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Immigration and the Dynamics of Peripheral Populations

ROBERT D. HOLT[1]

ABSTRACT. The influence of immigration upon the abundance and dynamics of peripheral populations should reflect the degree of genetic differentiation between residents and immigrants. The interplay of immigration, local dynamics, and natural selection in models of population growth is examined. Given that no genetic variation exists upon which local selection may act, and that a population is numerically stable, immigration should increase population size. In populations with discrete-time dynamics, immigration may either destroy or create local stability. If a population is unstable, an increase in the rate of immigration may reduce its average density. The introduction of haploid genetic variation dramatically changes the character of the relation between immigration rate and density. If fitnesses are density-dependent, in a stable, polymorphic population total density is independent of the rate of immigration. Decreasing the fitness of immigrants relative to residents may enhance the stabilizing influence of immigration. It is briefly argued that frequency-dependent fitnesses or diploid genetic variation with density-dependent fitnesses can produce an inverse relation between the rate of immigration and population size. These theoretical results suggest that the consequences of dispersal for population dynamics may be strongly influenced by the degree of local genetic adaptation that exists within a species.

INTRODUCTION

Patterns of dispersal are central to both island and continental biogeography, for the range ultimately occupied by a newly formed species depends upon that species' success as a colonizer (Williams, 1969). The importance of dispersal in other phenomena of ecology and evolution is not as well understood and has been the subject of considerable debate. Over the past two decades, evolutionists and ecologists have moved in curiously opposite directions in their views on the significance of dispersal in natural populations. In 1963, Ernst Mayr in *Animal Species and Evolution* strongly argued that "gene flow is the main factor responsible for genetic cohesion among the populations of a species . . . [and] one of the principal reasons for the slow rate of evolution of common widespread species." This view of gene flow as a significant homogenizing force was accepted evolutionary doctrine for many years but has recently come under increasing attack. The empirical and theoretical studies of Antonovics (1968), Endler (1977), Levin and Kerster (1974) and Slatkin (1978) (to note just a few prominent landmarks) have demonstrated that gene flow does not as a general rule effectively counter spatially varying selection. Many evolutionary biologists are now persuaded that even though gene flow can provide an important source of variation upon which selection might act, in most natural populations rates of gene flow are usually not great enough to prevent the evolution of local adaptation.

Until the early 1970's theoretical ecology consisted largely of glosses on the elegant mathematical edifice erected by Vito Volterra and Alfred Lotka fifty years earlier. This body of theory, designed to analyze the dynamics of spatially homogeneous populations, neglec-

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[1] Museum of Natural History and the Department of Systematics and Ecology, University of Kansas, Lawrence, Kansas 66045, U.S.A.

ted the possible significance of movement patterns in population processes. But in recent years the role of dispersal in local dynamics and interspecific interactions has become the focus of much research activity by theoretical ecologists (e.g., Levin, 1978; Okubo, 1980). Empirical evidence is steadily mounting that movement patterns affect both the mean density of populations and the pattern of fluctuations around that mean (Gaines and McClenaghan, 1980; Taylor and Taylor, 1977; Tamarin, 1977). We are left in the slightly awkward position of appearing to believe that dispersal is important in local ecological dynamics, but not in local evolutionary dynamics!

There is one circumstance for which all seem to agree that dispersal can be an important conservative evolutionary force. Peripheral populations in an ecotone often exist in low densities adjacent to populations at much higher densities. In such peripheral populations, natural selection favoring locally adapted alleles can be readily swamped by rates of immigration which are low in absolute numbers of individuals per unit time, but high in proportion to the peripheral population's low abundance (Antonovics, 1976). Mayr (1963) suggested that such regular disruption of local adaptations by immigration should be expected wherever a border population exists at low densities, and he argued that this process could produce evolutionary stasis at a species' border.

It is premature to judge the empirical adequacy of Mayr's model, as too little is known about the causes and dynamics of species' borders. However, the scenario is consistent with analytic studies of the countervailing influence exerted by gene flow upon local selection in low-density populations (e.g., Nagylaki, 1978). Hence, it is possible that gene flow neither accounts for the genetic cohesion of a species over its entire range, nor as a rule prevents local adaptation, yet does confer a kind of evolutionary stability upon that species' border.

In this paper I explore an ecological question suggested by Mayr's evolutionary hypothesis. What is the relationship between the rate of immigration into a population and that population's size? I will argue that the answer to this question should depend upon the existence and character of genetic variation in the species. Given that residents and immigrants are genetically identical, it seems intuitively reasonable to expect that as the number of immigrants increases, so should population size. Conversely, if immigrants and residents differ genetically, the average immigrant should be less fit in the local environment than is the average resident. The more immigrants there are, the lower the mean fitness of the population should be. We may reasonably conjecture that a sufficient reduction in mean fitness will decrease the size of the population.

