

Effects of Releasing Maladapted Individuals: A Demographic-Evolutionary Model

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Submitted December 22, 1999; Accepted May 18, 2001

ABSTRACT: A model of the joint dynamics of change in population size N and evolution in a quantitative trait z , as a result of a general form of density dependence, local stabilizing selection, and immigration of individuals deviating from the local optimum, is analyzed. For weak selection and migration, a reduction in total equilibrium population size below the initial level without immigration, K , is shown to occur if the immigrants deviates more than $\sqrt{8} = 2.83$ genetic standard deviations from the optimum and if the rate of migration m is sufficiently large relative to the strength of stabilizing selection s . For the Lotka-Volterra form of density dependence, two additional equilibria are shown to exist below K , provided that the strength of selection is large relative to the strength of density dependence. Reintroduction of an initially extinct population is possible if the immigrants are not too maladapted and if the genetic variance is sufficiently large. For a simplified version of the model corresponding to competition between similar species or different haplotypes, the equilibrium population size is always exactly at K if $m < Ksz_i^2/2$ and is above K otherwise, which shows the importance of including recombination in the model.

Keywords: migration, stabilizing selection, population regulation, genetic variation.

The size of many populations in the wild are declining as a result of habitat destruction and other human activities. To prevent further reductions, people have sought to enhance many such populations by supplementing them with other populations considered to be more healthy. These supplementary populations, however, often differ genetically from the population one wishes to rescue (Tessier et al. 1997; Unwin and Glova 1997). This has led to the concern that supplementation can have various indirect negative effects on population viability. Such concerns also

apply in cases in which people attempt to reintroduce species that are extinct in the wild by releasing individuals from populations kept in captivity and, in the case of harvested populations, by supplementing wild populations with individuals born in captivity in hopes of increasing the harvest (Fleming and Gross 1993).

An increasing number of species are also used in cultivation. Often, in particular in the case of salmonid fishes used in marine aquaculture, large numbers of cultivated individuals escape accidentally from closed-culture operations or are released intentionally in the context of sea ranching (Hindar et al. 1991). Cultivated populations can differ from wild populations as a result of intentional artificial selection for traits that are of economic importance and as a result of unintentional natural selection in the culture environment that differs from the selective regime in the wild (Fleming and Eium 1997). This has led to similar concerns about the possible genetic effects this may have on the wild populations (Hindar et al. 1991). In contrast to this view, however, it has been argued that the genetic effects are of little importance and that immigration through the accidental release of cultivated individuals actually acts as a form of beneficial supplementation through its direct effect on population size.

Several different forms of potentially negative genetic effects have received attention in the literature. Small effective population size (Ryman and Laikre 1991) and intentional and unintentional selection may lead to long-term reductions in genetic variability in the population used for supplementation, which, in turn, may reduce the recipient population's ability to adapt to environmental changes (Lande and Shannon 1996). Outbreeding depression may also occur if different coadapted gene complexes evolve in different subpopulations (Allendorf and Waples 1996; Lynch 1996). However, while these processes are important in the long-term, loss of genetic variation and evolution of coadapted gene complexes are both relatively slow processes. Therefore, genetic change as a result of continual immigration of individuals not adapted to the local environment may be of more immediate importance. However, because most life-history

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traits are polygenic, the classic theory of gene frequency evolution cannot be directly applied to understand the consequences of this but needs to be understood through models based on quantitative genetics (Lande 1982).

Here, I consider the effects of immigration on population dynamics and the evolution of a quantitative trait, in a local population subject to stabilizing selection and a general form of density dependence. The phenotypic mean of the immigrants deviates from the local phenotypic optimum. For a simple limiting case of the model, I show that a reduction in total population size at the joint demographic and evolutionary equilibrium, below the carrying capacity without migration, is possible provided that the deviation of immigrants from the local optimum is sufficiently large and the rate of migration exceeds a critical threshold. I also show, using numerical methods and assuming a specific form of population regulation, that additional stable and unstable equilibria below the carrying capacity can exist as a result of a form of positive feedback in the model, given the additional condition that the strength of density dependence is weak. The existence of these additional equilibria are related to the question of whether reintroduction of an initially extinct population is possible. For reintroduction strategies based on a constant low rate of immigration, reintroduction of an adapted population is shown to be possible, even with immigrants that have a negative intrinsic rate of increase, unless the immigrants are too maladapted and the genetic variance is too small.

