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MAINTENANCE OF POLYGENIC VARIATION VIA A MIGRATION–SELECTION BALANCE UNDER UNIFORM SELECTION

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Population subdivision is often invoked to explain the large amount of heterozygosity found at single loci in natural populations (Felsenstein 1976; Hedrick et al.,1976; Karlin 1982; Hedrick 1986). Surprisingly, relatively few studies describe the effects of population structure on the maintenance of genetic variance for polygenic (quantitative) traits. Felsenstein (1977) and Slatkin (1978) presented models in which additive genetic variance can be maintained via migration along a cline (see also Barton and Turelli 1989). Goldstein and Holsinger (1992) used simulations to show that variance for quantitative traits could be maintained under uniform selection in a population subject to isolation by distance (see also Lande [1991]), and Slatkin and Lande (1994) demonstrated that the segregation variance generated by between-population crosses depends on how variance is generated within each population. Here I analyze the amount of genetic variance that can be maintained deterministically via a migration–selection balance under uniform selection and conclude that a potentially large amount of variance can be generated in this way. This is true only when migration is very weak, so as not to overcome the influence of selection. When variance is maintained, it is maximal at the critical balance between migration and selection.

The deterministic interaction between migration and selection has been the subject of a great deal of analysis in the context of Wright's shifting-balance theory (Crow et al. 1990; Barton 1992; Kondrashov 1992; Phillips 1993). These studies have shown that migration can be very effective at overcoming the effects of selection and driving populations to uniformity. For the shifting-balance process, this means that once a population has undergone a peak shift, it might be expected to drive peak shifts in neighboring populations, depending on the details of the genetic system and population structure (Barton 1992; Phillips 1993). The purpose here is to explore regions of the parametric space in which this does not happen, but instead both populations remain polymorphic. Results from this deterministic approach will be contrasted with models that include stochastic effects and make somewhat different predictions (Lande 1991; Goldstein and Holsinger 1992; Barton and Rouhani 1993).

Uniform stabilizing selection on an additive character generates disruptive selection at the genetic level because various combinations of alleles can yield the same optimal phenotype, but the marginal fitness of any allele depends on the genetic background in which it is found (Wright 1935). This is called "genetic redundancy" by Goldstein and Holsinger [1992]). Two populations can thus display the same phenotype but be fixed for different genotypes. If these populations were to exchange migrants, the mixing of the different genotypes would generate variance within each population. This would be a somewhat cryptic source of genetic variation because there would be no obvious differentiation between the populations.

Depending on the strength of migration, most of the variance generated by migration would then be quickly eliminated by selection, creating a migration-selection balance. This is the multilocus equivalent of a migration-selection polymorphism generated by underdominance at a single locus (Karlin and McGregor 1972). Because many characters are assumed to be under stabilizing selection, and because population structure is undoubtedly an important feature of natural populations, the interaction of migration and selection could obviously be an important influence on the maintenance of genetic variance.

The Model

To facilitate comparisons with models of mutation-selection balance, I will use a model of Gaussian phenotypic stabilizing selection on an additive character. In this model, a character, z, is assumed to be under stabilizing selection toward a single optimum, z_0. Individual fitness is determined by a Gaussian curve with variance $1/s$ centered at this optimum, $W = \mathrm{Exp}[-s(z - z_0)^2/2]$. The value of the character is determined by n diallelic loci, with each locus having an identical effect α on the character (i.e., each allele contributes either $-\alpha/2$ or $+\alpha/2$ to the character). The trait is assumed to be completely heritable, although as is pointed out in the Discussion, both selection and the per-locus effects can be scaled by the environmental variance. The dynamics of migration between two populations will be studied. Both populations begin with the same optimal phenotype, but are fixed for different underlying genotypes (i.e., a different allele at each of the n loci). The gene frequency dynamics of this model can be determined numerically using the migration–selection equations given by Crow et al. (1990) and Phillips (1993). Briefly, these equations describe the exact dynamics of multilocus gamete frequencies with arbitrary linkage relationships in an infinite population with discrete, nonoverlapping generations. Here free recombination between all loci

