Genet. Res., Camb. (1980), **36**, *pp.* 29–40
Printed in Great Britain

The effect of migration and recombination on the equilibrium structure of populations subject to a common symmetric selection regime

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(*Received* 20 *September* 1979 *and in revised form* 22 *April* 1980)

SUMMARY

The effect of migration and recombination on the equilibrium structure of populations subject to a common symmetric selection regime in all habitats is studied. Attention is restricted to a class of symmetric polymorphic equilibria which have been studied in two-deme systems by Bazykin (1972) and Karlin & McGregor (1972) for one locus and by Christiansen & Feldman (1975) for two loci. With increased migration and recombination the heterozygosity increases unless it is already at the maximum level. Although the populaton system as a whole is always at linkage equilibrium, the magnitude of linkage disequilibrium in the individual demes may either increase or decrease with more migration and recombination. In general, the less the migration and the less the recombination between interacting loci, the greater the possibilities of polymorphic equilibria.

1. INTRODUCTION

Subdivided populations often manifest different allele and gamete frequencies in different demes. Although the disparities may be due to migration mitigating selection which favours different alleles or gametes in different habitats as has been studied extensively as clines (e.g. Haldane, 1948; Karlin & Richter-Dyn, 1976), such disparities may also be present when the same selection regime is in force in all the habitats (Bazykin, 1972; Karlin & McGregor, 1972; Christiansen & Feldman, 1975). We extend the models of these three papers to more habitats, more loci, and more alleles. In particular, we present restrictions on the viability parameters, migration rate, and recombination distribution which allow the existence of a stable polymorphism with allele (and gamete) frequencies varying among the demes.

This paper offers a complementary perspective on one of the models developed in our previous paper (Karlin & Campbell, 1978). In that paper we studied the stability of the central polymorphism (equal frequencies of all gamete types in all demes) when a symmetric selection regime (that of Lewontin & Kojima (1960) or generalizations to more loci and/or alleles (Karlin, 1979)) is in force in each habitat, but the selection regime varies among the habitats. One conclusion was that, although the central polymorphism can be either stable or unstable for all recombination distributions and migration rates for appropriate selection parameters, if the viability parameters are such that the stability of the central equi-

0016-6723/80/2828-8110 $01.00

librium depends on the recombination and migration rates, then more recombination and/or migration transforms the central equilibrium from unstable to stable.

In the present work we assume that a common symmetric selection regime is manifested in all the habitats. With suitable constraints on the selection regime, recombination distribution, and migration rate, there will be a stable equilibrium configuration which will display polymorphism in all demes; but each deme will be distinguished from the others by which gamete type or collection of gamete types is most prevalent. We note that the equilibria studied here can only exist if the central polymorphism is unstable for all recombination distributions and migration rates; when they do exist, more migration and or recombination will cause the disparity between the gamete frequencies in the various demes to diminish. (Concomitantly these equilibria will become unstable and then cease to exist.)

One facet of population systems which our previous study of central polymorphic equilibria does not encompass is linkage disequilibrium, since equal frequency of all gamete types necessarily entails linkage equilibrium. However, the persistent nature of linkage disequilibrium has long been recognized (Robbins, 1918) although there is no general agreement on its definition when more than two loci are involved (see Bennett, 1954, and Hill, 1976). Many authors have investigated how pervasive linkage disequilibrium should be in subdivided populations (e.g. Sinnock & Singh, 1972; Nei & Li, 1973; Prout 1973; Feldman & Christiansen, 1975). Because of the symmetry assumptions we impose as well as the fact that we have not determined the whole equilibrium structure for the selection–migration regimes we consider, quantitative conclusions concerning the likelihood of linkage disequilibrium in subdivided populations are not appropriate. However, some features of linkage disequilibrium are illustrated by the model.

