



Single Locus Clines

Sergey Gavrilets

Evolution, Vol. 51, No. 3. (Jun., 1997), pp. 979-983.

Stable URL:

<http://links.jstor.org/sici?sici=0014-3820%28199706%2951%3A3%3C979%3ASLC%3E2.0.CO%3B2-E>

Evolution is currently published by Society for the Study of Evolution.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/ssevol.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

BRIEF COMMUNICATIONS

Evolution, 51(3), 1997, pp. 979–983

SINGLE LOCUS CLINES

SERGEY GAVRILETS

Departments of Mathematics and Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1300
E-mail: gavrila@math.utk.edu

Key words.—Clines, frequency-dependent selection, postmating isolation, premating isolation.

Received March 27, 1996. Accepted February 14, 1997.

Bazykin (1969) found the form of a single locus cline arising from viability selection against heterozygotes when two populations, initially fixed for alternative alleles, come into contact in a continuous, one-dimensional habitat. Here I have generalized Bazykin's results for the case of postmating reproductive isolation in the form of fertility selection as well as premating reproductive isolation.

Analysis of natural zones of hybridization has become a very popular field of research in recent years. This analysis provides insights into the nature of species, the development of barriers to gene exchange, the strength and mode of natural selection, the number of genes involved, and the dynamics of the speciation process (Endler 1977; Barton and Hewitt 1981, 1985, 1989; Harrison and Rand, 1989; Harrison 1990, 1993; Barton and Gale 1993). Many hybrid zones are thought to be maintained by a balance between selection and dispersal. Selection could act in many different ways, of which a very common one is selection against hybrids, recombinants, and rare phenotypes (Barton and Hewitt 1981, 1985, 1989; Barton and Gale 1993). A classical model for a hybrid zone in a one-dimensional, continuous habitat arising from selection against heterozygotes at a single locus was proposed and solved by Bazykin (1969). Mallet and Barton (1989) have shown that Bazykin's cline describes hybrid zones arising in a simple model of selection against rare phenotypes. Further studies (e.g., Slatkin 1973, 1985; Nagylaki 1975, 1976, 1994; Barton 1979a,b, 1983, 1986; Barton and Begtsson 1986; Mallet and Barton 1989; Barton and Gale 1993) of more complex models have advanced the understanding of hybrid zones in many directions. The purpose of this note is to generalize Bazykin's results for the case of fertility selection and premating reproductive isolation. These are very common types of reproductive isolation mechanisms which, however, were left outside the scope of recent developments in the hybrid zone theory. At the end of this note, I will show that single locus clines arising from fertility and viability selection against heterozygotes also describe hybrid zones arising in some models of selection against rare phenotypes.

SYMMETRIC VIABILITY SELECTION AGAINST HETEROZYGOTES

Consider an autosomal locus with two alleles **A** and **a**. Suppose homozygotes have equal viability, while heterozygotes have lower viability than homozygotes. One can assign viabilities (i.e., probabilities of survival from zygote stage to maturity) 1, $1 - s$, and 1 to genotypes **AA**, **Aa**, and **aa**, respectively. If selection against heterozygotes is weak ($0 < s \ll 1$), the dynamics of the frequency of allele **A**, p , in a

single randomly mating population are described by a differential equation

$$\frac{dp}{dt} = spq(p - q), \quad (1)$$

where $q = 1 - p$ is the frequency of allele **a**. Equation (1) has two stable monomorphic equilibria and an unstable polymorphic equilibrium at $p = \frac{1}{2}$. The population evolves to fixation of allele **A** (or **a**) if initially $p > q$ (or $p < q$). Consider now a population occupying a continuous, one-dimensional uniform habitat. Assuming that dispersal is equally likely in both directions, the dynamics of $p(x, t)$, the frequency of allele **A** at time t at spatial location x , can be described by

$$\frac{\partial p}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial x^2} + spq(p - q), \quad (2)$$

where σ^2 is the variance in distance between parent and offspring (Bazykin 1969).

