CLINES WITH ASYMMETRIC MIGRATION*

THOMAS NAGYLAKI

Department of Biophysics and Theoretical Biology, The University of Chicago,
920 East 58th Street, Chicago, Illinois 60637

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ABSTRACT

The consequences of asymmetric dispersion on the maintenance of an allele in a one-dimensional environmental pocket are examined. The diffusion model of migration and selection is restricted to a single diallelic locus in a monoecious population in the absence of mutation and random drift. It is further supposed that migration is homogeneous and independent of genotype, the population density is constant and uniform, and Hardy-Weinberg proportions obtain locally. If dispersion is preferentially out of an environmental pocket at the end of a very long habitat, the condition for maintaining the allele favored in the pocket becomes less stringent than for symmetric migration; dispersion preferentially into the pocket increases the severity of the condition for polymorphism. If an allele is harmful in large regions on both sides of an environmental pocket, the probability for polymorphism is decreased by asymmetric migration. The criterion for the existence of a cline is independent of the sense of the asymmetry; the cline itself is not. These phenomena are studied both analytically and numerically.—It is shown for symmetric migration and variable population density that the more densely populated parts of the habitat are more influential in determining gene frequency than the others. Thus, the higher the population density in an environmental pocket, the more easily an allele beneficial in the pocket will be maintained in the population.

THERE has been much interest recently in the amount and pattern of genetic variability maintained by the joint action of migration and selection. Research concerning populations distributed in clusters is discussed in detail in NAGYLAKI (1977a). Considerable progress has been made in the study of continuously distributed populations. The problem of the existence, uniqueness, and stability of clines in the simplest case of uniform population density and homogeneous and isotropic migration was investigated by CONLEY (1975), FLEMING (1975), NAGYLAKI (1975, 1977b), and FIFE and PELETIER (1977). Some work has been done on clines involving two loci (SLATKIN 1975) and quantitative characters (SLATKIN 1977), and the exploration of random genetic drift in a cline has begun (FELSENSTEIN 1975; SLATKIN and MARUYAMA 1975; NAGYLAKI 1978).

If a cline exists, there must be sufficient environmental heterogeneity to reverse the direction of natural selection at least once. Not infrequently, such spatial diversity must also be reflected in inhomogeneities in the migration pattern and carrying capacity. This motivated the analysis of the consequences of

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a discontinuity in the migration rate (NAGYLAKI 1976) and the diffusion treatment (NAGYLAKI 1976) of SLATKIN's (1973) geographical barrier model. Using SAWYER's (in preparation) recent results, we shall study the effects of a jump in population density in Section III.

Asymmetry in the dispersion rate may exist for plants due to prevailing winds or asymmetric migration of pollinating insects and for animals owing to a gradient of suitability over the habitat, as may be associated with more food, better terrain, more desirable temperatures, etc. MAY, ENDLER, and MCMURTRIE (1975) have examined the step and linear selection gradients with numerical and scaling methods. They found a "downwind" displacement (*i.e.*, in the direction of preferential migration) of the cline in both cases, but a significant broadening of the cline only for the step environment. We shall derive some qualitative properties of clines with asymmetric migration in Section I. The effect of the asymmetry on the conditions for the existence of clines will be investigated in Section II.

I. QUALITATIVE RESULTS

The analyses in this paper will be confined to one spatial dimension. They apply, therefore, to two distinct biological circumstances. Organisms are frequently restricted to the immediate neighborhood of a river, seashore, etc., or may live in a river or narrow valley. Alternatively, the distribution of the population may really be two-dimensional, but only one of the coordinates may have genetic relevance. This would happen, *e.g.*, if only latitude matters on a geographic scale, or locally if individuals exist at various elevations on a mountain range. Previous work (HANSON 1966; NAGYLAKI 1975) indicates that the difference between one and two dimensions, though not negligible, is neither surprising nor extremely large.

We denote the mean and variance of the migrational displacement per generation by the genotype-independent constants $m(-\infty < m < \infty)$ and σ^2. Let us assume that the population density is constant and uniform and Hardy-Weinberg proportions obtain locally. The population is monoecious, with the alleles A_1 and A_2 segregating at the locus under consideration. We neglect mutation and random drift, and suppose that at position x the Malthusian parameters of the genotypes A_1A_1, A_1A_2, A_2A_2 have the form $sg(x)$, $hsg(x)$, $-sg(x)$. Thus, $s\ (>0)$ is the strength of natural selection, and $h\ (-1 \leq h \leq 1)$ specifies the degree of dominance, assumed to be independent of location. Over- and underdominance are excluded for simplicity; to infer their effects, see NAGYLAKI (1975).

The equilibrium frequency, $p(x)$, of A_1 at x satisfies (NAGYLAKI 1975)

$$\frac{1}{2}\sigma^2 p'' - mp' + sg(x)f(p) = 0, \qquad (1)$$

where

$$f(p) = p(1-p)(1+h-2hp), \qquad (2)$$

and primes indicate derivatives with respect to x. Care must be exercised in imposing conditions at the boundaries of the habitat. If the population density is ρ, the flux of individuals is $m\rho-(1/2)\sigma^2\rho'$ (NAGYLAKI 1975). Hence, zero-flux boundary conditions cannot be stipulated with asymmetric migration *and* uniform population density. Suppose, however, that the population density is controlled by reduction everywhere to ρ at regular short time intervals. Then we can study continuous variation only in the gene frequency, and requiring the finiteness of its time derivative at the boundary yields

$$p'=0. \tag{3}$$

This boundary condition was deduced by FLEMING and SU (1974) in the neutral case, but one can see easily that their argument still applies in the presence of selection.