The equilibria which we study often manifest linkage disequilibrium. In some cases more migration and/or recombination increases the amount of linkage disequilibrium while under other circumstances increasing migration and/or recombination decreases the amount of linkage disequilibrium (for selection values which provide stability for these equilibria). But the linkage disequilibrium is a local phenomenon associated with the individual demes. The symmetry assumptions which we employ provide that the population-system as a whole is at linkage equilibrium, in particular at the central polymorphism which would be unstable if all the demes had the same gamete frequencies. This illustrates the Wahlund effect which in the absence of selection allows global linkage disequilibrium despite local linkage equilibrium due to random drift in the allele frequencies as well as global linkage equilibrium with local disequilibrium (Feldman & Christiansen, 1975).

As with our previous paper (Karlin & Campbell, 1978), the following results are attained employing the Kronecker (tensor) product structure which is inherent to the symmetric selection regimes which we consider here and provides many insights into the nature of genetic frequency transformations (Karlin & Liberman, 1976, 1978; Karlin, 1978, 1979; Karlin & Avni, 1980). It is neither the purpose of

this paper nor appropriate to this journal to present the analytic machinery here. Instead, we merely state the available analytic results which are needed for the analyses presented below.

The high degree of symmetry which is built into these models in order to allow tractable analytical results does not compromise these results since the models are structurally stable (*sensu* Karlin & McGregor, 1972) providing validity for qualitative conclusions when the assumptions are not quite satisfied. Although the equilibria are not of interest in their own right when they are not stable, they help delineate the total equilibrium structure, and thus when they degenerate into the central equilibrium is of interest.

We commence the sequel with a review of one-locus disruptive selection in two habitats (Bazykin, 1972; Karlin & McGregor, 1972) and the *bona fide* multi-locus case studied by Christiansen & Feldman (1975). We then indicate how the extant results are extended with examples entailing three loci in two habitats; two and three loci in four habitats, and three loci in eight habitats. The discussion considers how these results apply to more general systems than discussed in the main body, including several alleles per locus, different numbers of demes, and applications to numerical studies.

2. THE PROTOTYPE: ONE LOCUS WITH TWO ALLELES

The possibility of maintaining a spatially inhomogeneous polymorphism (i.e. the allele frequencies vary among the demes) by selection-migration balance in a subdivided population in a uniform environment (i.e. the viability parameters are the same in all habitats) was demonstrated by Bazykin (1972) and Karlin & McGregor (1972). They posited a single locus with two alleles (say A and a) in a population divided into two demes. Both the selection regime and the migration pattern were symmetric. We shall represent the symmetric selection regime common to both environments with the viability parameters:

$$\begin{aligned} \alpha &= \text{homozygous } (AA \text{ or } aa) \text{ viability}, \\ \beta &= \text{heterozygous } (Aa) \text{ viability}. \end{aligned} \tag{1}$$

Migration is specified by the backward migration matrix

$$M = \begin{pmatrix} 1-m & m \\ m & 1-m \end{pmatrix}. \tag{2}$$

If $\beta > \alpha$ (overdominance) and $0 < m < 1$, it was shown that the only stable equilibrium entails equal frequency of both alleles in each deme: the central polymorphism. The fixation states (either the A-allele is fixed in both demes or the a-allele is fixed in both demes) are unstable equilibria. However, if $\alpha > \beta$ (underdominance) and $(\alpha-\beta)/\beta > 6m-4m^2$, there is a stable polymorphic equilibrium with the frequency of the A-allele in one deme equal to the frequency of the a-allele in the other (these frequencies are given by $\frac{1}{2} \pm \sqrt{[1-4m\alpha/(\alpha-\beta)]}$). These equilibria approach the central polymorphism as migration increases, but they

become unstable (at $m = \frac{1}{4}\{3-\sqrt{[9-4(\alpha-\beta)/\alpha]}\}$) before they degenerate into the central polymorphism (at $m = (\alpha-\beta)/4\alpha$).

