ASSORTATIVE MATING GENES SELECTED ALONG A GRADIENT

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Received 21. viii. 80

SUMMARY

A population genetics model of a gene locus that is pleiotropic in the sense that it causes assortative mating and also affects fitness on an environmental gradient shows that assortative mating substantially alters the adaptive response of the population. Assortative mating loci are not likely to be polymorphic at a given locale because the genotypes of the minority allele are less likely to find mates. As an assortative mating type such as an early flowering plant colonises along a selection gradient, minority disadvantage inhibits the adaptive response of the population. If selection is not intense, the population will not adapt. Once the colonial population reaches a locale where selection overcomes monority disadvantage, divergence occurs. Once initiated, divergence is accelerated by assortative mating. The combined effects of selection and assortative mating can result in rapid speciation (elimination of heterozygotes) or in the formation of a stable hybrid zone between mating types.

1. INTRODUCTION

A GENE that causes assortative mating could be pleiotropic in the sense that it affects fitness in some additional way. For example, several plant species have evolved early flowering inland and late flowering coastal ecotypes in California (Clausen, 1951): early flowering is part of an adaptive complex that enables inland races to survive summer drought. Turesson (1922) listed several Scandinavian species in which the opposite condition obtains; *i.e.*, coastal ecotypes flower earlier than inland ecotypes—presumably inland habitats experience frost later in the spring. When a plant species colonises a region where natural selection favours a shift in flowering time, the simple adaptive response of the population might be considerably altered because a shift in flowering time could cause assortative mating. The complexity stems from the fact that a mutant coloniser that flowers at an odd time, although favoured by selection, is unlikely to find another plant to cross-pollinate. Although this pleiotropic phenomenon is most obviously exemplified in flowering plants, the argument is certainly more general; *viz*, when a gene is selected along a gradient, its frequency will not behave according to simple selection models if that gene also affects assortative mating.

2. MODEL

This note reports some results from a one-locus-two-allele population model where the alleles in question cause assortative mating but also affect fitness differentially over a geographical range. The geographical range comprises a linear sequence of nine locales, each capable of supporting a deme. In each discrete generation, fractions of size $m/2$ of each deme migrate one locale to the left and right while the fraction $(1-m)$ remains. For

the two end demes (1 and 9), this rule is modified such that a fraction $m/2$ migrates to the adjacent interior deme (2 and 8, respectively), whereas the fraction $(1-m/2)$ remains. The selection pattern is varied in the analysis, but, generally AA homozygotes are favoured in the left part of the range whereas $A'A'$ homozygotes are favoured to the right (fig. 1, bottom panels).

Assortative mating is assumed to be of the mass-action form as defined by Karlin and Scudo (1969). Analysis of the mass-action model was extended by Moore (1979). The model envisages the following situation: Three assortative mating genotypes AA, AA' and $A'A'$ encounter one another at frequencies equal to the products of their genotypic frequencies. Given that two genotypes encounter, they mate with probability 1, α or β ($\beta \leqq \alpha \leqq 1$), depending on whether they share 2, 1 or 0 alleles at this locus. The essential feature of the mass-action model is that the least frequent allele is at a disadvantage because its genotypes are less likely to find mates. The mass-action model shows that the majority allele becomes fixed in the population and that a mutant allele will not increase in frequency unless it is favoured sufficiently by selection to overpower its minority disadvantage due to assortative mating (Moore, 1979).

The theoretical population genetics of a single gene locus with two alleles selected along a gradient has been studied in detail (Haldane, 1948; Fisher, 1950; Jain and Bradshaw, 1966; Endler, 1973, 1977; Slatkin, 1973; May *et al.*, 1975; Nagylaki, 1975). The selection component of the present model is essentially identical to these earlier models, but these models did not consider assortative mating. Endler (1977), and Caisse and Antonovics (1978) investigated two-locus models wherein a fitness locus was selected along a gradient, and the resultant behaviour of a functionally and genetically independent assortative mating locus was determined. In both studies, the constant-fraction assortative mating scheme proposed by O'Donald (1960) was used. There is no minority disadvantage in the constant-fraction scheme, and this leads to results that contrast with those of a mass-action scheme—particularly with regard to the evolution of reproductive isolation (Moore, 1979). Crosby (1970) modelled "speciation" with a polygenic system of fitness loci and an independent polygenic assortative mating system. He apparently was unaware of the minority disadvantage inherent in his assortative mating scheme; consequently, it is unclear whether reproductive isolation evolved in his simulations because hybrids were selected against or because the initial assortative mating polymorphism was unstable. The theoretical population genetics of a mass-action assortative mating system selected along a geographical gradient has not been investigated. Such an investigation is worthwhile because many genes that are ecologically selected (*e.g.* flowering time genes) must effect some assortative mating, and the minority disadvantage inherent in the mass-action model may be common in plants (Levin, 1972), and animals as well (Moore, 1979). The situation envisaged here is one where a species is colonising along an ecological selection gradient. The single locus modelled is selected along the gradient, but this locus also affects assortative mating.