Positivity is the only property of $f(p)$ required for the following qualitative results. We assume that $g(x)$ is continuous; we may think of the step environments of Section II as limiting cases.

1. *Maxima and minima*

In view of the downwind displacement of clines mentioned above and analyzed below, it is perhaps not entirely obvious that maxima and minima of $p(x)$ can occur only where A_1 is advantageous and deleterious, respectively. Since $p'=0$ at a stationary point of $p(x)$, (1) shows that $\operatorname{sgn} p''(x)=-\operatorname{sgn} g(x)$, where $\operatorname{sgn} x=x/|x|$, thereby establishing that $p(x)$ can have maxima and minima only where $g(x)\geq 0$ and $g(x)\leq 0$, respectively.

2. *sgn* g(x) = *sgn* x

Let us restrict ourselves to a single reversal of the direction of natural selection, choosing $\operatorname{sgn} g(x)=\operatorname{sgn} x$ without loss of generality. We enforce (3) at any boundaries of the habitat. If there is no boundary for $x<0$, then $p(-\infty)=p'(-\infty)=0$. With no boundary for $x>0$, $p(\infty)=1$ and $p'(\infty)=0$. With no boundaries, intuition, experience (FLEMING 1975; NAGYLAKI 1975, 1977b; FIFE and PELETIER 1977) and related work (SAWYER, in preparation) lead us to expect, at most, one stable cline. With at least one boundary, we expect at most one stable and one unstable cline.

(a) *Monotonicity*: In spite of preferential dispersion, we expect intuitively that the cline is monotone nondecreasing. To prove this, assume the contrary, *i.e.*, $p'(x_0)<0$ for some x_0. If $g(x)$ is nonzero near the boundaries (or nonzero for sufficiently large $|x|$, if $x=\pm\infty$ is a "boundary"), we have from (1) and (3) $\operatorname{sgn} p''(x)=-\operatorname{sgn} g(x)=-\operatorname{sgn} x$, and hence $p'(x)\geq 0$ sufficiently close to the boundaries. Therefore, $p(x)$ must have a maximum at some $x_M<x_0$ and a minimum at some $x_m>x_0$, whence $x_M<x_m$. But Result 1 implies $x_M>0$ and $x_m<0$, demonstrating our assertion by contradiction.

(b) *Downwind displacement*: In view of the above monotonicity, we may roughly define the location, $\bar{x}$, of a cline as the position of the greatest slope.

Then $p''(\bar{x}) = 0$ and (1) inform us that $mp'(\bar{x}) = sg(\bar{x})f[p(\bar{x})]$. Therefore, with symmetric dispersion, $m = 0$. we obtain $\bar{x} = 0$. For $m \neq 0$ we find $\operatorname{sgn} \bar{x} = \operatorname{sgn} g(\bar{x}) = \operatorname{sgn} m$ because $p'(\bar{x}) \geq 0$. This establishes the downwind displacement observed numerically for the step and linear selection gradients by MAY, ENDLER, and MCMURTRIE (1975).

3. *Scaling*

We posit that the habitat is unbounded (*i.e.*, very long for both $x > 0$ and $x < 0$ compared to m and σ). and seek the controlling dimensionless measure of the asymmetry of dispersion. Taking d as the characteristic length of the environmental variation, we consider the special case ($\mu \geq 0$)

$$g(x) = \begin{cases} -1 \quad, & x < -d/2, \\ -(-2x/d)^{\mu}, & -d/2 < x < 0, \\ +(\ \ 2x/d)^{\mu}, & 0 < x < d/2, \\ +1 \quad, & x > d/2, \end{cases} \tag{4}$$

of odd $g(x)$. With $m = 0$ we derived the characteristic length

$$w = (l^2 d^{\mu})^{1/(\mu+2)} = l(d/l)^{\mu/(\mu+2)} = d(l/d)^{2/(\mu+2)} \tag{5}$$

for the cline (NAGYLAKI 1975, 1977b). In (5), $l = \sigma / \sqrt{s}$, the width of the cline for the step environment (SLATKIN 1973). Setting $x = w\xi$ in (1) and dividing by $\sigma^2 / (2w^2)$, we see that the coefficient of the first derivative becomes

$$\tilde{m} = 2mw / \sigma^2 . \tag{6}$$

Manifestly, $|\tilde{m}| << 1$ and $|\tilde{m}| >> 1$ correspond to small and large asymmetries. For the step ($\mu = 0$) and linear ($\mu = 1$) selection gradients, $\tilde{m}$ agrees with the critical asymmetry parameters of MAY, ENDLER, and MCMURTRIE (1975). For a neutral belt separating the regions where A_1 and A_2 are favored, $\mu = \infty$, so $w = d$ and $\tilde{m} = 2md / \sigma^2$. Only in this case is $\tilde{m}$ independent of the selection intensity s. Otherwise, (5) and (6) show $\tilde{m}$ is a monotone decreasing function of s. Thus, weak selection enhances asymmetry. The asymmetry parameter is a monotone decreasing function of σ and a monotone increasing function of d.