Using verbal arguments alone it is difficult to gauge the relative magnitude of these two opposing consequences of immigration. I have therefore explored the effect of immigration upon the dynamics of peripheral populations in three classes of population models. In order of increasing complexity, these are continuous-time and discrete-time ecological models: 1) without genetics, 2) with haploid genetic variation, and 3) with diploid genetic variation. This paper discusses the first two classes of models. My studies of the third class of models—by far the most complicated—will be presented elsewhere, along with certain technical details of the models described below.

PERIPHERAL POPULATION MODELS: GENETICALLY HOMOGENEOUS POPULATIONS

The two general growth models to be discussed are

$$\frac{dN}{dt} = F(N) + I \qquad (1)$$

and $N(t + 1) = G(N(t)) + I$, or, equivalently,

$$\Delta N = G'(N(t)) + I \qquad (2)$$

where N is population density, F(N) and G(N) are growth functions, $G'(N) \equiv G(N) - N$, and I denotes immigration. Throughout this paper the rate of immigration is assumed to be temporally invariant, and the growth functions F and G are assumed to be continuous. A continuous-time differential equation such as (1) is strictly appropriate as a growth model only for populations with completely overlapping generations, negligible time lags and no variation in survivorship or fecundity with age. The quantity I is an instantaneous rate of immigration. The discrete-time difference equation (2) best describes populations in which age-classes or growth stages are temporally segregated, so that only one class is present at any time. If dispersal occurs during a single stage in the life history of the organism, and the population is censused immediately following each pulse of dispersal and immigration, equation (2) is an appropriate model for studying the influence of immigration upon population dynamics. Both models assume that there are no qualitative differences, including genetic differences, between residents and immigrants.

The three standard steps in the analysis of growth models such as (1) and (2) are as follows: 1) solve for point equilibria, N^*; 2) determine the local stability character of each equilibrium; 3) for model (2), attempt to understand the often complex dynamical behavior that may exist when populations do not have a stable point equilibrium. For any biologically reasonable model, in the absence of immigration there will be an equilibrium N^* of maximal size—the carrying capacity, K—above which the population has a negative growth rate. The number of equilibria found at densities below K is determined by the specific details of particular models.

IMMIGRATION AND POPULATION EQUILIBRIA

In model (1), equilibria are found by solving $F(N^*) + I = 0$. The local stability of each equilibrium is determined by the slope of the growth curve,

$$\lambda \equiv \frac{d}{dN}\left(\frac{dN}{dt}\right) = \frac{dF}{dN}$$

where the derivative is evaluated at $N = N^*$. If $\lambda < 0$, the equilibrium is locally stable, and if $\lambda > 0$ it is unstable. A population nudged away from an unstable equilibrium will converge asymptotically to a stable equilibrium. How does immigration shift the position of each equilibrium? By applying the chain rule of differentiation to (1) we have

$$\frac{dN^*}{dI} = -\left(\frac{dF}{dN}\right)^{-1} = -\lambda^{-1}, \left(\frac{dF}{dN} \neq 0\right).$$

Hence, the slope λ of the growth curve at an equilibrium determines both the stability of the equilibrium population and the way in which immigration shifts its density. Immigration increases the density of populations at locally stable equilibria and decreases the densities at which unstable equilibria occur. The quantity $|\lambda|$ measures the strength of density-dependence in the population; increasing $|\lambda|$ reduces the sensitivity of population size to changes in immigration rate. Regardless of the detailed form of the growth model, however, if a peripheral population is at its carrying capacity, $\lambda < 0$ and immigration will always increase that population's size.

A similar relation between the rate of immigration and equilibrial density holds in the discrete-time growth model. We find the equilibria by solving $G'(N^*) + I = 0$. By linearizing around N^* in the usual way it can be shown that the local stability properties of each equilibrium are set by the sign and magnitude of

$$\lambda' = \frac{dG'}{dN},$$

where the derivative is evaluated at N*. In general, three classes of equilibria are possible: 1) $\lambda' > 0$. A population deviating by a small amount from N* will monotonically diverge away from N*. 2) $-2 < \lambda' < 0$. The equilibrium is locally stable. 3) $\lambda' < -2$. The negative density-dependence at the equilibrium is so severe that the population repeatedly overshoots the equilibrium then crashes to low densities. The population ultimately settles into sustained oscillations around the locally unstable equilibrium; the character of these fluctuations depends upon the specific details of the full, nonlinear model. (May, 1976).

Applying the chain rule of differentiation again, we have

$$\frac{dN^*}{dI} = -\left(\frac{dG'}{dN}\right)^{-1} = -(\lambda')^{-1}$$

where $\frac{dG'}{dN}$ is evaluated at N*. Hence, if $\lambda' > 0$, immigration reduces the density at which equilibrium occurs, and if $\lambda' < 0$, population size increases with immigration.