3. Results

The dynamics of colonisation and adaptation are illustrated in fig. 1 for two selection regimes. Results were obtained by reiteration of the
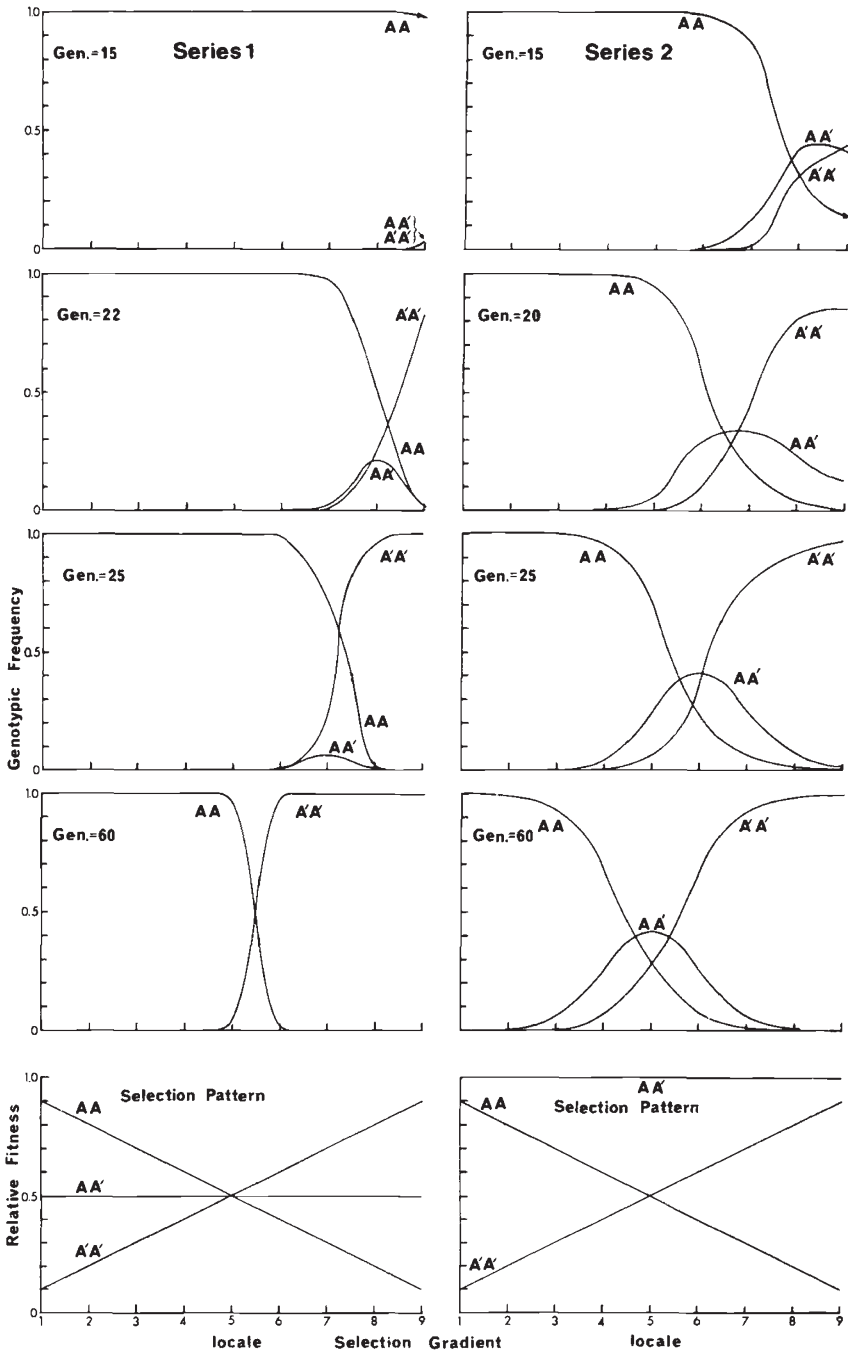
FIG. 1.—The evolution of assortative mating in species colonising along two distinct selection gradients. The selection regimes are illustrated in the bottom panels. Series 1: heterozygotes have intermediate fitness. Series 2: heterozygotes are favoured by selection. Colonisation proceeds from left to right in both reiteration series, as indicated by the arrows in the top panels.