II. QUANTITATIVE ANALYSIS

We seek criteria for the existence of clines. One expects to observe many of the relevant biological phenomena with semi-infinite and infinite habitats and no dominance ($h = 0$). The conditions we shall obtain are certainly sufficient (SAWYER, in preparation), and probably also necessary (NAGYLAKI 1975). For stability we can rely on SAWYER (in preparation), but uniqueness we must conjecture. No numerical evidence was found against necessity or uniqueness. Generalization to an arbitrary degree of dominance is straightforward, but, at least for $h < -\frac{1}{3}$, we do not expect the sufficient conditions to be necessary (NAGYLAKI 1975).

1. *Semi-infinite cline*

We suppose the habitat is the half-line $0 \leq x < \infty$. The geometry envisaged here would apply to fresh-water organisms in a river flowing into a body of salt water, organisms distributed over a region bounded on one side by a mountain range, river, or seashore, etc. Assume A_1 is beneficial in $0 \leq x < a$ and harmful in $x > a$, the ratio of the uniform selection intensities being α^2:

$$g(x) = \begin{cases} 1, & 0 \leq x < a, \\ -\alpha^2, & x > a. \end{cases} \tag{7}$$

We introduce the dimensionless coordinate $\xi = x/a$ and redefine p and g as $p(\xi)$ and

$$g(\xi) = \begin{cases} 1, & 0 \leq \xi < 1, \\ -\alpha^2, & \xi > 1. \end{cases} \tag{8}$$

From (1), (2), and (3) we obtain

$$p'' - \beta p' + k^2 g(\xi) p(1-p) = 0, \qquad \xi > 0, \tag{9}$$

$$p'(0) = 0, \qquad p(\infty) = 0, \tag{10}$$

where primes now signify derivatives with respect to ξ, $\beta = 2am/\sigma^2$ $(-\infty < \beta < \infty)$ is the crucial dimensionless asymmetry parameter, and $k^2 = 2sa^2/\sigma^2$ controls the behavior of the cline without asymmetry (NAGYLAKI 1975).

A cline will exist if $k > \kappa$, where κ is the smallest positive eigenvalue of the linearized equation

$$p'' - \beta p' + k^2 g(\xi) p = 0, \qquad \xi > 0, \tag{11}$$

with the boundary conditions (10) (SAWYER, in preparation). The solution of (11) in (0,1) is a linear combination of exponentials; in $(1,\infty)$ it is a decaying exponential. The constants in the exponents are determined by substitution into (11). Imposing $p'(0) = 0$ and continuity of $p(\xi)$ and $p'(\xi)$ at $\xi = 1$ permits the elimination of the normalization constants and leads to the eigenvalue equation

$$F(\lambda) \equiv \alpha^2 y \coth(y/2) - (\beta^2 + \alpha^2\lambda)^{1/2} - \beta(1+\alpha^2) = 0, \tag{12}$$

where $\lambda = 4k^2$ and $y = (\beta^2 - \lambda)^{1/2}$. By using $\exp(\beta\xi/2)$ and $\xi \exp(\beta\xi/2)$ as the linearly independent solutions in (0,1), it is easy to verify that the special case $k = \beta/2$ is given correctly by taking the appropriate limit in (12). The reader unfamiliar with the procedure described above (12) will find the detailed solution of a similar problem in Section IV.5 of NAGYLAKI (1975) helpful.

We can calculate κ explicitly by iteration for small asymmetry, $\beta \to 0$. Noting that $\coth iz = -i \cot z$, we easily obtain from (12) the Maclaurin series

$$F(\lambda) = 2\alpha k(\alpha \cot k - 1) - \beta(1 + \alpha^2) + O(\beta^2). \tag{13}$$

Therefore, (12) and (13) inform us that

$$\kappa = \tan^{-1} \alpha + O(\beta), \tag{14}$$

the leading term agreeing with our previous result for isotropic migration (NAGYLAKI 1975). From (12) and (13) we deduce

$$\kappa = \tan^{-1}\left[\alpha - \frac{\beta(1+\alpha^2)}{2\kappa}\right] + O(\beta^2) \ .$$

$$= \tan^{-1}\alpha - \frac{\beta}{2\tan^{-1}\alpha} + O(\beta^2), \tag{15}$$

upon inserting (14) and expanding in powers of β. Clearly, we may neglect the uncalculated second order term in (15) if $|\beta| << (\tan^{-1}\alpha)^2$.

We observe that for sufficiently small β preferential dispersion into the environmental pocket ($\beta < 0$) raises κ, thereby increasing the stringency of the critical condition $k > \kappa$, as expected from the influx of A_2 genes. But excess migration out of the pocket ($\beta > 0$) eases the requirement for polymorphism. This result is recognized as biologically reasonable if it is recalled that the population density is regulated in this model, so that an efflux of individuals from the pocket raises the frequency of A_1 in the rest of the habitat without depopulating the pocket. We shall see numerically that the conclusions of this paragraph apply without restrictions on the magnitude of β. The fact that the change in κ is of $O(\beta)$ may be established for any selection gradient $g(\xi)$ by perturbation theory (see, *e.g.*, MATHEWS and WALKER 1964, Chapter 10). For the special case (8) of $g(\xi)$, (15) was derived completely independently in that manner.