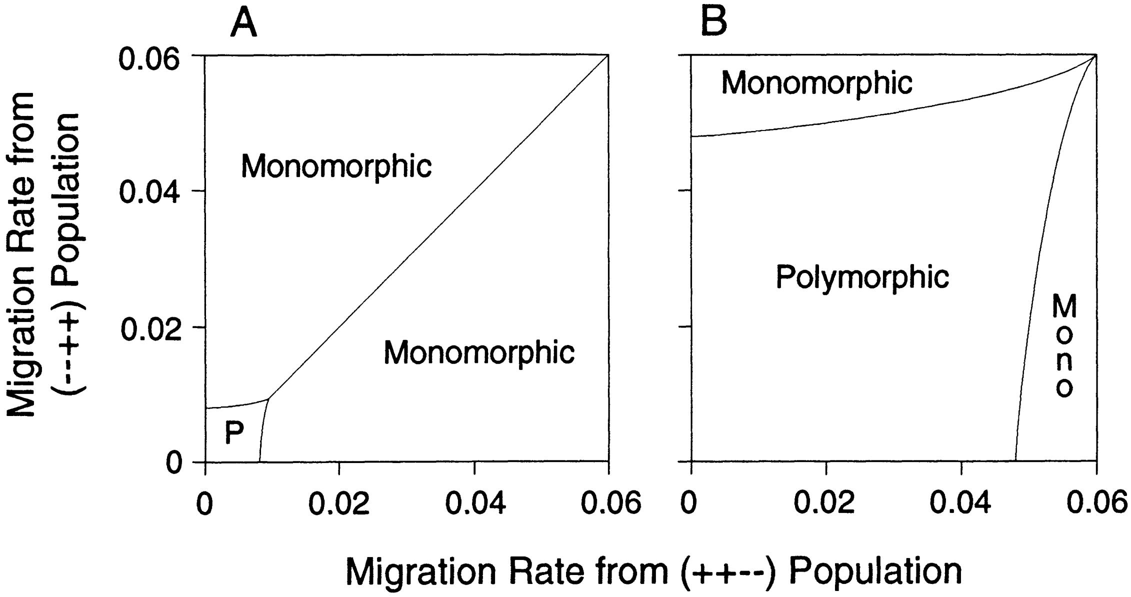

FIG. 1. Phase plots for a four-locus model of Gaussian stabilizing selection. The model is symmetrical; thus, only two qualitatively different outcomes are possible: (1) a monomorphic equilibrium of either of the genotypes in each population, or (2) a polymorphic equilibrium within each population. (A) "Weak" selection, $s\alpha^2 = 0.2$. (B) "Strong" selection, $s\alpha^2 = 5.0$. Increasing the strength of selection expands the region of polymorphic equilibria (strong and weak selection are relative to one another—the weak selection case might actually be fairly strong compared to natural populations).

is assumed, although any linkage disequilibrium generated by selection is included in the model.

There are two possible outcomes when two populations initially fixed for different optimal genotypes exchange migrants: (1) both populations can become fixed for one of the two original genotypes, or (2) the populations can attain a polymorphic equilibrium maintained by a balance between migration and selection. The range of migration rates that leads to these outcomes can be described using a phase diagram that divides the parameter space of migration rates into these two regions, as shown in Figure 1. Because here we are only interested in the region of polymorphic equilibria, and because this region is highly symmetrical, it is expedient to concentrate solely on the critical migration rate at which unidirectional migration from one population to the other causes a change from a polymorphic to a monomorphic equilibrium (Crow et al. 1990). This value is conservative because, as long as the migration rates from both populations are below this value (even if they are asymmetrical), the populations will always attain a polymorphic equilibrium (Fig. 1). The results will therefore be presented in terms of a single parameter, m_c, describing the migration rate from the fixed to the polymorphic population. There will also be some slightly higher, balanced migration rates that fall in the region of polymorphic equilibria, but describing the region as a box rather than a complex shape greatly simplifies interpretation.

