we may work with the numbers c_i, where c_i is the proportion of the total survivors to be found in the i-th niche, and $\Sigma c_i = 1$. To complete the model, we suppose that at the time of reproduction the survivors leave the niches, and that mating is at random in the entire population. If we denote by q' the frequency of A in this mating population, then $q' = \Sigma c_i q_i$, where q_i is the frequency of A in the i-th niche after selection.

It can easily be seen that under this model Δq is the weighted mean of the Δq's for the individual niches, so that

$$1) \qquad \Delta q = q' - q = q(1-q)\Sigma c_i \frac{(1-V_i) + (W_i + V_i - 2)q}{V_i + 2(1-V_i)q + (W_i + V_i - 2)q^2}$$

The factor $q(1-q)$ gives a trivial equilibrium at $q = 0$ and $q = 1$. The function $h(q) = \Delta q/q(1-q)$ will have the same sign as Δq for $0 < q < 1$. Since $h(q)$ is continuous, if $h(0)$ is positive and $h(1)$ is negative, there will be at least one q between 0 and 1 for which $h(q) = 0$ and hence at least one point of stable equilibrium. Setting $q = 0$ we find $h(q) = \Sigma c_i(1 - V_i)/V_i$, which is positive if

$$2) \qquad 1 + \Sigma c_i \frac{1-V_i}{V_i} \equiv \Sigma c_i \frac{1}{V_i} > 1.$$

Setting $q = 1$ we find $h(1) = \Sigma c_i(W_i - 1)/W_i$, which is negative if

$$3) \qquad 1 - \Sigma c_i \frac{W_i - 1}{W_i} \equiv \Sigma c_i \frac{1}{W_i} > 1.$$

Conditions 2 and 3 are equivalent to the conditions that the weighted harmonic means of the W_i and of the V_i (the reciprocals of expressions 2 and 3) be less than one. Since the harmonic mean is less than the arithmetic mean except when all the numbers being averaged are equal, there will, *a forteriori*, be a stable equilibrium if the weighted arithmetic means of the W_i and V_i are less than one. For a single niche, this reduces to W_i and V_i both less than one, which is known to be a necessary and sufficient condition for a stable equilibrium. For more than one niche, conditions 2 and 3 are sufficient but not necessary. For example, with two niches and $c_1 = c_2 = \frac{1}{2}$, $W_1 = 2$, $V_1 = 1.1$, $W_2 = 0.5$, $V_2 = 1.1$, if initially $0 < q < 0.6$, equilibrium will be reached with $q = 0.35$, while if $q > 0.6$, A′ will be eliminated; in other words 0.35 is a point of stable equilibrium and 0.6 is a point of unstable equilibrium. In this example, the harmonic mean of V is $1.1 > 1$. On the other hand, with $c_1 = c_2 = \frac{1}{2}$, $W_1 = 2$, $V_1 = 1.2$, $W_2 = 0.5$, $V_2 = 1.2$ there is no equilibrium point between zero and one. An example fulfilling conditions 2 and 3 is $c_1 = c_2 = \frac{1}{2}$, $W_1 = \frac{3}{2}$, $V_1 = \frac{2}{3}$, $W_2 = \frac{2}{3}$, $V_2 = \frac{3}{2}$, giving a stable equilibrium at $q = \frac{1}{2}$. Note that in this example the weighted arithmetic means are greater than one, although the weighted harmonic means are less than one. For this last example the location of the equilibrium point at $\frac{1}{2}$ can be found by considerations of symmetry, but in general the actual value of the equilibrium point must be found by trial and error or some other approximate method.

The model here proposed is obviously not realistic; however, if it is modified by supposing that individuals move preferentially to niches they are better fitted for, or that there is a tendency for mating to occur within a niche rather than at random over the whole population, conditions will be more favorable for equilibrium, so that in a sense we are considering the worst possible case. For another rather artificial model with variable population size, which will be discussed elsewhere, equilibrium is attained under similar conditions.

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