3. BALANCED HALF-CENTRAL SYMMETRIC EQUILIBRIA

The above example was extended to two loci with two alleles at each locus (say A, a and B, b, respectively) by Christiansen & Feldman (1975). They posited the same symmetric migration structure as above and the symmetric Lewontin–Kojima (1960) selection regime specified by the viabilities

α = viability of double homozygotes (e.g. $AABB$),

β_1 = viability if A-locus is heterozygous and B-locus is homozygous (e.g. $AaBB$),

β_2 = viability if A-locus is homozygous and B-locus is heterozygous (e.g. $AABb$),

γ = viability if both loci heterozygous (i.e. $AaBb$). (3)

Among the equilibria which they studied were complementary equilibria:

$$\text{freq}(AB) = \text{freq}(ab) = [(1+\eta)/4]\,\text{freq}(Ab) = \text{freq}(aB) = (1-\eta)/4 \quad \text{in deme 1},$$
$$\text{freq}(AB) = \text{freq}(ab) = [(1-\eta)/4]\,\text{freq}(Ab) = \text{freq}(aB) = (1+\eta)/4 \quad \text{in deme 2}$$
$$(-1 \leqslant \eta \leqslant 1), \tag{4}$$

which are analogs of the one-locus equilibria. They gave the necessary condition for existence of a stable equilibrium of this nature with sufficiently slight migration and recombination, which is $\alpha+\gamma-\beta_1-\beta_2' > 0$. As migration and recombination increase, the equilibria approach the central polymorphism (η approaches 0), but the equilibria become unstable before the central polymorphism is attained.

It is noteworthy that the magnitude of the local linkage disequilibrium decreases as migration and recombination increase (hence η decreases) although the population as a whole is always in linkage equilibrium.

A natural generalization of the Lewontin–Kojima selection regime for more loci is the generalized symmetric selection regime of Karlin (1979). Viabilities depend solely on which loci are heterozygous (versus homozygous) and not which alleles are present at the particular loci. For up to three loci it is specified by viability parameters

α = viability if all loci homozygous,

β = viability if exactly one locus is heterozygous,

γ = viability if exactly two loci are heterozygous,

δ = viability if exactly three loci are heterozygous. (5)

In order to allow differences among the loci we shall append subscripts to the β's indicating which locus is heterozygous and subscripts to the γ's indicating which locus is homozygous. A more concise notation extending to an arbitrary number of loci is available in Karlin (1979).

Equilibrium for generalized symmetric selection regimes with no recombination in a panmictic population which entail exactly half the possible gametic types in

equal frequency have been dubbed half-central symmetric equilibria by Karlin (1979) (all of the alleles may or may not be present). For two alleles per locus, these equilibria include frequency $(A) = 1$ for one locus, frequency $(AB) =$ frequency $(ab) = \frac{1}{2}$ for two loci, and frequency $(ABC) =$ frequency $(Abc) =$ frequency $(aBc) =$ frequency $(abC) = \frac{1}{4}$ for three loci. There are 2 half-central symmetric equilibria for one locus, 6 for two loci, and 14 for three loci; a catalogue of these equilibria for two and three loci appears in Karlin & Liberman (1976).

The above examples for one and two loci entail balancing complementary half-central equilibria in two-deme systems (i.e. both equilibria together contain all possible gamete types). The allele frequencies in each deme are an average of the frequencies of the central polymorphism and the frequencies of one of the half-central equilibria. Analogous equilibria ensue from complementary half-central equilibria with any number of loci. We present the existence and stability criteria for these equilibria for the particular half-central equilibria (and their complements) cited above. These formulae require slight modification for different choices of the constituent half-central equilibria. Notation is chosen to reflect the unity of this problem with respect to the number of loci.

It is convenient to introduce two statistics of the selection regime

$$\gamma_\Sigma = \begin{cases} \alpha+\beta & \text{(for one locus)}, \\ \alpha+\beta_1+\beta_2+\gamma & \text{(for two loci)}, \\ \alpha+\beta_1+\beta_2+\beta_3+\gamma_1+\gamma_2+\gamma_3+\delta & \text{(for three loci)}, \end{cases} \tag{6}$$

$$\gamma_\Delta = \begin{cases} \alpha-\beta & \text{(for one locus)}, \\ \alpha-\beta_1-\beta_2+\gamma & \text{(for two loci)}, \\ \alpha-\beta_1-\beta_2-\beta_3+\gamma_1+\gamma_2+\gamma_3-\delta & \text{(for three loci)}. \end{cases} \tag{7}$$