When two geographically disjoint populations, one fixed for allele **A** and another fixed for allele **a**, come into contact, a narrow zone where hybrids are produced arises. The resulting cline in allele frequencies is given by the equilibrium solution of (2)

$$p(x) = \frac{1}{2} \left\{ 1 + \tanh \left[\sqrt{\frac{s}{2a^2}} (x - x_0) \right] \right\}, \quad (3)$$

where x_0 is the (arbitrary) center of the cline at which $p = \frac{1}{2}$ (Bazykin 1969). The width of the hybrid zone can be characterized as the inverse of the gradient of p at the center of the cline, which for cline (3) is

$$w = 4\sqrt{\sigma^2/2s} \quad (4a)$$

(Barton 1979b). In this model, the difference in mean fitness between populations at the center and the edge of the cline is $s^* = s/2$. Using s^* , the width of the hybrid zone can alternatively be represented as

$$w = 2\sigma/\sqrt{s^*} \quad (4b)$$

(Barton and Gale 1993). As selection increases and dispersal decreases, the hybrid zone narrows. Given that two of the three variables w , σ^2 , and s^* are known, equations (4) allows one to predict a third variable. Besides cline width, cline shape can also be used in analyzing hybrid zone. On a logit scale (i.e., using $z = \ln(p/q)$ instead of p), the cline given by (3) follows a straight line with slope

$$\partial z/\partial x = 4/w \quad (5)$$

(Barton and Gale 1993). Both (4) and (5) have been widely

used in analyzing natural hybrid zones (Barton and Hewitt 1985; Barton and Gale 1993). The equations given above are based on several simplifying assumptions (weak and symmetric selection, uniform environment, no density effects, etc.). A number of these assumptions have been relaxed (e.g., Slatkin 1973, 1985; Nagylaki 1975, 1976, 1996; Barton 1979b; Christiansen et al. 1995). Another crucial assumption is that heterozygotes have reduced probability of survival from zygote to maturity (i.e., selection against hybrids is in the form of viability selection). Reduced viability of hybrids is only one of several possible manifestations of hybrid inferiority observed in nature, and is not necessarily the most common (see Table 1 in Barton and Hewitt 1985; Table 2 in Harrison 1990). In many cases, hybrids and recombinants are equally viable as individuals from parent populations, but have reduced (or zero) fertility. In some cases, hybrids are even more viable than individuals from parent populations (the phenomenon known as heterosis). Sometimes hybrids are perfectly viable and fertile, but their formation in natural populations is prevented by some premating isolating mechanisms (Harrison 1990, 1993). The viability selection model leading to hybrid zone description (eqs. 3–5) is obviously not appropriate in these cases. A model including both viability and fertility differences is described in the next section.

SYMMETRIC VIABILITY AND FERTILITY SELECTION AGAINST HETEROZYGOTES

Fertility selection models are known for their complex dynamic behavior (classical papers: Owen 1953; Bodmer 1965; Haderler and Liberman 1975; for more recent results: Liberman and Feldman 1985; Holsinger et al. 1986; Koth and Kemler 1986; Nagylaki 1987; Twomey and Feldman 1990; Lessard 1993, 1994). For example, a single-locus population can have two different stable polymorphic equilibria simultaneously (Owen 1953; Bodmer 1965) and can even evolve to a stable limit cycle (Haderler and Liberman 1975; Koth and Kemler 1986). In general, under fertility selection the genotype frequencies are not at Hardy-Weinberg proportions.

Consider a single, randomly mating population with non-overlapping generations. Let x , y , and z be the frequencies of genotypes **AA**, **Aa**, and **aa** at a certain generation, and v_i be (relative) viabilities of the three genotypes ($i = 1, 2, 3$ corresponding to genotypes **AA**, **Aa**, and **aa**, respectively). Fertility differences can be incorporated into the modeling framework by assigning different fertilities F_{ij} to matings between males with genotype i and females with genotype j . Let $f_{ij} = (F_{ij} + F_{ji})/2$ be the average of two fertilities of two reciprocal matings involving genotypes i and j . Note that $f_{ij} = f_{ji}$ for all i, j . Then in the next generation

$$\phi x' = v_1(f_{11}x^2 + f_{12}xy + 1/4f_{22}y^2), \quad (6a)$$

$$\phi y' = v_2(f_{21}xy + 2f_{13}xz + f_{23}yz + 1/2f_{22}y^2), \quad (6b)$$

$$\phi z' = v_3(f_{33}z^2 + f_{32}zy + 1/4f_{22}y^2), \quad (6c)$$

where ϕ is a normalizing factor such as $x' + y' + z' = 1$ (Bodmer 1965). If $f_{ij} = f_{ji}$ for all i, j (i.e., if fertilities are multiplicative), the model reduces to the standard viability selection model (Bodmer 1965).