We seek to characterize the size of the region of polymorphic equilibria and to determine how much genetic variance can be maintained when the migration rates are within this region. Bazykin (1973) provides the conditions for the existence of a migration-selection balance using a two-locus model of stabilizing selection with equal migration rates under the assumption of linkage equilibrium. For more than two loci, however, an approach such as his is prohibitive because of the complexity of the analysis. Nevertheless, the dynamics of the multilocus model can be determined exactly using the equations given by Phillips (1993). Unfortunately, for more than a few loci, the calculations become computationally as well as analytically difficult. Therefore, exact results for a small number of loci will be compared to two multilocus approximations, based on the extremes of strong and weak selection.

Weak Selection and Migration Approximation.—The first approximation for weak selection is based on an approach first presented by Wright (1935) in an analysis of the balance between mutation and selection under a quadratic-optimum model. The solution is identical except for a small factor introduced by the difference in fitness models ($s\alpha^2$ in the quadratic model is replaced by $s\alpha^2/2$ in the Gaussian model [Barton 1986]). Assuming that selection is weak (and therefore that the critical migration rate is also small) and that the population mean is at the optimum, Wright (1935, Eq. 43) showed that the equilibrium gene frequency of an allele at the ith locus that is initially fixed in the population receiving migrants from a population fixed for the other allele is

$$q_i = \frac{1}{4}\left(3 \pm \sqrt{1 - \frac{16m}{s\alpha^2}}\right) \quad \text{or} \quad 0. \tag{1}$$

The polymorphic equilibrium exists when the migration rate is below the critical value, $m_c < s\alpha^2/16$. The allele frequency at the stable equilibrium is approximately $q_i \approx 1 - 2m/s\alpha^2$. With weak selection and many loci, linkage disequilibrium can be neglected (Bulmer 1980; Lande 1984), and the genetic variance in the population is given by

$$V_g = \sum_i 2\alpha^2 p_i q_i; \qquad (2a)$$

$$\approx 4nm/s. \qquad (2b)$$

Equation (2b) is identical to previous results for mutation-selection balance (Wright 1935; Latter 1960; Bulmer 1972; Turelli 1984), except that n refers to the number of loci that differ between populations, not the total number of loci, and that the variance is maintained by the input of migrants, not new mutations. Barton and Rouhani (1993) also obtained this result under the assumption that, for their model, populations will differ, on the average, at half of their loci. The maximum variance that can be maintained occurs when the population is receiving migrants exactly at the critical rate. In this case, the variance is approximately $3n\alpha^2/8$.

Strong Selection Approximation.—When selection is very strong, any genetic variance introduced by migration is immediately eliminated by selection. This is obviously an extreme situation, but by using a strong selection approximation, an upper bound on the critical migration rate can be obtained.

Very strong selection means that only individuals with the optimal phenotype can survive. Thus, only genotypes that combine with the residents or immigrants to yield the optimal phenotype will persist. In any generation, then, the only viable genotypes will be the residents, the migrants, and a subset of recombinants resulting from mating between these two. By and large, however, these recombinants will be lost from the population the generation after they are created, as they recombine with other individuals and thereby become selected against. If we represent the frequency of the resident gamete by x, the frequency of the migrant gamete by y, and the frequency of recombinants between x and y with the optimal phenotype by z, then recursions for very strong selection are, to a good approximation, given by

$$\begin{aligned} x' &= (1 - m)\,(x^2 + c_1xy)/(x + y + z)^2, \\ y' &= (1 - m)(y^2 + c_2xy)/(x + y + z)^2 + m, \\ z' &= (1 - m)(2c_3xy)/(x + y + z)^2. \end{aligned} \qquad (3)$$

where $c_1 = c_2 = 1/2^{n-1}$ is the probability that resident and migrant gametes will not recombine, and $c_3 = [\binom{n}{n/2} - 2]/2^{n-1}$ is the probability that a recombination event between the resident and migrant gametes will yield a gamete (other than the original types) that will combine well with the resident gametes. I have been unable to obtain a general solution to (3), but if one makes the assumption that the frequency of the resident genotype is high relative to the probability of no recombination (which will be true if the number of loci is large), then one can set $c_1 = 0$, and a solution is possible. This solution, obtainable from the author, is fairly complex, and not directly relevant except to note that it only exists when the migration rate is less than