Because we only present examples for three or fewer loci here, the concise representation of recombination given in Karlin & Liberman (1978) is not necessary and we shall employ the standard parameters

$$r \quad \text{(for two loci)} \tag{8}$$

and

$$\left.\begin{array}{ll} r & \text{(for the split } A/BC) \\ s & \text{(for the split } C/AB) \\ t & \text{(for the split } B/AC) \end{array}\right\} \text{(for three loci)}. \tag{9}$$

A necessary condition for existence of stable equilibria as specified above (cf. Table 1) is

$$\gamma_\Delta > 0. \tag{10}$$

This reduces to $\alpha > \beta$ for one locus (underdominance). It is a necessary condition for the stability of the half-central equilibrium in a single panmictic deme with no recombination (Karlin & Liberman, 1976; Karlin, 1979; Karlin & Avni, 1980).

The value for η (actually values since symmetry provides that $\pm\eta$ describe the

Table 1

	Gamete type	Two demes: Deme I	Two demes: Deme II	Four demes: Deme I	Four demes: Deme II	Four demes: Deme III	Four demes: Deme IV
One locus	A	$\frac{1+\eta}{2}$	$\frac{1-\eta}{2}$	Does not apply			
	a	$\frac{1-\eta}{2}$	$\frac{1+\eta}{2}$				
Two loci	AB	$\frac{1+\eta}{4}$	$\frac{1-\eta}{4}$	$\frac{1+\eta+\zeta+\theta}{4}$	$\frac{1+\eta-\zeta-\theta}{4}$	$\frac{1-\eta+\zeta-\theta}{4}$	$\frac{1-\eta-\zeta+\theta}{4}$
	Ab	$\frac{1-\eta}{4}$	$\frac{1+\eta}{4}$	$\frac{1-\eta-\zeta+\theta}{4}$	$\frac{1-\eta+\zeta-\theta}{4}$	$\frac{1+\eta-\zeta-\theta}{4}$	$\frac{1+\eta+\zeta+\theta}{4}$
	aB	$\frac{1-\eta}{4}$	$\frac{1+\eta}{4}$	$\frac{1-\eta+\zeta-\theta}{4}$	$\frac{1-\eta-\zeta+\theta}{4}$	$\frac{1+\eta+\zeta+\theta}{4}$	$\frac{1+\eta-\zeta-\theta}{4}$
	ab	$\frac{1+\eta}{4}$	$\frac{1-\eta}{4}$	$\frac{1+\eta-\zeta-\theta}{4}$	$\frac{1+\eta+\zeta+\theta}{4}$	$\frac{1-\eta-\zeta+\theta}{4}$	$\frac{1-\eta+\zeta-\theta}{4}$
Three loci	ABC	$\frac{1+\eta}{8}$	$\frac{1-\eta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$
	ABc	$\frac{1-\eta}{8}$	$\frac{1+\eta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$
	AbC	$\frac{1-\eta}{8}$	$\frac{1+\eta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$
	Abc	$\frac{1+\eta}{8}$	$\frac{1-\eta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$
	aBC	$\frac{1-\eta}{8}$	$\frac{1+\eta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$
	aBc	$\frac{1+\eta}{8}$	$\frac{1-\eta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$
	abC	$\frac{1+\eta}{8}$	$\frac{1-\eta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$
	abc	$\frac{1-\eta}{8}$	$\frac{1+\eta}{8}$	$\frac{1+\eta+\zeta+\theta}{8}$	$\frac{1+\eta-\zeta-\theta}{8}$	$\frac{1-\eta+\zeta-\theta}{8}$	$\frac{1-\eta-\zeta+\theta}{8}$

Gamete frequencies for the balanced half-central and quarter-central equilibria ($0 \leqslant \eta, \zeta, \theta \leqslant 1$). The choice $\eta = \zeta = \theta = 0$ gives the central polymorphism. When the equilibria are stable η, ζ, and θ are close to 1. We specialize to $\eta = \zeta = \theta$ for the explicit calculations in the text.