I will assume that relative viabilities are 1, $1 - s$, and 1 and that the matrix of relative fertilities f_{ij} has the form

$$\begin{pmatrix} 1 & 1 - a & 1 - b \\ 1 - a & 1 - c & 1 - a \\ 1 - b & 1 - a & 1 \end{pmatrix}. \quad (7)$$

The latter is a symmetric fertility model introduced by Haderler and Liberman (1975). It assumes that fertilities of matings between similar homozygotes are the same and normalized to be 1, that fertilities of matings between a F_1 hybrid and either homozygote is $1 - a$, that fertilities of matings between different homozygotes is $1 - b$, and that fertility of hybrid-hybrid matings is $1 - c$. I will assume that differences in both viabilities and fertilities are small, that is, that $s, a, b, c \ll 1$ (weak selection approximation). In this case, deviation of zygote frequencies from Hardy-Weinberg proportions can be neglected (Nagylaki 1987) and the dynamics of the frequency of allele **A** ($p = x + y/2$) can be described by a differential equation

$$\frac{dp}{dt} = pq(p - q)(A + Bpq), \quad (8)$$

where

$$A = s + a, \quad B = b + 2c - 4a. \quad (9)$$

If there is no fertility differences (i.e., if $a = b = c = 0$), (8) reduces to (1). Note that the mean fitness of the population, which is given by the product of the mean fertility and the mean viability (Nagylaki 1987), is

$$\bar{w} = 1 - 2(2a + s)pq + 2(4a - b - 2c)p^2q^2. \quad (10)$$

I will be interested in situations where the dynamics of a randomly mating population have two stable monomorphic equilibria and a single unstable polymorphic equilibrium at $p = 1/2$, as was the case in the viability selection model. For this to be the case, one has to require that $A \geq 0$ and $A + B/4 \geq 0$ or, equivalently,

$$s + a \geq 0, \quad s + (b + 2c)/4 \geq 0, \quad (11)$$

where at least one inequality should be strict. (If both inequalities in (11) are reversed, the single polymorphic equilibrium at $p = 1/2$ is stable. If only the former inequality is reversed, there are two additional polymorphic equilibria (at p such that $pq = [b + 2c - 4a]/[s + a]$), which are unstable, while both monomorphic equilibria and the polymorphic equilibrium at $p = 1/2$ are stable. If only the latter inequality is reversed, the two additional polymorphic equilibria are stable, while three remaining equilibria are unstable).

Consider now a population occupying a continuous, one-dimensional, uniform habitat. An analog of (2) with both viability and fertility selection is

$$\frac{\partial p}{\partial t} = \frac{\sigma^2}{2} \frac{\partial^2 p}{\partial x^2} + pq(p - q)(A + Bpq). \quad (12)$$

When two geographically disjoint populations, one fixed for allele **A** and another fixed for allele **a**, come into contact, a narrow zone where heterozygotes are produced arises. The resulting cline in allele frequencies is given by the equilibrium solution of (12), which can be found analytically. The

width of the hybrid zone characterized as the inverse of the gradient of p at the center of the cline is

$$w = 4 \sqrt{\frac{\sigma^2}{2(s + a/3 + b/6 + c/3)}} \quad (13)$$

(cf. 4a). In describing the cline shape, I will use an independent variable x' , the deviation from the center of the cline normalized to the half of the width of the hybrid zone, $x' = (x - x_0)/(w/2)$. If $B = 0$, the equilibrium solution of (12) is given by (3) with A taking place of s . If $A = 0$ and $B \neq 0$, this solution is