To begin the general analysis of (12), let us show that $F(\lambda)$ is monotone decreasing wherever it is finite. For $\lambda \leq \beta^2$, we have

$$F'(\lambda) = -\left[\frac{\sinh y - y}{4y\sinh^2(y/2)} + \frac{\alpha^2}{2(\beta^2 + \alpha^2\lambda)^{1/2}}\right],$$

which is indeed negative because $\sinh y \geq y$ for $y \geq 0$. If $\lambda > \beta^2$, we define $\eta = (\lambda - \beta^2)^{1/2}$ and compute

$$F'(\lambda) = -\left[\frac{\eta - \sin\eta}{4\eta\sin^2(\eta/2)} + \frac{\alpha^2}{2(\beta^2 + \alpha^2\lambda)^{1/2}}\right],$$

again demonstrating $F'(\lambda) < 0$ since $\eta \geq \sin\eta$ for $\eta \geq 0$.

Monotonicity enables us to find bounds on κ. By direct calculation we prove that

$$F(0) > 0 \quad \text{if and only if} \quad \beta < \beta_0 \equiv \ln(1+\alpha^2), \tag{16a}$$

$$F(\beta^2) > 0 \quad \text{if and only if} \quad \beta < \beta_1 \equiv 2[1 - (1+\alpha^2)^{-1/2}], \tag{16b}$$

$$F(\beta^2 + \pi^2) > 0 \quad \text{if and only if} \quad \beta < \beta_2 \equiv -\pi(1+\alpha^2)^{-1/2}, \tag{16c}$$

$$F(\beta^2 + 4\pi^2 -) = -\infty. \tag{16d}$$

Employing the variable $b = (1 + \alpha^2)^{1/2} - 1$ and the elementary inequality $(b > 0)$ $\ln(1 + b) > b/(1 + b)$, we conclude trivially that $\beta_0 > \beta_1$; obviously $\beta_1 > 0 > \beta_2$. To understand what happens as $\beta \to \beta_0-$, note that for $\beta > 0$ (12) gives

$$F(0) = \alpha^2\beta \coth(\beta/2) - \beta(2+\alpha^2),$$

whence

$$\frac{\partial}{\partial\beta}F(0) = -\frac{4\sinh^2(\beta/2) + \alpha^2(e^{-\beta} + \beta - 1)}{2\sinh^2(\beta/2)} < 0. \tag{17}$$

Hence, $\kappa \to 0+$ as $\beta \to \beta_0-$. Therefore, if dispersion out of the pocket reaches or exceeds the critical value β_0, a cline will be maintained by any nonzero selection intensity. Together with (16), this yields the following limits on the critical value κ:

$$\beta < \beta_2 \quad \text{implies} \quad (1/2)(\beta^2 + \pi^2)^{1/2} < \kappa < (1/2)(\beta^2 + 4\pi^2)^{1/2}, \tag{18a}$$

$$\beta_2 \leq \beta < \beta_1 \quad \text{implies} \quad (1/2)|\beta| < \kappa \leq (1/2)(\beta^2 + \pi^2)^{1/2}, \tag{18b}$$

$$\beta_1 \leq \beta < \beta_0 \quad \text{implies} \quad 0 < \kappa \leq (1/2)\beta, \tag{18c}$$

$$\beta \geq \beta_0 \quad \text{implies} \quad \kappa = 0. \tag{18d}$$

We observe also that if A_1 is lethal outside the pocket, *i.e.*, as $\alpha \to \infty$, (12) reduces to the simpler equation

$$y \coth(y/2) = \beta. \tag{19}$$

As $\beta \to -\infty$, (18a) suggests that $\kappa \to (1/2)(\beta^2 + 4\pi^2)^{1/2}$. To check this, we apply the bound (18a) to (12) and infer that $\eta \cot(\eta/2) \to -\infty$ as $\beta \to -\infty$, whence $\eta \to 2\pi$, as required.

L. A. PELETIER has pointed out (private communication) that sufficient asymmetry destroys the cline even in an infinite habitat. In the special case studied here, we can easily confirm this interesting result and derive the critical range for the asymmetry parameter. A_1 might be swamped by A_2 for sufficiently large negative m. The critical condition (12) is clearly unaltered by shifting the pocket in (7) to the left by a. Hence, if $a \to \infty$, then $\beta \to -\infty$, and the result below (19) requires $k > -1/2\,\beta$, *i.e.*, $m > -\sigma\sqrt{2s}$. To preserve A_2, m must not exceed a critical value depending on the selection coefficient, $s\alpha^2$, favoring A_2. Thus, by analogy with the above criterion, $m < \alpha\sigma\sqrt{2s}$, and we conclude that a cline exists if

$$-\sigma\sqrt{2s} < m < \alpha\sigma\sqrt{2s}.$$

Notice that in terms of the scaled asymmetry parameter, $\tilde{m}$, in (6) this condition

$$-2\sqrt{2} < \tilde{m} < 2\sqrt{2}\,\alpha.$$

reads

TABLE 1

Critical values κ for the semi-infinite cline

$\beta \backslash \alpha$	1/2	1	2	∞
—10	5.51	5.54	5.58	5.66
—2	1.71	1.82	1.98	2.26
—1	1.18	1.34	1.55	1.90
—1/2	0.870	1.08	1.33	1.73
—1/10	0.563	0.848	1.15	1.60
0	0.464	0.785	1.11	1.57
1/10	0.341	0.720	1.06	1.54
1/2	0	0.396	0.874	1.42
1	0	0	0.615	1.27
2	0	0	0	1.00
10	0	0	0	0.07