A simple graphical illustration of this conclusion is shown in Figure 1. The solid line marks a growth curve G(N) of an isolated peripheral population. There are two stable nontrivial equilibria (points 1 and 3 in the figure) and one unstable equilibrium (point 2). In a comparable but less isolated population with I immigrants entering per generation, the growth curve is G(N) + I. Adding a constant rate of immigration I to the growth equation is geometrically equivalent to a rigid, vertical translation of the growth curve graph by I units. The dashed line in the figure portrays the growth curve of the less isolated population. It can be seen that the influx of immigrants has pushed the population well above its carrying capacity and has caused the paired equilibria at lower densities to disappear entirely. As the rate of immigration is increased, populations are less likely to be trapped at such low-density equilibria.

IMMIGRATION AND POPULATION STABILITY IN DISCRETE-TIME GROWTH MODELS

Given that a population is locally stable, we have seen that immigration should increase population size. But if negative density-dependence is too severe at high densities, populations may exist in a permanent state of fluctuation around an unstable point equilibrium. This suggests the following two questions about the impact of immigration upon a peripheral population. Can immigration destabilize an otherwise stable population, or, conversely, can immigration impose stability onto an unstable, fluctuating population? Given that a

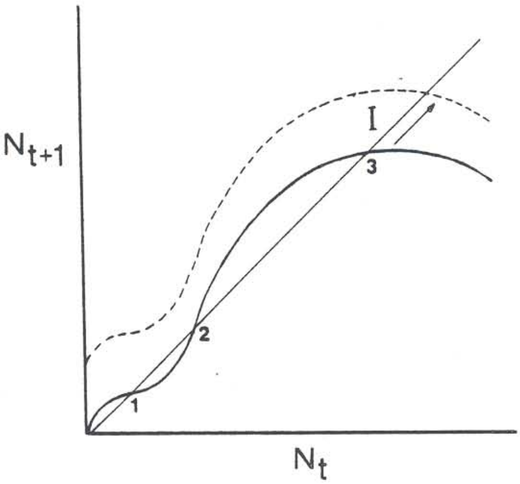

Figure 1. The effect of immigration upon equilibrium density in a discrete-time model. Equilibria occur where G (N), the curved line, crosses the straight, 45° line. Adding a constant amount of immigration raises the growth curve uniformly and equilibrium 3 increases, whereas the other equilibria vanish.

population is varying cyclically or chaotically, how does immigration modify the distribution of densities shown by the population over time?

As immigration increases, the slope of the growth curve at an equilibrium where $\lambda' < 0$ changes according to

$$\frac{\partial \lambda'}{\partial I} = \left(\frac{d^2G}{dN^2}\right)\left(\frac{dN^*}{dI}\right).$$

Given a growth curve that is concave downward,

$$\frac{d^2G}{dN^2} < 0 ,$$

immigration will push the population toward levels of increasingly severe density-dependence and may even destabilize an intrinsically stable peripheral population. Conversely, immigration may stabilize a population whose growth curve is concave upward—

$$\frac{d^2G}{dN^2} > 0.$$

Therefore the effect of immigration upon population stability is determined by the concavity of the growth curve G(N).

Standard discrete-time models provide ready examples of both effects. One model for which immigration is destabilizing is the discrete logistic equation

$$N(t+1) = N(t)\,(1 + r - \frac{r}{K}\,N(t)) + I \quad (3)$$

where r is the intrinsic growth rate. The stability properties of this model without immigration are well–understood (May and Oster, 1976; Roughgarden, 1979). In the Appendix, I outline the stability character of the discrete logistic with immigration. Figure 2 depicts the stability domains of this model. (The dashed and dotted lines are explained in the Appendix.) The overall impression from this figure is that immigration reduces or eliminates stability in the peripheral population.

By contrast, in other models immigration may stabilize an intrinsically unstable population. Figure 3 shows the results of a local stability analysis of the following model:

$$N(t+1) = N(t)\exp[r(1 - N(t)/K)] + I \quad (4)$$

With no immigration and $r < 3$, the dynamics of this model resemble those of (3) May (1976). As immigration increases, the domain of unstable behavior diminishes. The contrast between Figures 2 and 3 is striking. In a more detailed analysis it can be shown that the opposing consequences of immigration for the two models are due to the downward concavity of (3) and the upward concavity of (4) at high values of r and N.