$$p(x) = \frac{1}{2} \left(1 + \frac{x'}{\sqrt{1 + x'^2}} \right). \quad (14a)$$

If $A > 0$ and $B \neq 0$, the cline $p = p(x)$ is implicitly defined by

$$x' = \frac{1}{2} \sqrt{1 + C} \ln \left(\frac{p}{q} \frac{1 + 2Cq + \sqrt{1 + 4Cpq}}{1 + 2Cp + \sqrt{1 + 4Cpq}} \right), \quad (14b)$$

where $q = 1 - p$ and $C = B/(6A) > -1$. If $C = 0$, equation (14b) produces Bazykin's cline (3), while if $C \rightarrow \infty$, it produces cline (14a). Equations (13–14), which generalize classical Bazykin's (1969) results for the case of both viability and fertility selection, represent the main theoretical results of this note. In the next section I discuss the differences between Bazykin's clines and those described by equations (13–14).

COMPARISON OF CLINES FROM VIABILITY SELECTION WITH CLINES FROM VIABILITY/FERTILITY SELECTION

Cline Width

In the case of both fertility and viability selection, the difference in mean fitness between populations at the center of the cline and the edge is

$$s^* = (4s + 4a + b + 2c)/8. \quad (15)$$

Comparing this with (13), one can see there is no simple relation between s^* and w similar to (4b).

Let us denote by w_B the cline width produced by viability selection only with $s = \Delta$, where Δ is the heterozygote's reduction in fitness. Then in a model where viability selection is absent ($s = 0$) and the reductions in fertility of matings between different genotypes are the same ($a = b = c = \Delta$), the cline width $w = \sqrt{6/5}w_B$. In a model with both viability and fertility selection with $s = a = b = c = \Delta$, $w = \sqrt{6/11}w_B$. This and the form of (13) suggest that for comparable strength of selection, the width of the hybrid zone is only slightly affected by incorporating fertility selection. As expected, any type of hybrid or recombinant deficiency makes the hybrid zone narrower, but different types of selection have different efficiency. Parameters s (reduction in heterozygotes' viability) and b (reduction in fertility of matings between parental genotypes) have the most and the least influence, respectively, while parameters a (reduction in fertility of matings between a parental genotype and a hybrid) and c (reduction in fertility of matings between hybrids) have intermediate (and equal) influence.

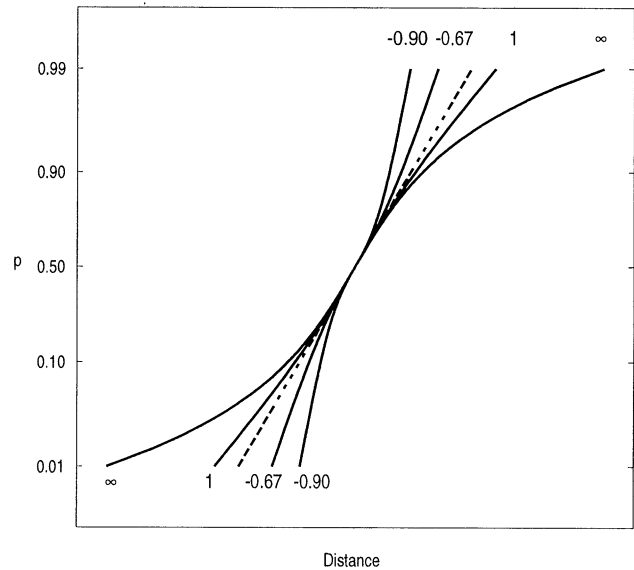


FIG. 1. Clines maintained by a balance between dispersal and viability-fertility selection on a single locus. Allele frequencies are plotted against distance on a logit scale; the clines are scaled so all have the same position and width. Numbers give the corresponding C -values.