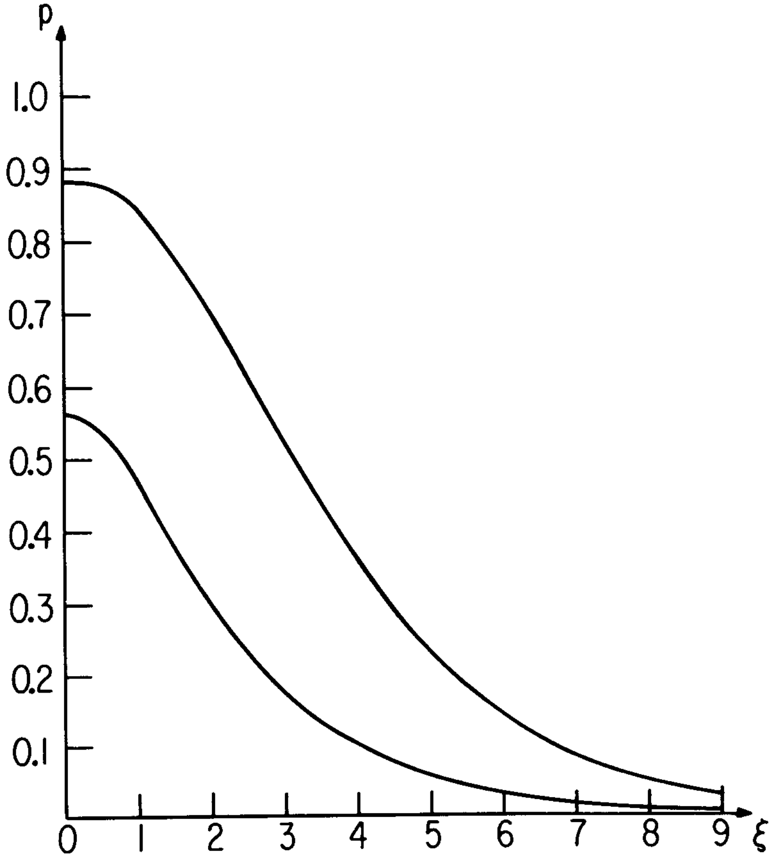

FIGURE 1.—Two semi-infinite clines: $\alpha = 1$, $\beta = \frac{1}{2}$, $k = 0.8$ (lower curve) and $\alpha = 2$, $\beta = 2$, $k = 0.6$ (upper curve).

We exhibit typical critical values κ, computed from (12) and (19), in Table 1. The values of the critical asymmetry parameter β_0 corresponding to $\alpha = 1/2$, 1, 2 are 0.223, 0.693, 1.609. The numbers in the table conform to (18), agree closely with (15) for $\beta = \pm 1/10$, and indicate that κ is a monotone increasing function of α and a monotone decreasing one of β, as expected and discussed above.

Evidently, there are three distinct cases: $0 < k < \kappa$, no cline; $k > \kappa > 0$, a cline exists; $k > \kappa = 0$ $(\beta > \beta_0)$, a cline exists. An example of each situation was chosen by referring to Table 1. Indeed, for $\alpha = 2$, $\beta = 1/2$, $k = 0.7 < \kappa = 0.874$, a thorough study of (9) and (10) revealed no cline. For $\alpha = 1$, $\beta = 1/2$, $k = 0.8 > \kappa = 0.396$, the unique lower solution in Figure 1 was found. Finally, with $\alpha = 2$, $\beta = 2$, $k = 0.6 > \kappa = 0$, the unique solution is the upper one in Figure 1. (Both curves are accurate to at least 1 part in 1000.)

2. *Infinite cline*

We are concerned here with $g(\xi)$ such that A_1 is favored in a finite interval $(g > 0)$ and deleterious elsewhere $(g < 0)$. In contradistinction to the case of symmetric migration, due to the asymmetric first derivative term in (9), we cannot obtain the infinite cline even for $g(-\xi) = g(\xi)$ by reflecting the semi-infinite one about the origin. We shall first prove some results for arbitrary environments.

With suitable scaling, the exact and linearized differential equations are still (9) and (11), but now $-\infty < \xi < \infty$ and the boundary conditions are $p(\infty) = p(-\infty) = 0$. With zero boundary conditions at infinity, the linear differential operator

$$\frac{d^2}{d\xi^2} - \beta \frac{d}{d\xi} + k^2 g(\xi) \tag{20a}$$

appearing in (11) is the adjoint of the operator

$$\frac{d^2}{d\xi^2} + \beta \frac{d}{d\xi} + k^2 g(\xi) \ . \tag{20b}$$

Therefore, (11) and the problem with the sense of the asymmetry reversed have nontrivial solutions for precisely the same values of k (CODDINGTON and LEVINSON 1955, p. 292). Hence, we conclude that the critical value κ is independent of the sign of β. The reader who does not find this biologically surprising should recall that we did *not* assume that $g(-\xi) = g(\xi)$, which would have made the result trivial, and the cline itself [*i.e.*, the solution of (9) with a fixed $k > \kappa$], as our examples will show, definitely depends on the sign of β.