Numerical studies of a number of discrete-time models were carried out in order to ascertain how immigration modifies the temporal distribution of densities in cyclic or chaotic populations. In such populations, a reasonable measure of abundance is the arithmetic time-average of densities

$$<N> = \frac{1}{T}\sum_{t=1}^{T} N(t).$$

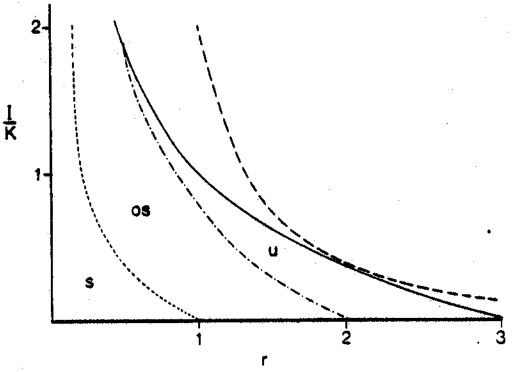

Figure 2. Stability regions for the discrete logistic (3). s = monotonic return to equilibrium. os = oscillatory return to equilibrium. u = locally unstable (stable cycles or chaos). The solid line is the largest value of I allowing non-negative numbers for G(N). The dashed line is the outer bound of the unstable region for the modified logistic model discussed in the Appendix.

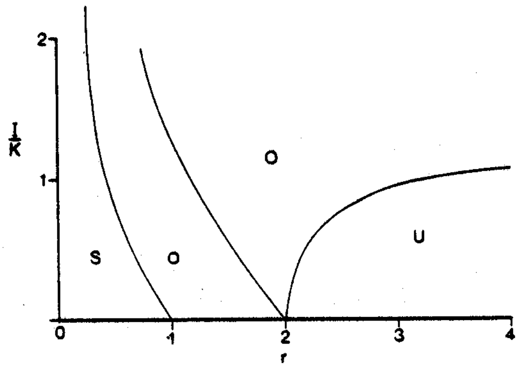

Figure 3. Stability regions for the exponential logistic (equation 4). s = monotonic stability. o = oscillatory stability. u = unstable. The central line in the o region separates parameter choices where an increase in I decreases the rate of return to an equilibrium (to the left) from those parameters where I effects a faster return (to the right).

In cyclic populations the appropriate value for T is one cycle length, whereas in a chaotic population a large number of generations per run starting from a number of initial conditions may be required to fully characterize <N>.

What is the relationship between average density and the rate of immigration? An example of a pattern that emerged repeatedly in the simulations is depicted in Figure 4. The model used for this figure has been extensively exploited by insect ecologists (e.g., Hassell, 1975). With an added immigration term the growth model is

$$N(t + 1) = N(t)e^{r} (1 + dN(t))^{-b} + I. \quad (5)$$

The four curves in the figure correspond to four values for the intrinsic growth rate, r. At I=0 and high r, populations obeying equation (5) fluctuate, sometimes greatly, around an unstable point equilibrium. In these unstable populations, <N> does not increase monotonically with I. The influx of a few immigrants per generation may dramatically increase <N>, and a yet greater rate of immigration may actually *decrease* <N>.

This nonmonotonic relation between <N> and I has a simple explanation. In discrete-time growth models such as (5), populations with high intrinsic growth rates tend to exhibit chaotic behavior (May, 1976). Time-series of populations in chaos typically show overshoots of K followed by precipitous declines in abundance. Following each population crash, several generations may elapse before population numbers are sufficiently large to produce a high total growth rate, culminating in another explosive overshoot and crash. Even a slow trickle of immigrants can greatly reduce the number of generations between successive overshoots. In model (5), population growth is essentially geometric at densities well below K. If N(0) is the number in the population immediately following a crash, the population size t generations later is approximately

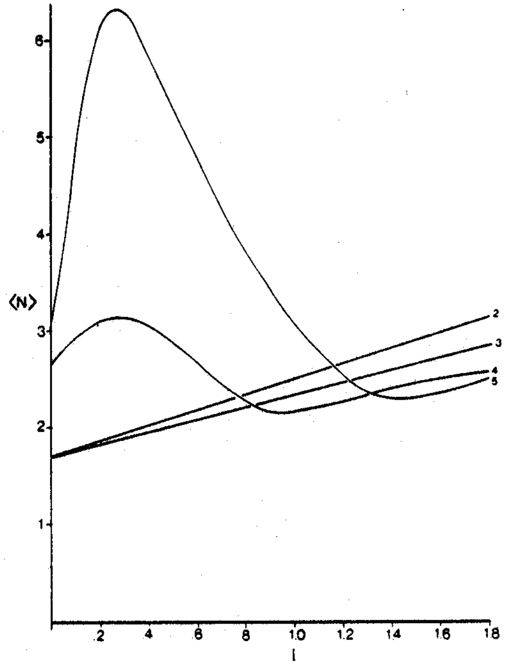

Figure 4. Time-averaged densities for model 5. The numbers labelling the curves are the intrinsic growth rates. The other parameters are d = 1, and b = r. For populations exhibiting chaotic behavior, the lines represent the average over many runs of 5,000 generations length, starting over a range of initial densities.

$$N(t) \cong N(0)e^{rt} + I\sum_{s=0}^{t-1} e^{rs}$$

given that numbers remain low enough for negative density-dependence to be negligible. From this expression it is clear that the time required to reach a given $\tilde{N}$ (e.g., an $\tilde{N}$ such that $G(\tilde{N}) > K$) from N(0) may be substantially shortened by regular immigration. This reduction in the amount of time needed for recovery from a population crash increases the number of generations at high densities, and therefore increases <N>. At higher rates of immigration, density-dependence among the immigrants themselves tends to diminish the magnitude of the overshoot. In model (5), this diminution leads to a decrease in <N>.