$$m_c < (1 - c_2)^2/[9 - c_2(6 - c_2) + 8(1 - c_2)c_3]. \qquad (4)$$

An alternative approach is to assume an infinite number of loci, in which case the probability that gametes from the resident and migrant populations will produce viable recombinants is essentially zero (i.e., $c_3 = 0$ in eq. 3). The recursion then simplifies to

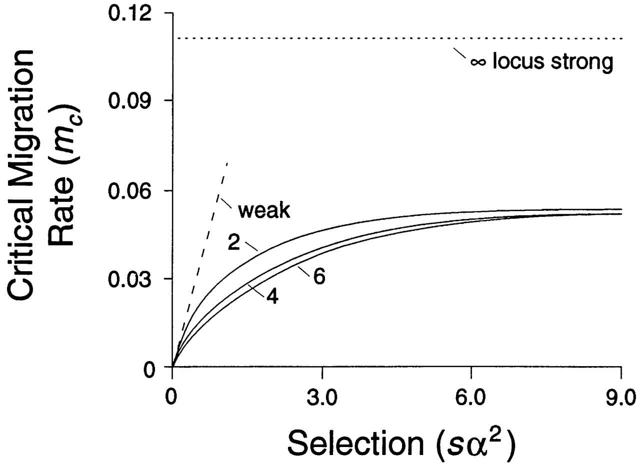

FIG. 2. Critical migration rates for the Gaussian stabilizing-selection model. Solid lines show exact results for two, four, and six loci. The dashed and dotted lines show the weak- and strong-selection approximations, respectively. This shows that the region of polymorphic equilibria shown in Figure 1 is bounded above as selection increases.

$$\begin{aligned} x' &= (1 - m)x^2/(x + y)^2, \\ y' &= (1 - m)y^2/(x + y)^2 + m \end{aligned} \qquad (5)$$

(cf., Crow et al. 1990, eq. 7; see also Kondrashov 1992). The solution to these equations for a stable, polymorphic equilibrium is

$$\begin{aligned} x &= \left(5 + 3\sqrt{(1 - 9m)(1 - m)} - 9m\right)\Big/8 \\ y &= \left(1 - \sqrt{(1 - 9m)(1 - m)} + 3m\right)\Big/8. \end{aligned} \qquad (6)$$

This solution exists only when the migration rate is below the critical value, $m_c < 1/9$. This is consistent with the relationship in (4), because both c_2 and c_3 go to zero with an infinite number of loci.

Exact Results.—The effect of the strength of selection on the critical migration rate is shown in Figure 2. As can be seen, the migration rate must usually be very low if variance is to be maintained in the population; otherwise, the loci go to fixation. Thus, there is a limit on how large the area of polymorphic equilibria can be. Even when selection is very strong, a migration rate much above 0.1 (1/9) precludes a migration-selection balance (this value is much lower when only a few loci are involved). The predicted critical migration rate for the infinite locus approximation is substantially higher than the exact results for a few loci because with a finite number of loci, recombination between the migrants and residents creates other equally fit genotypes that segregate in the population at a reasonably high frequency ($\sim m$). This effect is illustrated in Figure 3, which represents the critical migration rate under strong selection as predicted by Equation (4). This equation overestimates the actual critical migration rate when the number of loci is small, as might be expected from the approximation that was made (although numerical solution of Equation (3) for two loci produces a reasonably good value). It does show, however, that the actual m_c will be much lower than infinite locus prediction even when the number of loci is