Model and Results

Rationale

Although traits that have been subject to directional artificial selection in culture may also be under directional selection in the wild, artificial selection will generally, as a result of trade-offs, create indirect responses in correlated traits and a net decrease in fitness under natural conditions. This follows from the fact that the joint evolution of the set of all life-history traits as a result of natural selection, under quite general conditions, maximizes the intrinsic growth rate of a population (Lande 1982). Any change in a set of correlated traits away from this optimum will, therefore, lead to some reduction in mean fitness. Although natural selection and immigration in this situation affect several traits simultaneously, a univariate model based on a simple form of stabilizing selection like the one considered here will be an appropriate model if certain idealized conditions hold approximately.

Weak Selection and Migration

In general, when the genotypic means differ between the immigrants and the local population, migration will generate strong, positive linkage disequilibrium that inflates the genetic variance and creates departures from normality. This linkage disequilibrium is gradually broken down by recombination during reproduction. Here, I begin by analyzing the simple limiting case of weak selection and a low rate of migration relative to the rate of recombination. The population will then remain approximately in linkage equilibrium provided that the deviation of the immigrants from the mean in the local population is not too large. The analysis also relies on the infinitesimal model (Fisher 1918; Bulmer 1980); that is, I assume that z depends on a large number of genes with small additive effects, so that allele frequencies and the genetic variance at linkage equilibrium V remain approximately constant. This assumption and the above assumptions of weak selection and migration also imply a normal distribution of breeding values z (Bulmer 1980). We then only need to consider the dynamics of the size of the population $N(t)$ and the evolution of the mean of the breeding values $\bar{z}(t)$.

For stronger selection and migration, we can obtain exact predictions for the migration-selection balance for stronger migration and stabilizing selection using Fourier-transform methods that fully take into account nonnormality and increased genetic variance caused by linkage disequilibrium (Turelli and Barton 1994, Tufto 2000). As I will note in the discussion, however, for important parameter values, as long as deviations of immigrants from local optimum are moderate and selection and migration are not too strong, numerical analysis (Tufto 2000) shows that approximations based on analysis of the limiting case of weak selection and migration produce reasonable results.

In general, to incorporate stabilizing selection and density dependence, the absolute fitness of an individual with breeding value z must be a function of both z and N . I assume that this function takes an additive form:

$$f(z, N) = r(N) - \frac{s}{2}(z - z_0)^2, \quad (1)$$

where z_0 is the local optimum, s is the strength of selection, and $r(N)$, to incorporate density dependence, is some decreasing function of population size N . Without any loss of generality, we can take the optimum to be 0, which corresponds to a simple translation of the model in terms of the trait z . If we take expectation over different genotypic values z and include immigration at rate m in the model, we find that the rate of change in population size with time becomes

$$\frac{dN}{dt} = \left[r(N) - \frac{s}{2}(V + \bar{z}^2) \right] N + m. \quad (2)$$

The mean per capita growth rate of the population (the sum in the square brackets) involves two load terms that reduce the rate of population increase: a genetic load, $sV/2$, associated with the genetic variance and a migrational load, $s\bar{z}^2/2$, proportional to the square of the deviation caused by the immigration of maladapted individuals. (The latter is similar to the evolutionary load in Lande and Shannon's [1996] model for evolution in changing environments.)

As in the haploid model that Holt and Gomulkiewicz (1997b) considered, the parameter m is defined here as the absolute number of individuals entering the population per unit time and is taken to be constant. Because population size changes over time, this means that the effect of migration on allele frequencies (and hence on the mean of the trait) will increase as population size N decreases. More precisely, the rate of change in $\bar{z}$ as a result of immigration, that is, what is usually referred to as the migration rate in the population genetic literature, will be equal to m/N . This is in contrast to most standard population genetic theory in which the genetic migration rate usually is taken to be constant. As we shall see, this assumption has some important consequences.

Let z_1 denote the mean breeding value among the immigrants relative to the phenotypic optimum. The rate of change in $\bar{z}$, including the standard term for the effect of stabilizing selection (Lande 1982) in continuous time, in the case of weak selection and a low rate of migration, is then

$$\frac{d\bar{z}}{dt} = -Vs\bar{z} - \frac{m}{N}(\bar{z} - z_1). \quad (3)$$

Equations (2) and (3) specify the joint dynamics of $N(t)$ and $\bar{z}(t)$.

From equation (3), it follows that at the joint evolutionary and population dynamic equilibrium for a given N , the mean of the trait is

$$\bar{z} = \frac{m/N}{Vs + m/N} z_1. \quad (4)$$

Thus, as the rate of migration relative to the rate of response to stabilizing selection increases, the equilibrium $\bar{z}$ approaches the mean of the immigrants z_1 .

To get an understanding of the effects of immigration on population size, it will be helpful to begin by considering the case of a small rate of immigration m . First, define the carrying capacity K as the population size N at

which $dN/dt = 0$ when there is no immigration ($m = 0$) and the mean is at the optimum ($\bar{z} = 0$) so that

$$r(K) - \frac{Vs}{2} = 0; \quad (5)$$

that is, the population growth rate, including the genetic load, is 0 at the carrying capacity K .

