NOTES AND COMMENTS

THE HYBRID SINK EFFECT

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THE population density at the centre of a cline maintained by a balance between dispersal and selection will usually be lower than the density in the surrounding regions. Under most circumstances, natural selection maximises the population density (though see Slatkin, 1978, for exceptions due to frequency-dependent fitnesses). Dispersal between two monomorphic areas will therefore reduce the density in the boundary region below its maximum value. If the cline between the two genotypes is maintained by hybrid unfitness, then the loss of hybrids will depress the population size, whilst if it is maintained by spatially varying selection, the population will be depressed by the presence of maladapted organisms which had moved across the cline. The negative effects of dispersal and selection will be counterbalanced by the density-dependent forces which regulate population size. Thus, the reduction in density at equilibrium will be given by the ratio between the selective load and the rate of return of the population to its equilibrium size. This argument assumes that selection is " hard ", and operates independently of the regulating forces; if there is competition between genotypes, giving frequency dependence, the population size will not be affected so much by the action of natural selection.

Hall (1973, 1977) has suggested that this local reduction in population density could strengthen the action of the cline as a barrier to gene flow at linked loci. The effect has also been discussed by Moran, Wilkinson and Shaw (1979). More organisms will migrate into the " hybrid sink " than migrate out, and so the cline will be narrowed. Recombinants produced there will tend to be swamped by the incoming parental gametes, reducing gene flow past the cline. Modifiers which are only advantageous in the cline will also be swamped, and so the adaptive reinforcement of, for example, premating isolation will also be slowed down. Any mechanism which could strengthen the barriers between diverging races clearly has great relevance to theories of speciation; however, a closer look at the hybrid sink effect indicates that it is probably not very significant.

Let us consider the simple model of a cline maintained by weak, hard selection against heterozygotes (s, $\ll 1$), at a single locus where two alleles are segregating at frequencies p, q (see Bazykin, 1969, Barton, 1979a). The average number of offspring, or absolute fitness, of the homozygotes will be some function of the population density, $W(\rho)$, say, whilst the fitness of the heterozygotes will be $(1-s)W(\rho)$. If the monomorphic population is maintained at a stable equilibrium density, ρ_0, at which $W(\rho_0) = 1$, we can

approximate the fitness function near this equilibrium by $W(\rho) \simeq 1 - r(\rho - \rho_0)/\rho_0$. (This expression is exact if the logistic model of population growth applies.) Hence, the dynamics of a mixed population can be described by $\bar{W}(\rho) = (1 - 2pqs)(1 - r(\rho - \rho_0)/\rho_0)$, and so, for $s \ll r$, $\rho = \rho_0(1 - 2pqs/r)$. The effect of dispersal in smoothing out this local reduction in density may be neglected if selection is weak.

This pattern of density variation can be superimposed on the equations for gene flow past a cline given in Barton (1979*b*). As expected, the additional terms which describe the hybrid sink effect lead to a reduction in cline width, and in gene flow. However, the extra terms are of order (s^2/r), and so the effect is negligible when selection is weak in comparison with the forces regulating population size.

Of course, significant barriers can only be generated if selection is strong. In that case, a stepping stone model of population structure is more appropriate than a continuous model, since the cline will be narrow. The centre of the cline will fall between demes, and so there will be little reduction in population size at the edges. Thus, the hybrid sink effect will again be negligible. Even if the organism is distributed more or less continuously, there will still be large local variations in population density, and these will probably have more effect on gene flow than will the self-generated density trough.

If many loci are involved in a set of coincident clines, the hybrid sink effect will be stronger. Selection at each locus will reduce the population density, and so the density trough will be correspondingly deeper. If there are n loci, the hybrid sink terms will be of the order (ns^2/r), provided that the actions of the various loci on density do not interact. It is possible that a set of clines might be wide enough not to fall between demes, and yet, despite the low selection needed to maintain such a wide cline, the reduction in population density at the centre might be large enough to make the sink effect significant ($s \ll M$, where M is the fraction of the population exchanged between demes in each generation, and yet $s \gg r/n$). However, this could only happen for a restricted range of parameters, since the loci must be far enough apart on the linkage map to act independently ($s \ll R/n$, where R is the total map length).

From these considerations, it would seem that the hybrid sink effect is not important in reinforcing barriers to gene flow.

References

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