same equilibrium under relabelling the demes) is given above (§2) for one locus. For two loci it is specified by

$$\eta^2 = [(1-2m)(\gamma_\Sigma + \gamma_\Delta - 4r\gamma) - \gamma_\Sigma]/\gamma_\Delta. \tag{11}$$

For three loci the equation is

$$\eta^2 = [(1-2m)(\gamma_\Sigma + \gamma_\Delta - 4r(\gamma_2+\gamma_3) - 4s(\gamma_1+\gamma_2) - 4t(\gamma_1+\gamma_3)) - \gamma_\Sigma]/\gamma_\Delta. \tag{12}$$

Employing these values for η^2, i.e. assuming we have determined the frequencies

https://doi.org/10.1017/S0016672300019649 Published online by Cambridge University Press

at the equilibrium, we can verify necessary conditions for stability of the equilibrium involving only the recombination parameters or only the migration rates. The former conditions are

$$[\gamma_\Sigma+\gamma_\Delta-4r\gamma][\gamma_\Sigma-\eta^2\gamma_\Delta]/[\gamma_\Sigma+\eta^2\gamma_\Delta]^2 < 1 \tag{13}$$

for two loci and

$$[\gamma_\Sigma+\gamma_\Delta-4r(\gamma_2+\gamma_3)-4s(\gamma_1+\gamma_2)-4t(\gamma_1+\gamma_3))(\gamma_\Sigma-\eta^2\gamma_\Delta)]/[\gamma_\Sigma+\eta^2\gamma_\Delta]^2 < 1 \tag{14}$$

for three loci. If we instead employ the parameter m the stability criterion is independent of the number of loci:

$$(1/[1-2m])\,[\gamma_\Sigma-\eta^2\gamma_\Delta]/[\gamma_\Sigma+\eta^2\gamma_\Delta] < 1. \tag{15}$$

These inequalities are expressed in terms of the recombination and migration parameters (and not η^2) if we substitute (11) or (12) into (13), (14), or (15) for η^2.

4. BALANCED QUARTER-CENTRAL SYMMETRIC EQUILIBRIA

The above methods are not restricted to two-deme systems. If two or more loci are present (we illustrate with two and three loci) there may be a stable equilibrium in a system of four demes with each deme manifesting an excess (compared to the central equilibrium) of exactly one quarter of the gamete types while the population system as a whole manifests the central polymorphism. The selection regime (5) and recombination distribution ((8), (9)) as described above are appropriate, but in order to incorporate four demes we must expand the backward migration matrix to

$$M = \begin{pmatrix} 1-3m & m & m & m \\ m & 1-3m & m & m \\ m & m & 1-3m & m \\ m & m & m & 1-3m \end{pmatrix}. \tag{16}$$

The equilibria we study are of the form given in Table 1. The frequencies in the individual demes are averages of the frequencies associated with the central polymorphism and the quarter-central equilibria given in Karlin & Liberman (1976). In particular, we employ the quarter symmetric equilibria freq $(AB) = 1$ for two loci, freq $(ABC) =$ freq $(abc) = \frac{1}{2}$ for three loci, and their complements (cf. Table 1).

The gamete frequencies for equilibria of the form given in Table 1 satisfy a system of three cubics in three variables. However, if we slightly strengthen the symmetry assumptions, the system collapses to a single cubic in one unknown which is readily solvable since one of the roots is zero. We assume

$$(1-2r)\gamma = \beta_1 = \beta_2$$

for three loci. Under these assumptions, an equilibrium of the type given in Table 1 (with $\eta = \zeta = \theta$) will satisfy

$$\eta^2(3\alpha-2\beta-\gamma)-(1-4m)\eta(2\alpha-2\beta)-(1-4m)(2\alpha+2\beta)+\gamma_\Sigma = 0 \tag{17}$$

https://doi.org/10.1017/S0016672300019649 Published online by Cambridge University Press

for two loci and

$$\eta^2(3\alpha+3\delta-3\beta-3\gamma)-\eta(1-4m)(2\alpha-2\beta+(2-8r)(\delta-\gamma)) \\ -(1-4m)\,(2\alpha+2\beta+(2-8r)\,(\gamma+\delta))+\gamma_\Sigma = 0 \quad (18)$$

for three loci.