Without making any detailed assumptions about the pattern of density dependence, it is clear that N will be close to the carrying capacity K when m is small, provided that the population growth rate decreases with increasing population size. Let $-\alpha/K$ denote the first derivative of $r(N)$ with respect to N at $N = K$. The parameter α thus measures the strength of density dependence near the carrying capacity. For small m and for N near K , we can then write equation (2), with the joint equilibrium value of $\bar{z}$ expressed as a function of N of equation (4) substituted in for $\bar{z}$, on the linearized form

$$\frac{dN}{dt} = -\alpha(N - K) + m. \quad (6)$$

Setting $dN/dt = 0$, we find that the size of the population at the joint equilibrium is

$$N = K + \frac{m}{\alpha}. \quad (7)$$

Thus, there is always at first an increase in the equilibrium population size equal to m/α . Essentially, this result arises because the migrational load term in equation (2) depends on the squared deviation from the optimum, which in turn, for small m , is directly proportional to m , whereas the direct demographic effect of migration on the equilibrium population size is directly proportional to m .

It may be possible, however, that once the migration rate and the deviation $\bar{z}$ from the optimum become sufficiently large, the total load may become sufficient to reduce the growth rate so much that the equilibrium population size becomes smaller than K , the equilibrium for no migration ($m = 0$). At the migration rate at which this happens, we must have $dN/dt = 0$, $d\bar{z}/dt = 0$, and $N = K$. Substituting equation (4) into equation (2) and noting that $r(N) - Vs/2$, by definition (5), yields 0 for $N = K$, yields

$$\frac{s}{2} \left(\frac{m/K}{m/K + Vs} z_1 \right)^2 K = m. \quad (8)$$

A simple interpretation of this condition is that if some rate of migration $m > 0$ at which $N = K$ exists, the indirect effect of the migrational load in reducing the population

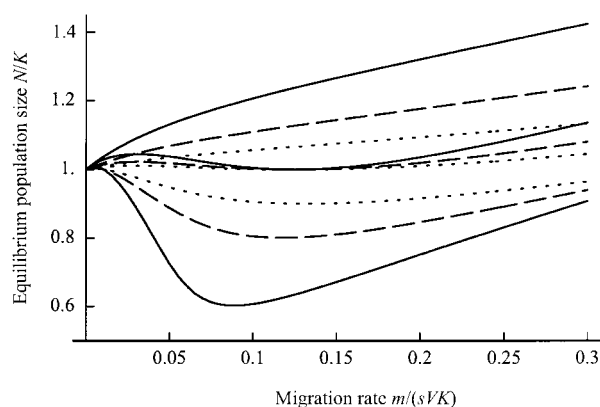


Figure 1: The equilibrium population size N/K for the Lotka-Volterra population model as function of $m/(sVK)$ for $z_1/\sqrt{V} = 2$, $z_1/\sqrt{V} = \sqrt{8}$, and $z_1/\sqrt{V} = 4$ (upper, middle, and lower group of curves, respectively) and $r/sz_1^2 = 1/4$, $r/sz_1^2 = 1/2$, and $r/sz_1^2 = 1$ (solid, dashed, and dotted curves, respectively, within each group). The effect of changing the strength of selection s is indicated by the dotted curves.

growth rate (the left-hand side of the above equation) must be matched by its direct demographic effect (the right-hand side).

Solving for equation (8), we find that this occurs for the migration rates

$$m^* = \frac{1}{4} Ks \left(z_1^2 - 4V - z_1 \sqrt{z_1^2 - 8V} \right), \quad (9)$$

$$m^{**} = \frac{1}{4} Ks \left(z_1^2 - 4V + z_1 \sqrt{z_1^2 - 8V} \right). \quad (10)$$

These migration rates only exist (i.e., are noncomplex) provided that

$$z_1 > \sqrt{8V} \text{ or } z_1 < -\sqrt{8V}; \quad (11)$$

that is, a reduction down to K for some $m > 0$ is only possible if the immigrants deviate more than $\sqrt{8} = 2.83$ genetic standard deviations from the optimum. For smaller deviations ($-\sqrt{8V} < z_1 < \sqrt{8V}$), the equilibrium population size is never at $N = K$ for any $m > 0$. Also note that the critical migration rates m^* and m^{**} do not depend on the strength α (nor the form) of density dependence around $N = K$; the only assumption made is that $r(N)$ is some decreasing function of N . One can show that m^* and m^{**} are always nonnegative provided that these solutions exist.