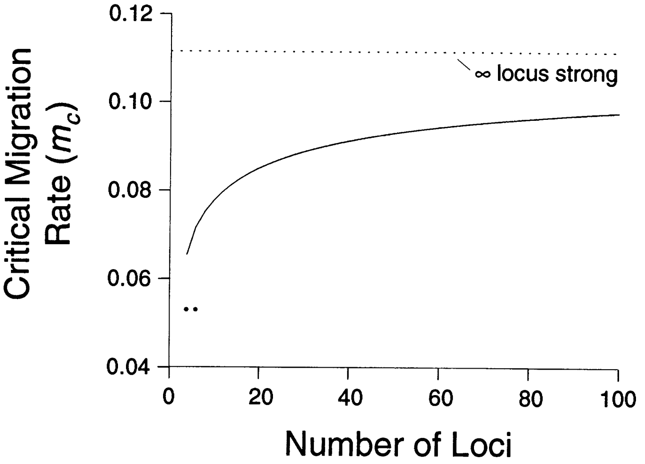

FIG. 3. Effect of the number of loci on the strong-selection approximation of the critical migration rate. The solid line is the approximation given in Equation (4). This line approaches the infinite locus approximation only very slowly with an increasing number of loci. The two dots represent the exact calculations given in Figure 2, and show that this approximation overestimates the critical migration rate when the number of loci is small.

large, because recombination between resident and migrant gametes produces recombinants that are of the most fit type ($[\binom{n}{n/2}]/2^{n-1}$; for $n = 100$ this yields a frequency of 8% of the total recombinants produced).

If the migration rate is below the critical rate, then some genetic variance can be maintained via a migration-selection balance. In general, the analytical approximations given above provide an adequate description of the nearly linear relationship between migration rate and variance when selection is weak and the migration rate is low (Fig. 4). As the migration rate approaches its critical value, more variance is maintained than is predicted by the linear model, but the variance is bounded above by the maximum given by the approximation. Increasing the strength of selection allows the critical migration rate to increase, potentially allowing more variants to enter the population. The increase in variance from this source is countered by the elimination of variation by selection, however; thus, there is actually a net loss in the maximum amount of variance that can be maintained as selection increases (Fig. 5). More variance is therefore generated with weak selection and low migration rates than with strong selection and high migration rates. However, strong selection masks a large amount of potential variation in the form of linkage disequilibrium (Bulmer 1974). If this disequilibrium were to be eliminated, say by a change in the direction of selection, then the variance present in the population would actually approach that obtained under the weak selection–low migration case (Fig. 5).

The above analysis is based on the assumption that the population mean is at the optimum. Barton (1986) has shown that other stable equilibria are possible under a mutation-selection balance when this assumption is violated. Migration among populations whose means are not at the optimum might therefore also be expected to generate genetic variance under uniform selection, but this situation should be far more unstable than the symmetrical case discussed above.

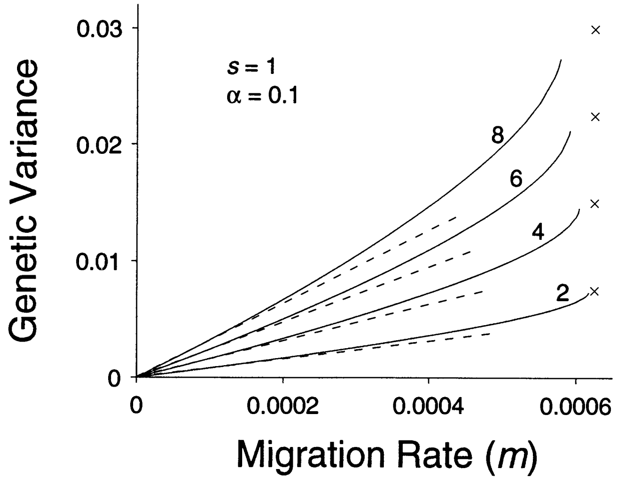

FIG. 4. Within-population genetic variance under a migration-selection equilibrium with weak selection. The solid lines show the variance for exact calculations of the Gaussian stabilizing-selection model with differing numbers of loci (indicated by the numbers next to each line). The lines end at the critical migration rate. The dashed line gives the weak-selection approximation, $V_g \approx 4nm/s$. The × shows the upper bound on the variance at the critical migration derived from the weak selection approximation, $V_g \approx 3n\alpha^2/8$. Here, $s = 1$ and $\alpha = 0.1$.