From our result, $\kappa(-\beta) = \kappa(\beta)$, we infer that

$$\kappa(\beta) = \kappa(0) + O(\beta^2) \tag{21}$$

as $\beta \rightarrow 0$. Thus, for weak asymmetry anisotropic dispersion has a much smaller effect in an infinite habitat that in a semi-infinite one. Equation (21) was also proved directly: a perturbation calculation (see. *e.g.*, MATHEWS and WALKER 1964, Ch. 10) demonstrates that the term linear in β vanishes identically.

We turn to the special case of an environmental pocket in $-a < x < a$ and a piecewise constant selection coefficient. With the definitions of ξ, β, and k for the semi-infinite habitat, we choose

$$g(\xi) = \begin{cases} -\gamma^2, & \xi < -1, \\ 1, & -1 < \xi < 1, \\ -\alpha^2, & \xi > 1. \end{cases} \tag{22}$$

We solve (11) in $(-\infty,\infty)$ with $g(\xi)$ given by (22). The solutions are decaying exponentials in $(-\infty,-1)$ and $(1,\infty)$ and a linear combination of exponentials in $(-1,1)$, the constants in the exponents being determined by (11). Enforcing continuity of $p(\xi)$ and $p'(\xi)$ at $\xi = \pm 1$ and simplifying tenaciously, we arrive at the eigenvalue equation

$$G(\lambda) \equiv (uv - \eta^2)\eta^{-1} \tan \eta + u + v = 0, \tag{23}$$

where $u = (\beta^2 + \gamma^2\lambda)^{1/2}$, $v = (\beta^2 + \alpha^2\lambda)^{1/2}$, and η was defined above (16). In the degenerate case $k = (1/2)\ \beta$, one must use the solutions $\exp(\beta\xi/2)$ and $\xi\exp(\beta\xi/2)$ in $(-1, 1)$. Since the equations for the normalization constants turn out to be inconsistent, we conclude that $(1/2)\ \beta$ is not an eigenvalue. This result is ensured automatically by the form of (23) because

$$G(\lambda) > 0 \qquad \text{if} \qquad k \leq (1/2)\,|\beta|\,. \tag{24}$$

Observe that only β^2 appears in (23), in accordance with the evenness of $\kappa(\beta)$ proved below (20). The invariance of κ under the interchange of $\alpha \leftrightarrow \gamma$ is not an independent result: this transformation amounts to the replacement $\xi \to -\xi$, which is manifestly equivalent to $\beta \to -\beta$.

For small asymmetry, $\beta \to 0$, (23) yields

$$\left\{\frac{\alpha+\gamma}{1-\alpha\gamma} - \tan\,(2k)\right\} + \frac{\beta^2}{8k^2}\left\{\left[\frac{(\alpha+\gamma)^2}{\alpha\gamma(1-\alpha\gamma)}\right]\tan\,(2k) + 2k\sec^2\,(2k) + \frac{\alpha+\gamma}{\alpha\gamma}\right\} + O(\beta^4) = 0, \tag{25}$$

whence

$$\tan\,(2k) = \frac{\alpha+\gamma}{1-\alpha\gamma} + O(\beta^2). \tag{26}$$

Therefore, we find

$$\kappa = (1/2)\,(\tan^{-1}\alpha + \tan^{-1}\gamma) + O(\beta^2). \tag{27}$$

Substituting (26) and (27) into the β^2 term in (25) and expanding in powers of β^2 yields

$$\kappa = (1/2)\,(\tan^{-1}\alpha + \tan^{-1}\gamma) + \frac{\beta^2(\alpha^{-1} + \gamma^{-1} + \tan^{-1}\alpha + \tan^{-1}\gamma)}{4(\tan^{-1}\alpha + \tan^{-1}\gamma)} + O(\beta^4). \tag{28}$$

If there is no asymmetry, (27) generalizes the critical condition (14) for a semi-infinite habitat. The latter applies to the infinite habitat if $\alpha = \gamma$. Note that (27) agrees with (21). With $|\beta| << 1$, (28) implies that asymmetric dispersion raises κ, increasing the stringency of the condition for existence of a cline. We shall see numerically that this conclusion holds for any β.