It should be noted that because the amount of linkage disequilibrium generated by migration depends not only on the rate of migration and selection but also on z_1 , the approximation on which equations (9) and (10) are based

will gradually break down for large z_1 at some point, depending on the strength of selection and rate of migration.

Lotka-Volterra Population Regulation

The existence of an equilibrium at $N = K$ does not preclude the existence of other stable and unstable equilibria below and above $N = K$. The existence of such equilibria, however, will depend on the population dynamics away from K . If we make the restrictive assumption that population regulation is on Lotka-Volterra form, that is, that $r(N) = r_0(1 - N/K)$, four lengthy, analytic, sometimes complex solutions for the equilibrium population size at the joint equilibrium can be obtained (these are not given here). Letting r denote the intrinsic growth rate $r_0 - sV/2$ of the population for $\bar{z} = z_0$, it follows, by rescaling the model, that the equilibrium population size over the carrying capacity, N/K , depends on three parameters only: $r/(sV)$, the intrinsic growth rate scaled against the rate of response to stabilizing selection, $m/(sVK)$, the rate of migration relative to the carrying capacity and the response to stabilizing selection, and $z_1/\sqrt{V}$, the number of genetic standard deviations the immigrants deviate from the local optimum.

The equilibrium population size for the Lotka-Volterra form of population regulation is shown in figure 1 as a function of $m/(sVK)$ for different values of $z_1/\sqrt{V}$ and $r/(sz_1^2)$. For all parameter values used, only one real joint equilibrium existed. Numerical evaluation of the eigenvalues of the stability matrix verified that this equilibrium was stable. Several other points can be noticed. For $z_1 < \sqrt{8V}$ (upper three curves), the equilibrium population size is always above $N = K$ for $m > 0$, and in general, the equilibrium population size, for given values of $m/(sVK)$, increases with decreasing values of $r/(sV)$.

It can also be noted that for the lowermost curve in figure 1 there is a sharp decline in N as m is increased above m^* . This is a result of a form of positive feedback in the system: by lowering the population mean growth rate, an increase in the rate of migration leads to a reduction in population size, which in turn leads to a further increase in the "genetic" migration rate. Consideration of some numerical cases indicates that this positive feedback mechanism can lead to additional stable and unstable equilibria for intermediate values of m provided that the strength of density dependence r is sufficiently small relative to the strength of selection and provided that condition (11) is satisfied (see fig. 2a, 2b). The low-population-size equilibrium in figure 2 corresponds to a situation in which $\bar{z}$ is kept near the mean z_1 of the immigrants as a result of a high genetic migration rate (because population size is low). This causes a large reduction in the population's intrinsic rate of increase, and so the population is maintained almost

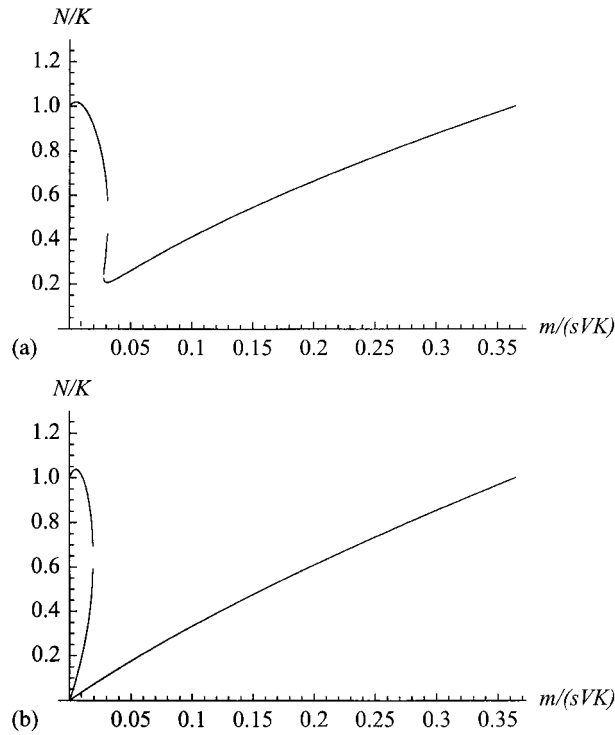


Figure 2: Equilibrium population sizes N/K for (a) $z_1 = 4\sqrt{V}$ and $r/(sz_1^2) = 1/8$ and (b) $z_1 = 4\sqrt{V}$ and $r/(sz_1^2) = 1/16$.

entirely by the immigrants. However, if population size is initially large, the genetic migration rate and the corresponding migrational load will be small, and so an equilibrium can exist at a large population size.