DISCUSSION

If a small number of migrants are being exchanged among a group of genetically differentiated subpopulations, genetic variance can be maintained within each subpopulation because incoming migrants tend to have a different genotype than the residents. This variance is maintained despite the

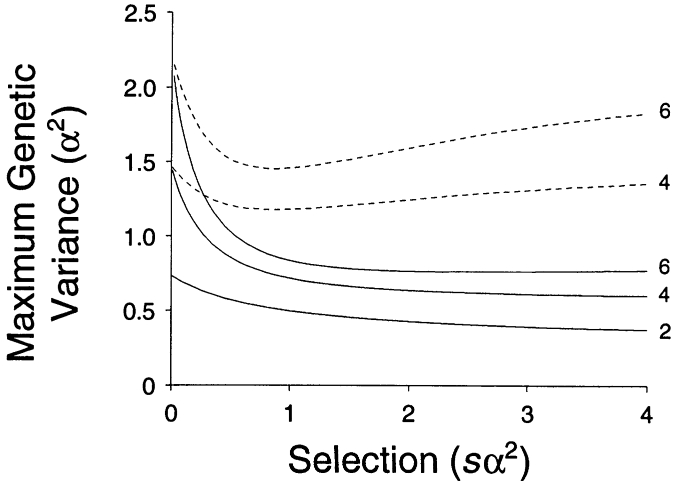

FIG. 5. Maximum attainable genetic variance under a migration-selection balance with one-way migration and Gaussian stabilizing selection. Solid lines show the genetic variance for different strengths of selection when the migration rate is within 0.1% of its critical value (see Fig. 2). The number of loci is given to the right of each line. The greatest variance can be maintained when both selection and migration are very weak. Dashed lines show the genetic variance that would ultimately be present in the population after selection is relaxed. The increase in variance is caused by the breakdown of linkage disequilibrium generated by selection. The dashed line for two loci is omitted for clarity.

fact that the pattern of selection is identical within each subpopulation (Lande 1991; Goldstein and Holsinger 1992; Barton and Rouhani 1993; Slatkin and Lande 1994). Here, migrants act in a fashion analogous to mutation, except migrants bring many new alleles into the subpopulation simultaneously. Migration would therefore appear to be a potentially important source of variance. Two factors work against this restricted form of migration-selection balance, however. First, the migration rate cannot be too high or the balance can not be maintained, even with very strong selection (Fig. 1). Depending on the fitness model, the migration rate must be very low for reasonable levels of selection ($m_c \approx s\alpha^2/16$), or the populations would be expected to become genetically homogeneous (for a more extreme fitness model with a critical migration rate of approximately 0.18, see Kondrashov [1992]). It is difficult to know how strong selection tends to be, but using values commonly referred to in the literature (Lande 1975; Turelli 1984; Barton 1986) and assuming that the input of new mutations is the same for every locus, a "typical" value for the strength of selection and allelic effects might be $s = 0.05/\mathrm{V_E}$ and $\alpha^2 = 0.1\mathrm{V_E}$. This yields a composite selection value of $s\alpha^2 = 10^{-3}$, well to the left side of Figure 2. Even if migration among populations was generally very low, periodic episodes of high migration would overwhelm the effects of selection (Barton 1992; Phillips 1993). Barton and Rouhani (1993) and Rouhani and Barton (1993) have extended this analysis to include drift, finding that if the migration rate exceeds $Nm > 1$, then the populations would be expected to go to a single peak.