To obtain bounds on κ, we put

$$H(\lambda) = uv - \eta^2 , \tag{29}$$

and show easily that

$$H(\lambda) > 0 \quad \text{if and only if} \quad (1 - \alpha^2\gamma^2)\lambda < \beta^2(2 + \alpha^2 + \gamma^2). \tag{30}$$

Let us define

$$\lambda_0 = \frac{\beta^2(2 + \alpha^2 + \gamma^2)}{1 - \alpha^2\gamma^2}, \qquad \lambda_1 = \beta^2 + \frac{\pi^2}{4}, \qquad \lambda_2 = \beta^2 + \pi^2 . \tag{31}$$

(If $\alpha\gamma = 1$, we may choose $\lambda_0 = \infty$.) Recalling (24), we see that there are three cases for $\beta \neq 0$ ($\lambda_0 = \beta^2$ if and only if $\beta = 0$):

(i) $\lambda_0 < \beta^2$ or $\lambda_0 \geq \lambda_2$:

In view of (30), $H(\lambda) \geq 0$ for $\beta^2 \leq \lambda \leq \lambda_2$. Then (23) and (29) tell us that $G(\lambda) > 0$, $\beta^2 \leq \lambda < \lambda_1$; $G(\lambda_1 \mp) = \pm\infty$; $G(\lambda_2) > 0$. Therefore

$$(1/2)\left(\beta^2 + \frac{\pi^2}{4}\right)^{1/2} < \kappa < (1/2)(\beta^2 + \pi^2)^{1/2}. \tag{32a}$$

(ii) $\beta^2 < \lambda_0 < \lambda_1$:

We infer from (30) that $H(\lambda) > 0$, $\lambda < \lambda_0$ and $H(\lambda) < 0$, $\lambda > \lambda_0$. Hence, $G(\lambda) > 0$, $\lambda \leq \lambda_0$ and $G(\lambda_1 -) = -\infty$. So

$$(1/2)|\beta|\left(\frac{2 + \alpha^2 + \gamma^2}{1 - \alpha^2\gamma^2}\right)^{1/2} < \kappa < (1/2)\left(\beta^2 + \frac{\pi^2}{4}\right)^{1/2}. \tag{32b}$$

(iii) $\lambda_1 < \lambda_0 < \lambda_2$:

Now $G(\lambda) > 0$, $\lambda < \lambda_1$; $G(\lambda_1 \mp) = \pm\infty$; $G(\lambda_0) > 0$. We deduce that

$$(1/2)\left(\beta^2 + \frac{\pi^2}{4}\right)^{1/2} < \kappa < (1/2)|\beta|\left(\frac{2 + \alpha^2 + \gamma^2}{1 - \alpha^2\gamma^2}\right)^{1/2}. \tag{32c}$$

If A_1 is lethal in $\xi < -1$, we let γ tend to ∞ in (23) and find

$$v\eta^{-1} \tan \eta = -1. \tag{33}$$

Should A_1 be lethal everywhere outside the pocket, we let $\alpha \to \infty$ in (33), whence $\tan \eta \to 0$ and $\eta \to \pi$. Thus, $\kappa \to (1/2)(\beta^2 + \pi^2)^{1/2}$. We expect the same result for very large asymmetry. Indeed, as $|\beta| \to \infty$, (30) informs us that case (i) applies, so (23) yields $\tan \eta \to 0$.

We display some representative critical values κ calculated from (23) in Table 2. Recall that

$$\kappa(\alpha,\gamma;\beta) = \kappa(\alpha,\gamma;-\beta) = \kappa(\gamma,\alpha;\beta). \tag{34}$$

Table 2 indicates that κ is a decreasing function of α, γ, and β. The bounds (32)

TABLE 2

Critical values κ for the infinite cline

α	γ	β 0	1/10	1/2	1	2	10
1/2	1/2	0.464	0.477	0.650	0.891	1.359	5.176
1	1/2	0.625	0.631	0.748	0.955	1.397	5.181
2	1/2	0.785	0.789	0.872	1.045	1.452	5.190
1	1	0.785	0.789	0.864	1.033	1.440	5.187
2	1	0.946	0.949	1.001	1.136	1.503	5.196
2	2	1.107	1.109	1.147	1.252	1.576	5.205

are satisfied, and the approximations for small and large β are quite accurate for $\beta = 1/10$ and $\beta = 10$.

In Figure 2 we exhibit two solutions of (9). Both have $\alpha = 2$, $\gamma = 1/2$, and $k = 3$. The graph with the higher peak corresponds to $\beta = -2$; the other to $\beta = 2$. Observe the downwind displacement discussed in Section I. The amount of this displacement and the shape of the cline depend strongly on the direction of the asymmetry. (Both curves are accurate to at least 1 part in 1000.)

III. DISCONTINUITY IN THE POPULATION DENSITY

To investigate the effect of variable carrying capacity in its simplest setting, we assume migration is symmetric, and the population density has the constant value ρ_0 for $x < 0$ and $\tau\rho_0$ ($\tau > 0$) for $x > 0$. If $\tau < 1$, we may imagine less food or water, more predators, less suitable climate, etc in $x > 0$. The equilibrium gene frequency satisfies (1) with $m = 0$:

$$(1/2)\sigma^2 p'' + sg(x)f(p) = 0, \qquad x \neq 0. \tag{35}$$

SAWYER (in preparation) has proved that the correct connection conditions between $x < 0$ and $x > 0$ read

$$p(0-) = p(0+), \qquad p'(0-) = \tau^2 p'(0+). \tag{36}$$

For piecewise constant environments, we can analyze the situation with the aid of the scaling device employed in the study of variable migration rates (NAGYLAKI 1976). Suppose

$$g(x) = \begin{cases} 1, & x < 0, \\ -\alpha^2, & x > 0, \end{cases} \tag{37}$$

in an infinite habitat, and there is no dominance ($h = 0$). With the new coordinate