Reintroduction

Both cases in figure 2 (and some cases in fig. 1) correspond to parameter combinations for which a population made up entirely from the immigrant genotypic distribution, in the absence of evolution and in the absence of further immigration, would go extinct in the wild; that is, we have $r - sz_1^2/2 < 0$. One question of interest is whether such a population (say a population of an endangered species maintained in captivity) can be used to reintroduce a healthy population in the wild. Here, only strategies based on releasing a constant number of individuals per unit time are considered. This will establish a population at some low population density that, given that the response to natural stabilizing selection is sufficiently large, may allow the local population to gain a positive growth rate. In fact, the nonexistence of any additional equilibria at low population densities for the parameter combination corresponding to the lowermost curve in figure 1 implies that this will happen.

However, it may also be that reintroduction will be impossible in cases in which immigrants are very maladapted. This possibility is indicated by the numerical example in figure 2b that shows that a low-population-size equilibrium, for this parameter combination, exists for rates of immigration all the way down to $m = 0$. If we rely on the supposition that a small, nonzero rate of immigration, in general, will be most favorable, it follows that the region in parameter space in which reintroduction in the deterministic sense is possible is the complement of the region in which the additional low-population-size equilibrium exists down to $m = 0$. This region of the parameter space, computed numerically, is shown in figure 3 delineated by the

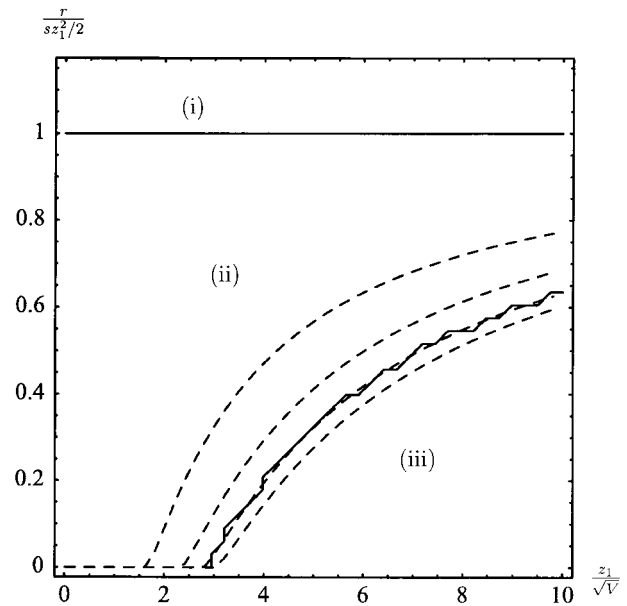


Figure 3: Different regions of the parameter space for which reintroduction is possible, with deviation of immigrants from local optimum measured in genetic standard deviations ($z_1/\sqrt{V}$) on the first axis and maximum attainable growth rate relative to initial maladaptation ($r/[sz_1^2/2]$) on the second axis. Different outcomes are delineated by solid lines. Reintroduction is possible whenever (i) the immigrants have a positive growth rate ($r < sz_1^2/2$) but also in some cases (ii) when the growth rate of the immigrants is negative, provided that the initial maladaptation (or strength of selection) and the deviation of immigrants from the optimum is not too large (iii). Note that reintroduction, in general, is always possible for $z_1 < \sqrt{8V}$. Reducing the genetic variance while keeping other parameters fixed corresponds to going from region (ii) to region (iii) and can thus make reintroduction impossible. The curve separating regions (ii) and (iii) was computed numerically by counting the number of real, positive, joint equilibrium solutions of equations (2) and (3) for $m/(sVK) = 0.0001$. The dashed lines delineate regions of the parameter space where reintroduction is possible and impossible based on the strategy of Gomulkiewicz and Holt (1995), that is, no migration after the initial generation, allowing population declines by factors of 2, 4, 7, and 10, respectively, before evolving a positive growth rate (upper-left to lower-right dashed curves).

solid lines. In general, in a large part of the parameter space (*i* and *ii*), reintroduction is possible, even with immigrants that have a negative growth rate ($r[sz_1^2/2] < 1$; *ii*). However, if the deviation of the immigrants from the local optimum is too large or if selection is too strong (*iii*), reintroduction of a locally adapted population will be impossible, at least with the above strategy (constant m).

In general, the possibility of reintroduction also depends on the genetic variance V being sufficiently large. If we keep all other model parameters constant, a reduction of V by a factor of say, four, increases $z_1/\sqrt{V}$ by a factor of two, such that reintroduction may become impossible (*iii*).

Gomulkiewicz and Holt (1995) considered a model similar to the one presented here but without density dependence and with no migration after the first initial generation. They showed that a population initially having a negative growth rate, for example, after a colonization event or after a human-mediated reintroduction, can evolve a positive intrinsic rate of increase before going extinct, provided that the genetic variance is sufficiently large and provided that immigrants are not too maladapted initially. For this to occur, initial population size N_0 also has to be sufficiently large relative to the minimum population size N_c , which is considered to be critical in terms of the risk of extinction as a result of demographic stochasticity.