We can summarize the above results as follows: 1) Given no genetic differentiation between immigrants and residents, immigration should increase the density of stable peripheral populations. 2) The concavity of the growth curve determines the relation between immigration rate and stability. And finally, 3) in fluctuating peripheral populations, an increase in the rate of immigration may decrease the average size of the population.

PERIPHERAL POPULATION MODELS: THE EFFECT OF HAPLOID GENETIC VARIATION

The conjecture to be examined is that genetic differentiation between immigrants and residents alters the functional relationship between the rate of immigration and population size. In the remainder of this paper I explore the properties of models which incorporate a particularly simple kind of genetics—haploid variation with two alternative alleles at a single locus. One allele—type 1—is fixed within the species' main range, and so all immigrants are type 1, whereas the other allele—type 2—is selectively favored in the peripheral population. To explore how the balance between selection and immigration affects both the gene frequency and population size, we modify models (1) and (2) as follows.

Counting gene *numbers*, the appropriate generalization of model (1) is

$$\begin{aligned} \frac{dN_1}{dt} &= N_1\, \phi_1\, (N_1, N_2) + I \\ \frac{dN_2}{dt} &= N_2\, \phi_2\, (N_1, N_2) \end{aligned} \tag{6}$$

where N_i is the density of type i (i=1,2), ϕ_i is the *per capita* instantaneous growth rate or the absolute fitness of type i, and I is the immigration rate of type 1. The total population size is defined as $N = N_1 + N_2$, the gene frequency of allele 1 is $p = N_1/N$, and the gene frequency of allele 2 is $q = 1 - p$. The mean fitness of the population is $\bar{\phi} = p\phi_1 + q\phi_2$. An alternative representation of system (6) is obtained by differentiating N and p with respect to t

$$\begin{aligned} &\frac{dN}{dt} N\bar{\phi} + I \\ &\frac{dp}{dt} = pq(\phi_1 - \phi_2) + q\frac{I}{N}. \end{aligned} \tag{6'}$$

In like manner, we may embody haploid genetic variation within the framework of the discrete-time model (2) as follows:

$$\begin{aligned} N_1(t+1) &= N_1(t)g_1(N_1, N_2) + I \\ N_2(t+1) &= N_2(t)g_2(N_1, N_2) \end{aligned} \tag{7}$$

or, equivalently,

$$\begin{aligned} \Delta N &= N(\bar{g} - 1) + I \\ \Delta p &= \frac{pq(g_1 - g_2) + q\frac{I}{N}}{\bar{g} + \frac{I}{N}} \end{aligned} \tag{7'}$$

where g_i is the per-capita growth rate or absolute fitness of type i and $\bar{g} = pg_1 +$

qg_2 is the mean fitness of the population. The analysis of these two models proceeds through the usual steps of first solving for equilibria (N^*, p^*), determining the local stability of each equilibrium, and then examining the behavior of the model away from equilibria. Models (6)′ and (7)′ explicitly display the genetic character implicit in models (6) and (7).

DENSITY-DEPENDENT SELECTION

It is difficult to make much headway without specifying in more detail the fitness functions ϕ_i and g_i. A selective regime that has received a great deal of attention from population biologists is density-dependent selection, for which ϕ_i and g_i may be written as functions of total density N, $\phi_i(N)$ and $g_i(N)$ (Roughgarden 1971, 1976; Charlesworth 1971, 1980; Asmussen, 1979). A significant finding of these theoretical studies is that if fitnesses are strictly density-dependent, and the population is stable, natural selection adjusts gene frequencies in such a way that population density is locally maximized at the joint demographic and genetic equilibrium.

First consider the continuous-time model (6). To simplify the analysis, I assume that each allele has a carrying capacity K_i such that $\phi_i(K_i) = 0$, and that there is negative density–dependence at all densities:

$$\frac{d\phi_i}{dN_i} < 0.$$

In the absence of immigration, it is straightforward to show that the allele with higher K excludes the alternate allele. Since type 2 is assumed to be locally favored, $K_2 > K_1$ and the population equilibrates at K_2.