Cline Shape

Figure 1 compares the cline shape in several models using a logit scale (i.e., using $\ln(p/q)$ instead on p ; cf. Figs. 2.1, 2.2 in Barton and Gale 1993). Given are Bazykin's cline (3) (corresponding to $C = 0$), the cline given by (14a) (corresponding to $A = 0$ or, equivalently, $C = \infty$), and several intermediate cases. The case with $A = 0$ can happen if both heterozygotes are viable ($s = 0$) and matings between a heterozygote and a parental genotype are fertile ($a = 0$), or if reduction in fertility of these matings is balanced by increased viability of heterozygotes (overdominance) such that $s > 0$, $a < 0$, $s + a \approx 0$. The case with $C = 1$ happens if $a = b = 0$, $s = \Delta$, $c = 3\Delta$, that is, if besides viability selection only heterozygote-heterozygote matings have reduced fertility. The case with $C = -2/3$ happens if $s = b = c = 0$, $a = \Delta$, that is, if the only type of selection is reduced fertility of matings between heterozygotes and parental genotypes. The case with $C = -9/10$ happens if $s = b = 0$, $a = \Delta$, $c = -1.4\Delta$, that is, if matings between heterozygotes and parental genotypes have reduced fertility, but matings between heterozygotes have increased fertility. Figure 1 shows that deviations of C from zero result in deviations of the cline shape from the straight line. If $C > 0$, the frequency of a rare allele reduces much slower with the deviation from the cline center than in Bazykin's cline. If $C < 0$, the frequency of a rare allele reduces much faster with the deviation from the cline center than in Bazykin's cline. Since $C > 0$ if $b + 2c > 4a$, the former case is expected when there is strong deficiency in fertility of matings between different parental genotypes and/or between heterozygotes. The latter case is expected when there is strong deficiency in fertility of matings between heterozygotes and parental genotypes. In general, the cline shape strongly depends on fine details of fertility selection.

PREMATING REPRODUCTIVE ISOLATION

The model leading to dynamic equations (6) implies that the probability of mating between a female and a male given that they have met does not depend on their genotypes. However mating between individuals can be prevented to some degree by premating reproductive isolation mechanisms. Let m_{ij} be the probability of mating between a male with genotype i and a female with genotype j given that they have met ($i, j = 1, 2, 3$). The dynamics of the genotype frequencies is now described by equations (6) with

$$f_{ij} = (F_{ij}m_{ij} + F_{ji}m_{ji})/2. \quad (16)$$

Note that, as before, $f_{ij} = f_{ji}$. Given the matrix $\{f_{ij}\}$ has form (7), all results from the previous section remain valid. In this model, effects of premating reproductive isolation are similar to those of fertility selection.

SYMMETRIC SELECTION AGAINST RARE PHENOTYPES

Gavrilets and Hastings (1995) introduced a symmetric model of linear frequency-dependent selection. In this model, the genotype fitnesses are linear functions of the genotype frequencies

$$w_{AA} = xW_{11} + yW_{12} + zW_{13}, \quad (17a)$$

$$w_{Aa} = xW_{21} + yW_{22} + zW_{23}, \quad (17b)$$

and

$$w_{aa} = xW_{31} + yW_{32} + zW_{33}, \quad (17c)$$

where $x = p^2$, $y = 2pq$, and $z = q^2$ are the frequencies of three genotypes, and the matrix of the coefficients W_{ij} characterizing the extent to which changes in the genotypes frequencies influence their fitnesses has form

$$\begin{pmatrix} \delta & \beta & \alpha \\ \gamma & \eta & \gamma \\ \alpha & \beta & \delta \end{pmatrix}. \quad (18)$$

For this symmetric model to produce feasible (i.e., non-negative) fitnesses, one has to assume that $\alpha, \gamma, \delta > 0$, $\beta > -\sqrt{\alpha\delta}$, $\eta > -\gamma$. If selection is weak, the dynamics of p in a single randomly mating population in this model are approximated by (8) with

$$A = \delta - \gamma, \quad B = -\delta - \alpha + 2\beta + 2\gamma - 2\eta. \quad (19)$$

If $\delta \geq \gamma$, $3\delta \geq \alpha - 2\beta + 2\gamma + 2\eta$, where at least one inequality is strict, the dynamics have two stable monomorphic equilibria and an unstable polymorphic equilibrium at $p = 1/2$. In this case, which corresponds to selection against rare phenotypes, results from the previous sections can be used for describing hybrid zones.