By reanalyzing Gomulkiewicz and Holt's (1995) model, for the continuous time formulation used here, an analytic expression can be derived for the relative decline in population size that occurs before the minimum population size N_c is reached (appendix; eq. [A4]). The dashed lines in figure 3 show in which regions of the parameter space reintroduction will be possible, allowing declines in population size by different factors N_0/N_c . As shown by this figure, for the strategy considered by Gomulkiewicz and Holt (1995), the condition for when reintroduction will be possible is qualitatively similar to the strategy considered here based on releasing a constant number of individuals per unit time (fig. 3). However, for Gomulkiewicz and Holt's (1995) strategy to be equally effective, one has to allow a decline in population size before the population is rescued by evolution by a factor of about seven. Again, these results depend on linkage disequilibrium being negligible. However, in the case of reintroduction, the increase in genetic variance as a result of positive linkage disequilibrium will increase the response to selection, only making the condition for when reintroduction can occur less restrictive.

Competing Species

The analysis has so far been based on the assumption that the additional variance due to linkage disequilibrium and deviation from the Hardy-Weinberg equilibrium is broken down sufficiently fast relative to the strength of selection

and the rate of migration, through random mating and recombination, so that the dynamics of the genetic variance and departures from normality can be ignored. It is interesting to contrast this case with a different form of the model in which the immigrants and the natives are different species that compete strongly (i.e., that are ecologically interchangeable) with the resident species and in which there is no hybridization between the immigrants and the native species. The state of the system, assuming that the variance within each species is small such that evolution can be ignored, is then characterized by the population size of each species: the number of native individuals, N_0 , and the number of individuals originating from the immigrants, N_1 .

The immigrants and the natives can also be considered to be different single-locus haplotypes of a haploid species with the immigrant haplotype suffering a reduction in fitness. The model is then identical to the model considered by Holt and Gomulkiewicz (1997b), except that I consider the behavior near the carrying capacity for a model with density dependence.

As before, assume that both immigrants and locals, through density dependence, produce the same reduction in individual fitnesses. We can then write

$$\frac{dN_0}{dt} = [r(N_0 + N_1)]N_0, \quad (12)$$

$$\frac{dN_1}{dt} = \left[r(N_0 + N_1) - \frac{sz_1^2}{2} \right] N_1 + m, \quad (13)$$

where the (negligible) component of the genetic load arising from the variance of z within each peak now is included in $r(N)$. As before, $r(N)$ is some decreasing function of N , and the carrying capacity K is defined as the equilibrium population size in the case of no migration ($m = 0$), so that $r(K) = 0$. From equation (12) and the definition of K , it immediately follows that the joint equilibrium values of N_0 and N_1 , provided that N_0 is nonzero, must satisfy

$$r(N_0 + N_1) = 0, \quad (14)$$

implying that the total population size (of both species)

$$N_0 + N_1 = K \quad (15)$$

at the joint equilibrium. Substituting equation (14) into equation (13), we find that the equilibrium population sizes are

$$N_1 = \frac{2m}{sz_1^2} K, \quad (16)$$

$$N_0 = \left(1 - \frac{2m}{sz_1^2}\right). \quad (17)$$

This is only possible if $m < Ksz_1^2/2$. If $m > Ksz_1^2/2$, it follows that the stable equilibrium value for N_1 takes some value greater than K (depending on the details of density dependence), whereas N_0 will be driven to extinction.

Thus, in contrast to the case with fast recombination, with only competition between different species, a reduction in total population size does not occur. Instead, we get either partial or complete displacement of the original population, with the total population size always at or above the carrying capacity K , respectively.

This result can be understood as following from the fact that the dynamics of the N_0 now are only disturbed by immigration through the effect of density dependence, such that N_0 grows until $N_0 + N_1 = K$, at which point the effect of density dependence reduces the growth rate of N_0 to 0.

Discussion

For a model of the joint dynamics of evolution in a trait z and population size N with a general form of density dependence, stabilizing local selection, and immigrants deviating from the local optimum, it has been shown that a reduction in equilibrium population size below the initial carrying capacity K is possible and that the condition for a reduction below K to occur requires that the deviation of the immigrants be larger than $\sqrt{8} = 2.82$ genetic standard deviations. For typical heritabilities of about $h = 0.5$ (Mousseau and Roff 1987), this corresponds to about two phenotypic standard deviations. The rate of migration also has to exceed a critical threshold proportional to the strength of stabilizing selection. This means that if the rate of migration is small or if the genetic variance is large, strong selection will prevent introgression of immigrating genes. However, strong selection can also have the effect of reducing population size if the genetic variance is too small and the rate of migration exceeds m^* .