We note that η does not occur in these quadratics solely as a square because changing the signum of η does not correspond to relabelling the demes as is the case with only two demes. The two-locus quadratic is not independent of the recombination rate because of the assumption $(1-2r)\gamma = \beta$.

The explicit stability criteria, although accessible, are not concise and are therefore omitted. However, we know by the theory of small parameters (Karlin & McGregor, 1972) that, since stability of the quarter symmetric equilibria in single panmictic population with no recombination and instability of the central polymorphism for all levels of recombination are necessary for the existence of balanced quarter symmetric equilibria, the equilibria will be stable (when they exist) for sufficiently slight migration and recombination, and they will become unstable before they merge into the central polymorphism as migration and recombination are increased.

As a complement to the circumstance with two loci in just two demes, two loci in four demes manifest negligible local linkage disequilibrium for negligible migration and recombination; but the amount of linkage disequilibrium initially increases with more migration and recombination although it reverts to zero as panmixia is attained.

5. BALANCED EIGHTH-CENTRAL SYMMETRIC EQUILIBRIA

Analogous to one locus in two demes and two loci in four demes, there are equilibria for three loci characterized by the prevalence of a different gamete type in each of eight demes for sufficiently slight migration and recombination if the fixation states are stable in single panmictic populations. The stability criterion for the fixation states (Karlin & Liberman, 1976) is

$$\alpha > \max(\beta, \gamma, \delta). \quad (19)$$

Equilibria of this type will become unstable and then merge into the central polymorphism with increased migration and recombination.

6. DISCUSSION

Bazykin (1972) and Karlin & McGregor (1972) demonstrated that an environment which allows only stable monomorphic equilibria for a panmictic population can maintain a stable polymorphism if the population is subdivided into demes. Christiansen & Feldman (1975) extended their result to two loci allowing the study of the effect of recombination as well as migration on polymorphism. We present the natural extension of these models to more demes, more loci, and more alleles.

The present work complements our previous study (Karlin & Campbell, 1978) which analysed the central polymorphism (equal frequency of all gamete types). In that work the selection and recombination regimes varied among the habitats and it was found that more migration and more recombination enhanced the stability of the central polymorphism. The present work assumes a common selection–recombination regime in all habitats and focuses on equilibria which only exist if the central polymorphism is unstable for all levels and forms of recombination.

Level of heterozygosity. Some of the equilibria which we studied (e.g. two loci in two demes) have the maximum level of heterozygosity ($\frac{1}{2}$) at each locus for all levels of migration and recombination as occurs with the central polymorphism. Other classes of equilibria (e.g. two loci in four demes), however, have negligible heterozygosity when migration and recombination are negligible which increases toward the maximum level with more migration and recombination. In no case does heterozygosity decrease with more migration and recombination.

Linkage disequilibrium. The system as a whole manifests the central polymorphism for all the equilibria studied here and hence global linkage disequilibrium is zero. However, the central polymorphism is not manifested in the individual demes and local linkage disequilibrium often occurs. In some cases (e.g. two loci in two demes) the magnitude of local linkage disequilibrium decreases with more migration and more recombination. Other circumstances (e.g. two alleles in four demes) provide an increase in the magnitude of local linkage disequilibrium with more migration and recombination if the level of migration and recombination is low.

Selection structure. The above examples have assumed two alleles at each locus with selection dependent solely on which loci are homozygous (versus heterozygous) and not which alleles are at the loci. (In fact, the worked-out examples assume that viability depends only on how many loci are homozygous and not which loci are homozygous.) The assumption of two alleles per locus has been made solely for clarity of exposition, inasmuch as the single-deme model for arbitrary numbers of alleles at each locus with fitness depending solely on which loci are homozygous has been analysed extensively (Karlin & Avni, 1980) and allows polymorphisms balanced by migration as presented above (more alleles require more demes).