As the rate of immigration increases, so does the frequency of type 1. However, given that the population is polymorphic for both alleles, population size is *independent* of the rate of immigration. For the population to be at its equilibrium (N^*, p^*) both growth rates in (6) must equal 0, so $N_2^*\phi_2(N^*) = 0$. As the population is assumed to be polymorphic, $N_2^* > 0$. Thus $\phi_2(N^*) = 0$. But by assumption, $\phi_2 = 0$ only when $N^* = K_2$. Therefore, the total population size remains at K_2 as the rate of immigration increases. Immigration does not change the total population size, but instead shifts the relative proportions of the two types. From (6′) we find that

$$p^* = \frac{-I}{K_2\phi_1\ (K_2)}$$

(since $K_2 > K_1$, $\phi_1(K_2) < 0$). Hence, a polymorphic equilibrium exists only if $I < |K_2\phi_1(K_2)|$. In the Appendix it is shown that the equilibrium

$$(N^*,\ p^*) = \left(K_2, \frac{-I}{K_2\phi_1(K_2)}\right)$$

is both locally and globally stable.

Thus we have completely characterized the interplay of immigration and selection in a general, haploid model of density-dependent selection. As long as $I < |K_2\phi_1(K_2)|$, immigration merely shifts the genetic composition of the peripheral population without changing its total density at all. The opposing ecological and genetic effects of immigration discussed in the introduction exactly cancel each other out.

By a parallel argument it can be shown that the comparative statistics of the discrete-generation model (7) are identical to those of the continuous-generation model. Given fitnesses that are density-dependent, equilibrial densities are independent of the rate of immigration in polymorphic populations. As with the purely ecological models discussed earlier, the principal difference between models (6) and (7) is that the latter may exhibit sustained oscillatory behavior. The point equilibrium of (7) is locally stable only if the magnitude of the real part of the dominant eigenvalue λ is less than unity. Let

$$a_{ij} \equiv \frac{\partial}{\partial N_j}(N_i g_i).$$

Then the two eigenvalues are

$$\lambda = [a_{11} + a_{22} \pm ((a_{11} - a_{22})^2 + 4a_{12}a_{21})^{1/2}]/2.$$

As both a_{12} and a_{21} are negative, the discriminant is positive and both eigenvalues are real numbers. We wish to understand how immigration alters the stability properties of a peripheral population, and how immigration perturbs average abundance in unstable populations. Substituting explicit fitness functions such as (3) or (4) leads to cumbersome masses of algebra from which it is difficult to extract necessary and sufficient conditions for local stability. However, it is plausible that if immigration reduces the frequency of a locally favored allele, the peripheral population could be made more stable. In discrete-time population models, the intrinsic growth rate r typically "tunes" the dynamic behavior of the model—the magnitude and period of oscillations usually increase with r. As immigrants are assumed to be less fit than residents, the values of r, or K, or both, for the immigrant should be lower. Diluting a population at high r with an admixture of immigrants with lower r should reduce the average r of the population as a whole, and therefore tend to stabilize an unstable peripheral population.

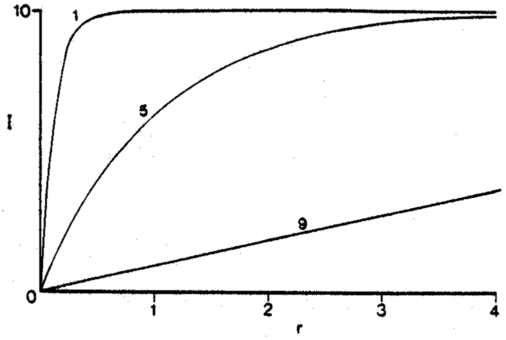

Figure 5. Maximum rate of immigration I permitting polymorphism in model 7 with equation 4 as a fitness function. K_2 = 10. $r_1 = r_2$. K_1 is denoted by the number marking each curve.

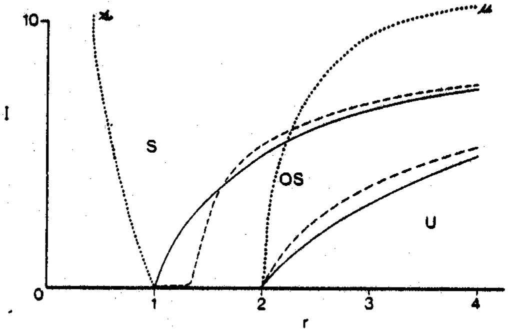

Figure 6. Stability regions of model 7 with fitnesses given by 4 . s = monotonically stable. os = damped oscillations. u = unstable. The solid lines mark the edges of stability regions for K_1 = 1, and the dashed lines for K_1 = 5. The dotted lines are from Figure 3 and depict the stability character of a population in which the immigrants are type 2.

In like manner, a lower tolerance of crowding in immigrants ($K_1 < K_2$) may enhance the stabilizing effect of immigration. As a particular example, consider a population with discrete generations in which the fitnesses of each type are described by $g_i(N) = \exp[r(1 - N/K_i)]$. The two alleles share the same r but differ in K. If the rate of immigration is too great, the polymorphism will not persist. As depicted in Figure 5, the maximum I consonant with polymorphism varies with both r and K_1. The local stability properties of this model are displayed in Figure 6. We have already observed that immigration is weakly stabilizing in this model when immigrants are of the same genetic type as the residents; the dotted lines, lifted from Figure 4, demarcate transitions from monotonic to oscillatory stability (left line) and from locally stable to unstable point equilibria (right line). The solid lines demarcate the edges of the corresponding stability regions for immigrants with $K_1 = 1$, and in like manner the dashed lines for $K_1 = 5$. Decreasing the carrying capacity of the immigrants heightens the stabilizing influence of immigration.