That one-way migration can have the somewhat counterintuitive effect of reducing population size is similar to the result of Kirkpatrick and Barton (1997) that a too large dispersal rate (or a too steep environmental gradient), under some conditions, can have the effect of confining a species range to a finite area (but not causing extinction). As in Kirkpatrick and Barton's (1997) model, the condition for this to happen is independent of the strength of stabilizing selection.

The analysis has for the most part been based on the assumption of weak selection and migration relative to the rate of recombination. A high rate of migration would generate large positive linkage disequilibrium and inflate the genetic variance and also, as Holt and Gomulkiewicz (1997a) noted, create departures from normality. It can be noted, however, that this would only increase the response to selection and reduce the deviation from the phenotypic optimum (Tufto 2000). In the case of natives and immigrants being different species or, alternatively, different single-locus haplotypes, there is no recombination of the genetic material of immigrants and natives. There is then also no reduction in total population size but, instead, either partial or complete displacement of the native population. This simplified version of the model thus illustrates the importance of including recombination and multilocus quantitative genetics in the model; the problem cannot, in general, be understood as a form of competition.

The source-sink, haploid, single-locus form of the model was also considered by Holt and Gomulkiewicz (1997b). In regards to the model presented here, Holt and Gomulkiewicz also made the assumption that the absolute number of individuals entering the population per unit time is constant. Focusing on the case of no density dependence, Holt and Gomulkiewicz (1997b) concluded that a sufficient criterion for the initial spread of a rare allele in a sink population is that its absolute fitness at low densities must be >1 , a result that differs from classical theory for gene-frequency evolution. However, as Holt and Gomulkiewicz (1997b) noted, with density dependence, the absolute fitness criteria, although remaining necessary, are no longer sufficient. Instead, as we show here in equation (17), regardless of the details of density dependence, the sufficient criteria is again that the coefficient of selection must exceed the rate of migration as in classical theory for gene-frequency evolution (e.g., Haldane 1930).

The dependency of the genetic migration rate on the population size does have important consequences for the joint evolutionary and demographic dynamics, however. While some of the results here are independent of this dependency, it creates a form of positive feedback, which, provided that density dependence is weak, leads to a fast drop in population size when the rate of migration exceeds the critical value m^* . When density dependence is weak relative to the strength of selection, multiple equilibria can exist. For parameter values for which the low-population-size equilibrium exists for rates of migration down to $m = 0$, this corresponds to a situation in which it will be impossible to reintroduce a population in an area where its intrinsic rate of increase initially is negative, if a strategy based on releasing a constant number of individuals per unit time is used. Because relatively little immigration, in

general, is thought to be sufficient to hamper local adaptation, it is somewhat counterintuitive that this strategy performs relatively well compared to the reintroduction strategy considered by Gomulkiewicz and Holt (1995), that is, no immigration after first establishing a sufficiently large population. However, unless the immigrants are very maladapted, a small rate of immigration m will be sufficient to establish a relatively large population N , which means that the genetic rate of migration m/N becomes sufficiently small relative to the rate of response to selection Vs such that evolution toward the optimum and a subsequent further increase in the population size can occur.

Numerous situations in conservation genetics for which the model presented here have potential applications exist (see, e.g., Avise and Hamrick 1996). However, nearly all studies investigating genetic differences between native populations and populations used for supplementation or as a basis for reintroduction have focused on supposedly neutral molecular genetic variation. For both theoretical (Lynch 1996) and empirical reasons (Cheverud et al. 1994; Waldmann and Andersson 1998), estimates of, for example, heterozygosities, cannot be easily used to infer adaptive features of population genetic structure. Few studies in conservation genetics report estimates of quantitative genetic parameters such as genetic variances and differences in means between populations for quantitative traits to be potentially important in local adaptation, although these parameters, as shown here, and as pointed out elsewhere (Storfer 1996), are of great interest. While one can never be sure to have included all traits of importance when differentiation has been generated by natural selection, studies based on many traits should generally give a good indication as to whether sufficiently large differences satisfying equation (11) exist.