difference equations on a digital computer. (Although cumbersome to write out, the appropriate difference equations are readily derived from Moore, 1979, table 6 by allowing the fraction $(1-m)$ of each genotype in each deme to remain and adding to this the fractions $m/2$ of each genotype from the two adjacent demes.) Both series were initiated with populations at locale 1. Colonisation is simulated in subsequent generations as migrants move across the geographical range from left to right. Allele A mutates to A' and *vice versa* at rate μ. Adaptively neutral mutations at a mass-action assortative mating locus are held at a low frequency by minority disadvantage (Moore, 1979). The selection patterns for the two reiteration series are illustrated in the bottom panels of fig. 1. The reiteration series differ only in selection pattern ($\alpha = \frac{1}{2}$, $\beta = 0$, $m = 0 \cdot 25$, $\mu = 0 \cdot 00001$).

In the first series, heterozygotes have intermediate fitness at all locales. AA homozygotes completely colonise the range before divergence is perceptible. An adaptive response is first evident at approximately generation 15 at the extreme right locale. Once the inertia of assortative mating is overcome, divergence proceeds rapidly (Gen. = 22, 25). A substantial number of heterozygotes occurs at the onset of divergence, but these are rapidly eliminated. Since AA and $A'A'$ cannot mate ($\beta = 0$), the elimination of heterozygotes is speciation. The species boundary initially occurs deep in the colonial range of the population but then flows back towards the centre as dictated by selection. A projected "history" much like the first reiteration series results when A' is dominant to A.

Heterozygote advantage hastens divergence and leads to the formation of a stable "hybrid zone" with regard to the assortative mating characteristic (fig. 1, series 2). Speciation does not occur here because heterozygotes in the central demes allow genes to be transmitted from one distal population to the other. Hybrid zones between maritime and inland plant races are also known (Turesson, 1922; Clausen, 1951). Numerous additional simulations were made for various parametric values (α, β, m and fitnesses); the results summarised in fig. 1 suffice to illustrate the most interesting implications of the model in terms of speciation and hybrid zones. In general, though, the inertial effect of mass-action assortative mating profoundly influences the dynamic aspects of divergence along a selection gradient and, in some cases, the equilibrium achieved. Initially, assortative mating retards adaptation and cline formation; however, once the colonising allele is carried, by selection, to a frequency greater than $0 \cdot 5$ in some part of the range, assortative mating accelerates further divergence. Thus, speciation by this mechanism can be very rapid once initiated; but, on the other hand, assortative mating could prevent the formation of a cline under conditions where selection alone would produce cline (Nagylaki, 1975). A cline fails to evolve if selection for the minority genotypes is not sufficient in at least some part of the range to overcome the minority disadvantage inherent to assortative mating.

4. DISCUSSION

I can summarise the predictions of this model with hypothetical, but very plausible, plant species. The progenitor species has a boreal maritime distribution and early flowering habit. Inland colonisers experience selection for delayed flowering due to frost risk. Colonisation goes well beyond the point where divergence would occur were assortative mating not inhibiting the adaptive response. Delayed flowering is first seen in marginal inland

populations. Once late flowering forms reach a threshold abundance, assortative mating accelerates divergence. Concomitantly, intermediate flowering types are eliminated from the population, and the incipient species boundary flows back towards the midpoint of the selection gradient where it stabilises. Once initiated, reproductive isolation evolves in less than ten generations. Other outcomes can occur: A stable hybrid zone can result if heterosis exists along all or part of the range. Alternatively, there may be no adaptation if selection is not intense. Obviously, considerable caution must be exercised in extending inferences from a one-locus-two-allele model to general evolutionary phenomena. A polygenic model would be more realistic but give less insight at this juncture because of the additional complexity; further, the choice of the specific polygenic model would be somewhat arbitrary (*i.e.*, additive effects, codominance, etc). I speculate that a polygenic assortative mating system would behave in much the same way provided it had the property of minority disadvantage; however, it would be possible for a population to become fixed for an intermediate genotype. Nevertheless, the present model, representing a single assortative mating locus selected along an ecological gradient, reflects a situation that must be common and could, therefore, represent a general process of speciation. It should be noted that the evolution of "premating" reproductive isolation in this model is quite *incidental* to the process of adaptation along the selection gradient.

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