The symmetry assumptions are incorporated to allow concise formulae. But the results have general qualitative applicability because the model is structurally stable (i.e. the qualitative behaviour of the system is not changed by small deviations in the parameter values).

The symmetry assumptions can be somewhat weakened if there are several alleles at the loci. This is accomplished by considering each locus as a cluster of tightly linked loci or superlocus (Karlin, 1979) so that each allele of the superlocus is a gamete type for the cluster of tightly linked loci. The above selection constraints on the constituent loci of the superlocus allow a more general selection regime on the alleles of the superlocus. The multilocus character is retained if

there are several superloci with negligible recombination among their constituent loci but significant recombination between the superloci.

Migration structure. The migration pattern is a form of island migration (Deakin, 1966) which superimposes a sedentary tendency on total panmixia. The uniformity of the selection regime allows that demes as physical entities are not important; rather, if clustering the demes provides the appropriate number (e.g. 2, 4, 8) of virtual demes and the net migration rates among the virtual demes reflect homing superimposed on panmixia, the above models are pertinent.

An important aspect of these models is that they allow contrasting equilibrium configurations under different subdivisions of the population. With several loci, finer subdivision of a population provides more types of symmetric equilibria which may exist. Although which equilibria are stable depends on the selection regime and recombination distribution, passing to a finer subdivision of a population will not destroy an equilibrium configuration or its stability, but may allow other (stable) equilibria with less heterozygosity and more (local) linkage disequilibrium to exist.

Other equilibria. Because the equilibrium structure becomes far more intricate as the dimension increases, we are not able to present the complete equilibrium structure as is done by Bazykin (1972), Karlin & McGregor (1972), and Christiansen & Feldman (1975). Even in those cases the symmetric equilibria described in this paper do not subsume all the possible equilibrium configurations. However, these symmetric equilibria which are interesting in their own right if stable are equally important if unstable for helping to delineate where stable equilibria must be.

This last feature is achieved most expeditiously by taking the results of this paper in concert with previously known results for the fixation states (Karlin & Liberman (1976) and the symmetric central polymorphism (Karlin & Campbell (1978)). As an example, we noted in Karlin & Campbell (1978) that because the central and fixation equilibrium can attain stability with more migration and more recombination, there must be other equilibria which lose their stability with more migration and more recombination. However, the non-central symmetric equilibria studied above can only exist if the central polymorphism is unstable for any level or form of migration (and no recombination); hence the central equilibrium remains unstable when these non-central equilibria become unstable with increasing migration and is still unstable when these non-central symmetric equilibria degenerate into it. Therefore, different equilibria must complement the stability of the fixation and symmetric equilibria. Of course, the existence of other (non-symmetric, non-fixation) equilibria is known; e.g. there can be four other equilibria with only one locus (Karlin & McGregor, 1972); even in a single deme there are other equilibria (Karlin, 1979). These formulae help delineate circumstances for their existence.

Computer simulation. In general, computer studies of multilocus, multiallele systems entail an unmanageable number of random parameters, and random methods for locating equilibria. While sacrificing the global equilibrium structure and putting constraints on the selection regime, these models permit the analysis

of symmetric equilibria which are easily characterized in systems entailing numbers of alleles and loci which would otherwise preclude analysis.

Effect of migration and recombination on the equilibrium structure. The transience of these non-central symmetric equilibria suggests a qualitative role which migration and recombination may play in the equilibrium structure of populations. Of course, drawing general conclusions from one class of equilibria is tenuous. But these equilibria are more likely to exist and be stable with low migration and tight linkage. Hence the notion that removing population structure in passing to one panmictic population and removing genome structure in passing to free recombination diminish the prospects for divers equilibria as posited in Karlin (1979) is supported.

Acknowledgement is especially due to Samuel Karlin for access to unpublished material as well as for productive discussions. The research on which this paper is based was conducted at Stanford University and supported in part by the National Institutes of Health (Grant GM10452-16) and the National Science Foundation (Grant MCS 76-80624-A01).

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