$$X = \begin{cases} x, & x < 0, \\ x/\tau^2, & x > 0, \end{cases} \tag{38}$$

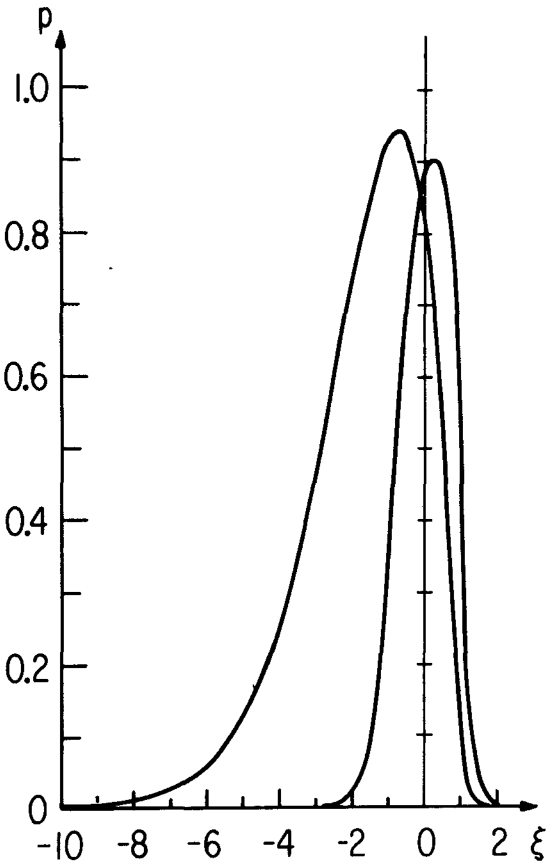

FIGURE 2.—Two infinite clines: $\alpha = 2$, $\gamma = \frac{1}{2}$, $k = 3$ for both; $\beta = -2$ (higher peak), $\beta = 2$ (lower peak).

the gene frequency and its slope are continuous at the origin, but α in (35) is replaced by $\tau^2\alpha$. Thus, the treatment of the jump in the migration rate in NAGYLAKI (1976) applies directly if the standard deviation ratio ν therein is replaced by the squared density ratio τ^2. In particular, the gene frequency p_0 at the origin is the unique root in $(0, 1)$ of

$$(1 + \tau^4\alpha^2)p_0^2(3 - 2p_0) = 1. \tag{39}$$

Considering $p_0 = p_0(\tau)$ as a function of τ and differentiating (39), we see easily that $p'_0(\tau) < 0$. Therefore, $p_0(\tau) \gtrless p_0(1)$ according as $\tau \lessgtr 1$. This means that the more densely populated part of the habitat is more influential in determining the gene frequency. Since the effect depends on the fourth power of the density ratio, it is a rather pronounced one.

In a semi-infinite habitat with no dominance and selection pattern

$$g(x) = \begin{cases} 1, & -a \leq x < 0, \\ -\alpha^2, & x > 0, \end{cases} \tag{40}$$

replacing ν by τ^2 in Eq. (19) of NAGYLAKI (1976), we infer that a cline will exist if

$$k > \tan^{-1}(\tau^2\alpha), \tag{41}$$

k still being defined as below (10). Therefore, if the pocket is more densely populated than the remainder of the habitat ($\tau < 1$), (41) is less stringent than for uniform population density. An allele is more difficult to maintain in an environmental pocket with low population density. These conclusions are expected both intuitively and from behavior of the infinite cline.

IV. SUMMARY

The consequences of asymmetric migration on clines were investigated. As with symmetric migration, maxima of the frequency of an allele must occur where that allele is favored. With a single reversal of the direction of natural selection, clines are displaced downwind, but are still monotonic. A rather general asymmetry parameter, m, was derived for an unbounded habitat by scaling in Eq. (6). Small and large asymmetry correspond to $|\tilde{m}| << 1$ and $|\tilde{m}| >> 1$. As discussed in the paragraph following Eq. (19), for asymmetry parameters outside an interval including 0, there is no cline.

If a semi-infinite habitat has an environmental pocket of length a at one end, the critical asymmetry parameter is $\beta = 2am/\sigma^2$, where m and σ^2 are the mean and variance of the migrational displacement. For selection intensity s, no dominance, and weak asymmetry ($\beta \to 0$), a cline exists if $k = 2sa^2/\sigma^2$ exceeds κ, given by (15). Preferential dispersion out of the pocket increases genetic variability; extra influx into the pocket decreases it.

With an environmental pocket in $(-a, a)$ in an infinite habitat, the condition for the existence of a cline is independent of the direction of the asymmetry, but the cline itself is not. For small asymmetry, the effect of the anisotropy on the critical value κ is second order in β, and hence fairly small. If the selection gradient is described by (22) and there is no dominance, κ has the value (28). Asymmetric dispersion lowers genetic diversity.

For symmetric migration and variable population density, regions of high population density influence gene frequencies more than sparsely populated areas. Thus, an allele is maintained more easily in a densely populated environmental pocket. With the semi-infinite habitat with selection coefficients and densities outside and inside the pocket having ratios $-\alpha^2$ and τ, respectively, and no dominance, a cline exists if $k > \tan^{-1}(\tau^2\alpha)$.

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