In the case when the immigrants differ from the local population mainly as a result of directional artificial selection, an estimate of the total response to selection in the trait under artificial selection may be available. This will also be the main parameter of interest in the more complicated case with indirect response to selection in correlated traits, which can be easily shown by considering a simple transformation of the full multitrait model. For Atlantic salmon (*Salmo salar* L.), a salmonid species used extensively in marine aquaculture, the total response to artificial selection for increased growth performance in the main breeding line used commercially in Norway is now, after six generations of selection, 3.28 genetic standard deviations, compared to the mean among the base population used when the breeding program was initiated in 1971 (Gjøen and Bentsen 1997; B. Gjerde, personal communication); that is, equation (11) is satisfied. This direct response to selection appears to be accompanied by somewhat smaller changes in a number of behavioral and morphological traits (Fleming and Einum

1997), which is consistent with the hypothesis that these traits are genetically correlated with growth performance. The largest difference between farmed and wild fish found in Fleming and Einum's (1997) study in the main principal component of several morphological traits would correspond to about 3.0 genetic standard deviation (based on the t -statistic in table 2 of Fleming and Einum 1997 and assuming a typical heritability of 0.5 [Mousseau and Roff 1987]), which indicates that genetic correlations, at least with some traits, are tight. These genetic changes appear to be accompanied by some reduction in fitness of farmed fish in the wild. Fleming et al. (2000) have estimated the lifetime success of newly escaped farmed salmon to 19% of that of native fish, but this figure probably includes large effects of differences in rearing environments. Estimates of the strength of stabilizing selection relative to genetic variances from other species typically suggest that $sV = 0.05$ (Turelli 1984). Relying on this figure and the above estimate for response to artificial selection and based on the discrete time model of stabilizing selection, this would imply a somewhat higher relative fitness of the farmed type equal to $\exp(-s/2z_i^2) = 0.76$ and, from equation (9), a critical rate of migration $m^*/K = 0.016$. The rate of immigration of farmed salmon into wild populations on the coast of Norway has, in recent years, been between 20% and 50% (Lund et al. 1996), thus exceeding the above critical value of 1.6%.

In addition to the lack of good estimates for some of the underlying parameters, it should be noted that the value of m^* also is approximate because it is based on the limiting case of weak selection and a low rate of selection. For moderate strength of selection and rates of migration, however, predictions based on this limiting case do provide a reasonable approximation. Numerical analysis of migration-selection balance under the infinitesimal model (Tufto 2000) that uses the Fourier-transform method of Turelli and Barton (1994) and that fully takes into account nonnormality and the increase in the genetic variance caused by migration, shows that the error in the predicted deviation of the mean $\bar{z}$ from the optimum, for the parameter values used in the above example, is only up to about 10%.

Broodstock from the Norwegian breeding line of Atlantic salmon, in part because of its increased growth performance, is now being exported for use in marine aquaculture to Washington, British Columbia, and Alaska. This means that large numbers of Atlantic salmon in the near future will escape into rivers inhabited by other salmonid species. This will have very different consequences, however, as was shown by contrasting the simplified model in which immigrants and natives are considered to be different species and the model in which there is slow selection and migration. In both cases, the consequences can be damaging: with random mating and recombination, immigration can significantly reduce the size of the total

population, whereas competition in the case of immigrants being a different species can lead to complete displacement and extinction of the native species.

My approach here has been to develop a simple model of evolutionary and demographic dynamics by ignoring processes such as loss of genetic variation due to limited effective population size (Ryman and Laikre 1991), outbreeding depression arising from the breakup of coadapted gene complexes (Lynch 1991), and demographic and environmental stochasticity (Lande 1993). The results derived here should, therefore, be applied to real conservation problems only in combination with other theories.

Acknowledgments

I thank N. H. Barton, K. Hindar, B.-E. Sæther, and the reviewers for helpful and critical comments on previous versions of the manuscript. This work was financially supported by a postdoctoral research fellowship from the Norwegian Research Council's program "Biological Diversity—Dynamics, Threats and Management."

APPENDIX

Reintroduction Based on Gomulkiewicz's Strategy

Without migration and with $\bar{z}$ initially at z_1 , we have

$$\bar{z} = z_1 e^{-Vst}. \quad (\text{A1})$$

The dynamics of N at low population densities is then given by

$$\frac{dN}{dt} = \left(r - \frac{s}{2} z_1^2 e^{-2Vst} \right) N. \quad (\text{A2})$$

If the population growth rate initially is negative, $r - sz_1^2/2 < 0$, the population declines until its growth rate becomes 0 at time

$$t_c = \frac{1}{-2Vs} \ln \frac{2r}{z_1^2}. \quad (\text{A3})$$

Substituting this expression for t_c into the expression for $N(t)$ obtained by solving equation (A2), we find that the minimum population size N_c at time t_c over the initial population size N_0 is given by

$$\ln \frac{N_c}{N_0} = -\frac{r}{2Vs} \ln \frac{2r}{sz_1^2} + \frac{r}{2Vs} - \frac{z_1^2}{4V}. \quad (\text{A4})$$

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Associate Editor: Michael J. Wade