Hybrid zones arising from selection against rare phenotypes have been studied by Mallet and others (Mallet and Barton 1989; Mallet et al. 1990; Mallet 1993). Mallet and Barton (1989) have considered two models representing partial cases of model (17). Their models describe the dynamics of warning and mimetic coloration assuming that when a form (e.g., of a butterfly) is rare, it is selected against because predators (birds) do not recognize it as unpalatable. One model considered by Mallet and Barton (1989, eq. 2) leads to C

= 0 and Bazykin's cline (3). Another model (their eq. 4 with $h = 1/2$) leads to $C = -1/2$. The model resulting in $C = -1/2$ assumes that predators identify heterozygotes as either homozygote with probability $1/2$. A simple model for situations where all three genotypes look different to the predator is to assume that

$$w_{AA} = 1 - \Delta(y + z), \quad (20a)$$

$$w_{Aa} = 1 - \Delta(x + z), \quad (20b)$$

and

$$w_{aa} = 1 - \Delta(x + y), \quad (20c)$$

where Δ is a positive parameter measuring the strength of selection. In this case, the dynamics of p ($= x + y/2$) in a single randomly mating population are described by (8,19) with $\delta = \eta = 1$, $\alpha = \beta = \gamma = 1 - \Delta$ resulting in $C = -1/2$. The cline is wider by a factor $\sqrt{2}$ than Bazykin's cline and the cline shape described by (14b) deviates from that of Bazykin's cline significantly.

CONCLUSION

In a classical paper, Bazykin (1969) found the form of a single locus cline arising from viability selection against heterozygotes when two geographically distinct populations, initially fixed for alternative alleles, come into contact in a continuous, one-dimensional habitat. Here I have generalized Bazykin's results for the case of postmating reproductive isolation in the form of fertility selection as well as premating reproductive isolation. Fertility differences and premating reproductive isolation influence both the width and the form of the cline. Any type of hybrid or recombinant deficiency makes the hybrid zone narrower, but overall the width of the hybrid zone (measured by the inverse of the maximum gradient of allele frequency) is only slightly changed by fertility differences. This agrees with Barton and Gale's (1993) assertion that the mechanism of selection has little effect on the width of the clines. Fertility selection, as well as premating reproductive isolation, have much more profound effect on the shape of hybrid zones, which strongly depends on fine details of isolating mechanisms. In general, with strong reduction in fertility and/or probability of matings between different parental genotypes and/or between heterozygotes, the frequency of a rare allele reduces much slower with the deviation from the cline center than in Bazykin's cline. Slight overdominance (increase in heterozygotes viability) can significantly broaden the area where rare alleles have non-negligible frequencies. On the other hand, with strong reduction in fertility and/or probability of matings between parental genotypes and heterozygotes, the frequency of a rare allele reduces much faster with the deviation from the cline center than in Bazykin's cline. The description of single locus clines developed here can also be used for clines arising from selection against rare phenotypes, as in systems of warning and mimetic coloration. For comparable parameter values this form of selection leads to sharper clines than in Bazykin's model. The model studied here is of a single locus under symmetric selection. Slight asymmetries in fitness cause the clines to move, but local inhomogeneities can trap them. Clines may be wider if selection acts on many

loci, and recombination breaks these apart so that selection acts on their (small) individual effects.

ACKNOWLEDGMENTS

I am grateful to M. Cruzan and anonymous reviewers for helpful comments on the manuscript.