Second, given that the migration rate is below some critical rate so that variance can be maintained, it is not clear how the populations move through the selective valley to become differentiated in the first place (Barton and Rouhani 1987, 1993), or whether this transition can occur in a reasonable amount of time (Phillips 1996). This is the contentious issue of how effective the first two phases of Wright's shifting–balance process (drift across an adaptive valley and mass selection toward a new peak) might be (Wright 1931, 1932, 1977). Barton and Rouhani (1993) have demonstrated that, for simple models, populations can in fact diverge even in the face of strong selection if $Nm \approx 1$. This also appears to be true of continuous populations, which can become structured under strong selection as long as the dispersal distance is not too large (D. Goldstein pers. comm. 1993; see also Lande 1991). Therefore, models including genetic drift indicate that as long as migration stays below a restricted level, subdivided populations should be able to diverge, and the divergent subpopulations should experience elevated levels of variance caused by a migration-selection balance. The apparent discrepancy between the stochastic and deterministic analyses arises because the stochastic results apply to the likelihood of divergence between populations, whereas the deterministic results presented here relate to the likelihood that they will remerge, given that they have already diverged. These two issues are somewhat different because in finite structured populations (Barton and Rouhani 1993), or with isolation by distance (Lande 1991; Goldstein and Holsinger 1992), there is a continuous dynamic of divergence and remerging that can apparently fuel the maintenance of variation even when we would not expect it on the grounds of a migration-selection balance. Furthermore, the total amount of variation maintained in a set of structured populations is likely to be much larger than the variance maintained within single populations, as was studied here.

When the migration rate is low enough relative to the amount of selection, results for the migration-selection balance are identical to those for a mutation-selection balance with the migration rate replacing the mutation rate ($V_g \approx 4nm/s$ for weak selection; Fig. 4). As the migration rate increases, this approximation rapidly breaks down, but variance continues to increase with migration rate, reaching a maximum exactly at the critical balance between selection and migration ($V_g \approx 3n\alpha^2/8$; Fig. 4). This may explain why Goldstein and Holsinger (1992) observed maximum individual heterozygosity at intermediate dispersal distances. Because migration rates are expected to be orders of magnitude larger than mutation rates, migration-selection balance under uniform selection could maintain a significant amount of variance, given that the populations have diverged for some reason (e.g., species and subspecies; Grant and Grant 1992). Furthermore, restrictions on the magnitude of the migration rate could be mitigated if the strength and direction of selection were to vary temporally or spatially (Slatkin 1978; but see Barton and Turelli 1989). However, very low levels of migration do not appear to be the rule in natural populations (Slatkin 1987), and thus a migration-selection balance in unlikely to make a significant contribution to the maintenance of genetic variance in most populations. At least for the somewhat specialized model of uniform selection, the contrast between predictions based on deterministic and stochastic approaches suggests drift will be the dominant player in determining the amount of variance maintained via a migration-selection-drift balance.

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ADAPTATION TO HEAVY METALS IN THE AQUATIC OLIGOCHAETE *LIMNODRILUS HOFFMEISTERI*: EVIDENCE FOR CONTROL BY ONE GENE

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This study is designed to understand the genetic architecture of resistance to metal in a metal-tolerant aquatic oligochaete. Our results suggest the control by one gene, and further support the genetic simplicity and potential evolutionary responsiveness of metal tolerance in animals. Toxic substances are potent media of natural selection and many field populations of resistant plants and animals have been discovered and described (Antonovics et al. 1971; Macnair 1987; Klerks and Weis 1987; Devonshire and Field 1991). Metals such as cadmium and lead are commonly released into terrestrial and aquatic environments, and metal-resistant populations have been found in both terrestrial plants (Antonovics et al. 1971; McNeilly 1968; Macnair 1983), terrestrial invertebrates (Posthuma 1990), freshwater invertebrates (Klerks and Levinton 1989a,b), marine seaweeds (Russell and Morris 1970) and marine invertebrates (Bryan and Hummerstone 1971, 1973; Weis et al. 1981).

Although extensive evidence exists for a genetic basis of metal adaptation in plants (Antonovics et al. 1971), genetic studies of animals have been relatively uncommon, especially in field populations (Klerks and Weis 1987; Klerks and Levinton 1992). Allozyme frequencies have been found to correlate with metal exposure (e.g., Lavie and Nevo 1982; Nevo et al. 1984), although the direct biochemical significance of the selective effects is not clear. Posthuma et al. (1993) found that springtails exposed to metals had a heritable component