In discrete-time haploid models such as (6), as in the purely ecological model (2) discussed above, instability may complicate the relation between immigration and population size. In numerical studies I have found that polymorphisms are difficult to maintain if the demographic attributes of each type lead to severe oscillations in monotypic populations. In a stable population, a low immigration rate produces a low frequency of the immigrant type. The same rate of immigration can lead to a much higher gene frequency and even fixation in an unstable population, for the simple reason that following a population crash a few immigrants may comprise a sizeable fraction of the total population. During these crashes the locally adapted type can go extinct because of genetic drift, while immigration steadily replenishes the less fit type. Gene flow should hamper local adaptation more readily in unstable than in stable peripheral populations.

If the polymorphism does persist, over the course of population fluctuations high densities are correlated with low frequencies of the immigrant type. In the particular model used for Figures 5 and 6, the time-average of density, <N>, seems to be independent of I, but in other haploid models <N> may decrease with increasing I.

From this analysis of density-dependent selection in haploid populations, we may conclude that 1) the rate of immigration does not affect the total density of stable, polymorphic populations; 2) decreasing the fitness of immigrants relative to residents strengthens the stabilizing effect of immigration upon population dynamics; and 3) the maintenance of local adaptation in the face of gene flow is unlikely in severely fluctuating populations.

OTHER GENETIC MODELS

Two obvious generalizations of this model are to employ more general fitness functions in (5) and (6) and to develop comparable diploid models. Space limitations preclude a full treatment of these extensions here, so I will merely outline a few salient changes in the results produced by these modifications in the models. If the absolute fitness functions in models (5) or (6) are functions of the separate densities of the two types rather than of their summed density, the selective regime is a mixture of density-dependent and frequency-dependent selection. Alternative stable states may exist (Fenchel, 1975). For the continuous-time model (6), if the population is at a stable equilibrium, it can be shown that

$$\frac{dN^*}{dI} = \frac{dN_1{}^*}{dI} \left(1 - \frac{\partial\phi_2/\partial N_1}{\partial\phi_2/\partial N_2}\right)$$

where the partial derivatives are evaluated at $(N_1{}^*, N_2{}^*)$. Since immigration increases the density of N_1, the overall effect of immigration upon the total population hinges upon the relative magnitudes of the derivatives $\partial\phi_2/\partial N_1$ and $\partial\phi_2/\partial N_2$. If absolute fitnesses are determined solely by the total density of the population,

$$\frac{\partial\phi_2}{\partial N_2} = \frac{\partial\phi_2}{\partial N_1},$$

and N^* is independent of I. Immigrants that exert a disproportionate effect on the fitness of residents, compared with the effect of residents upon themselves,

$$\frac{\partial \phi_2}{\partial N_1} > \frac{\partial \phi_2}{\partial N_2},$$

decrease the total size of the population.

Even without immigration the diploid equivalents of (6)′ and (7)′ can manifest a rich panoply of behaviors. Asmussen (1979) has analyzed a discrete-generation model of density-dependent selection in which (4) served as a fitness function. She demonstrated the existence of regular and chaotic cycling in both population size and gene frequency. In contrast to classical selection models, heterozygote superiority in crowding tolerance is not required for the maintenance of genetic variation in these cyclic populations. All these features are retained in the models with immigration. An additional feature of the diploid models is that the relationship between immigration and population size depends upon the dominance relations of alternative alleles in the peripheral population. For instance, consider an allele that is simultaneously genetically dominant yet locally unfit. An increase in the rate of immigration of individuals bearing that allele has three distinct effects, two of which were discussed above. First, there is the ecological effect of increasing density by increasing the influx of individuals into the population; this corresponds to a purely ecological model such as (1). Second, if fitnesses are density-dependent, this increase in density lowers the fitness of the locally favored genotype, the numbers of which will decline until the overall density of the population is unchanged; this accounts for the uncoupling of immigration rates and equilibrial densities in the haploid models (6) and (7). Third, since in a Mendelian population the average fitness of the offspring produced by a genotype is partially determined by the array of genotypes available for mating, the more immigrants there are, the more the fitness of the resident's offspring will be diluted by cross-matings. The number of residents declines even further to compensate for this mating effect. The final pattern is an inverse relation between immigration rate and population density. By contrast, if the immigrant allele is recessive the mating effect is greatly diminished, and, just as in the haploid model, population size may be essentially independent of the rate of immigration.