LITERATURE CITED

- BARTON, N. H. 1979a. Gene flow past a cline. *Heredity* 43:333–339.
- . 1979b. The dynamics of hybrid zones. *Heredity* 43:341–359.
- . 1983. Multilocus clines. *Evolution* 37:454–471.
- . 1986. The effect of linkage and density-dependent regulation on gene flow. *Heredity* 57:415–426.
- BARTON, N. H., AND B. O. BENGTSSON. 1986. The barrier to genetic exchange between hybridising populations. *Heredity* 56:357–376.
- BARTON, N. H., AND K. S. GALE. 1993. Genetic analysis of hybrid zones. Pp. 13–45 in R. G. Harrison, ed. *Hybrid zones and the evolutionary process*. Oxford Univ. Press, Oxford.
- BARTON, N. H., AND G. M. HEWITT. 1981. Hybrid zones and speciation. Pp. 109–145 in W. R. Atchley and D. S. Woodruff, eds. *Evolution and speciation: essays in honor of M. J. D. White*. Cambridge Univ. Press, Cambridge.
- . 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16:113–148.
- . 1989. Adaptation, speciation and hybrid zones. *Nature* 341:497–503.
- BAZYKIN, A. D. 1969. A hypothetical mechanism of speciation. *Evolution* 23:685–687.
- BODMER, W. F. 1965. Differential fertility in population genetic models. *Genetics* 51:411–424.
- CHRISTIANSEN, F. B., V. ANDREASEN, AND E. T. POULSEN. 1995. Genotypic proportions in hybrid zones. *Journal of Mathematical Biology* 33:225–249.
- ENDLER, J. A. 1977. *Geographic variation, speciation, and clines*. Princeton Univ. Press, Princeton, NJ.
- GAVRILETS, S., AND A. HASTINGS. 1995. Intermittency and transient chaos from simple frequency-dependent selection. *Proceeding of the Royal Society London B* 261:233–238.
- HADELER, K. P., AND U. LIBERMAN. 1975. Selection models with fertility differences. *Journal of Mathematical Biology* 2:19–32.
- HARRISON, R. G. 1990. Hybrid zones: windows on evolutionary process. Pp. 69–128 in D. Futuyma and J. Antonovics, eds. *Oxford surveys in evolutionary biology*, vol 7. Oxford Univ. Press, Oxford, U.K.
- , ED. 1993. *Hybrid zones and the evolutionary process*. Oxford Univ. Press, Oxford, U.K.
- HARRISON, R. G., AND D. M. RAND. 1989. Mosaic hybrid zones and the nature of species boundaries. Pp. 111–113 in D. Otte and J. Endler, eds. *Speciation and its consequences*. Sinauer Associates, Sunderland, MA.
- HOLSINGER, K. E., M. W. FELDMAN, AND L. ALTENBERG. 1986. Selection for increased mutation rates with fertility differences between matings. *Genetics* 112:909–922.
- KOTH, M., AND F. KEMLER. 1986. A one locus–two allele selection model admitting stable limit cycles. *Journal of Theoretical Biology* 122:263–267.
- LESSARD, S. 1993. Adaptive topography in fertility viability selection models—an alternative to inclusive fitness in kin selection models. *Theoretical Population Biology* 43:281–309.
- . 1994. Adaptive topography in fertility viability selection models—the haplodiploid case. *Theoretical Population Biology* 46:344–362.
- LIBERMAN, U., AND M. W. FELDMAN. 1985. A symmetric two locus model with viability and fertility selection. *Journal of Mathematical Biology* 22:31–60.
- MALLET, J. 1993. Speciation, raiation, and color patten evolution in *Heliconius* butterflies: evidence from hybrid zones. Pp. 226–260 in R. G. Harrison, ed. *Hybrid zones and the evolutionary process*. Oxford Univ. Press, Oxford.
- MALLET, J., AND N. BARTON. 1989. Inference from clines stabilized by frequency-dependent selection. *Genetics* 122:967–976.
- MALET, J. N. BARTON, G. M. LAMAS, J. C. SANTISTEBAN, M. M. MUEDAS, AND H. EELEY. 1990. Estimates of selection and gene flow from measures of cline width and linkage disequilibrium in *Heliconius* hybrid zones. *Genetics* 124:921–936.
- NAGYLAKE, T. 1975. Conditions for the existence of clines. *Genetics* 80:595–615.
- . 1976. Clines with variable migration. *Genetics* 83:867–886.
- . 1987. Evolution under fertility and viability selection. *Genetics* 115:367–375.
- . 1994. Geographic variation in a quantitative character. *Genetics* 136:361–381.
- . 1996. The diffusion model for migration and selection in a dioecious population. *J. Math. Biol.* 34:334–360.
- OWEN, A. R. G. 1953. A genetic system admitting of two distinct stable equilibria under natural selection. *Heredity* 7:97–102.
- SLATKIN, M. 1973. Gene flow and selection in a cline. *Genetics* 75:733–756.
- . 1985. Gene flow in natural populations. *Ann. Rev. Ecol. Syst.* 16:393–430.
- TWOMEY, M. J., AND M. W. FELDMAN. 1990. Mutation modification with multiplicative fertility selection. *Theoretical Population Biology* 37:320–342.

Corresponding Editor: A. Hastings