A third theoretical approach, and one that ultimately might be the most profitable, is to extend quantitative genetic models of phenotypic evolution (Lande, 1976) in order to examine how immigration by individuals with nonoptimal phenotypes in one or more character states influences population size in density-regulated populations. Antonovics (1976) and Slatkin (1978) suggest some promising lines of development for such a theory.

DISCUSSION AND CONCLUSIONS

I have argued that two characteristics of a peripheral population should mold the functional relation between immigration rate and population size—its dynamic stability, and the degree of its genetic adaptation to the local environment. To begin understanding the dynamics of a peripheral population we must first isolate those factors responsible for its low population density. It is widely believed that density-independent factors act more severely in peripheral than in central populations. For instance, Mayr (1963) asserts that "the border region is a place in the area of a species where density-dependent factors are of minor importance." Alternatively, the peripheral population may be rare because of an increase in the intensity of density dependence. In populations with delayed density-dependence, these two explanations for rarity at a species' border have fundamentally different implications. If rarity results from a high rate of density-independent mortality the intrinsic growth rate of the population will be low and the population will stably persist at its carrying capacity, at least in temporally constant environments. By contrast, if r is high but K is low, the population may exhibit fluctuations of considerable magnitude around K, sometimes to the point of extinction. As the demographic and genetic consequences of immigration depend upon the stability character of the peripheral population, the first step in gauging the role of immigration should be to try to understand the causal basis for population fluctuations at the species' border.

Immigration may not change, or may even decrease, the density of a population that has adapted to its local environment. Scant data exists for testing this idea, in part because the requisite evidence is technically difficult to obtain. As noted above, there recently has been a de-emphasis of gene flow as a constraint on the evolution of local adaptation. To the extent that this view is valid, we should expect the predicted phenomenon to be rarely observed. An additional reason for the rarity of relevant data, however, is that many ecologists simply assume that organisms are well adapted to their environment. Although usually reasonable, in peripheral or ecologically marginal populations this assumption may well be false. I know of two possible examples of local maladaptation in peripheral populations resulting from gene flow. Camin and Ehrlich (1958) argued that on islands in Lake Erie a balance between migration and selection maintained a polymorphism in banding patterns of water snakes (*Natrix sipedon*). A substantial fraction of the island populations had locally unfit banding patterns. Stearns and Sage (1980) have suggested that the life-history traits of one freshwater population of the mosquito-fish (*Gambusia affinis*) might be best interpreted as maladaptation to the freshwater environment. Gene flow from a nearby brackish-water population may account for the apparent lack of local adaptation in this population. In neither instance is anything known about the effect of the apparent maladaptation upon population density. Comparable situations might well exist in many organisms with passive dispersal or territoriality residing in locally heterogeneous environments. For instance, were the habitat of a species of *Anolis* a mosaic of high and low quality patches, territorial behavior could lead to a steady flow of individuals into low density patches. This influx could reduce the efficacy of selection for better adaptation to the low-quality patch type.

A critical and very difficult empirical problem is to gauge the relative magnitudes of spatial scales associated with dispersal, selection, and nonselective determinants of density. Slatkin (1973) has suggested that a useful quantity for understanding evolution in spatially structured populations is the ratio between the average dispersal distance and a measure of the gradient in selection. If this ratio is small, a species should closely track spatial variation in selection (Roughgarden, 1979); since immigrants into a population are drawn primarily from nearby populations, and nearby populations experience similar selective regimes, immigrants should genetically resemble residents. In this case the purely ecological models discussed above are appropriate. By contrast, if the ratio is large, many immigrants will be from relatively distant populations with different selection pressures, and immigrants may differ greatly from the locally favored type. Understanding the role of immigration in population dynamics in this case requires a blending of ecology with genetics.

For the rate of immigration to be large enough, relative to carrying capacity, to qualitatively perturb the abundance or dynamics of a peripheral population, there usually must be a second, more abundant population in reasonable proximity to the first—a sharp spatial gradient in densities should exist. This density gradient need not correspond to a comparable selection gradient, since many factors that affect density do so indirectly. For instance, a consumer such as a detritivore may be able to alter the abundance, R, but not the rate of renewal of its resource. Individual consumers are food–limited, and there is no direct interference among them, we can write the *per capita* consumer growth rate as some increasing function of resource abundance, Y(R). The consumer population should grow until its collective demand has reduced resource availability to some level, C, at which each consumer just replaces itself with a single descendent. If the parameters determining the form of Y and the quantity C are spatially invariant, selection will act uniformly on these parameters throughout the consumer's range. However, the number of consumers present at equilibrium is determined indirectly by the renewal rate of the resource, which might well vary greatly over space. Hence, a consumer's density may be highly variable in space even though selection is not; dispersal could then be of more consequence for the ecology than for the evolution of the species. In other circumstances, of course, density gradients may closely match selection gradients.

The degree to which ecological phenomena are influenced by intraspecific genetic variation is a problem of great current interest. I have here argued that the ecological consequences of dispersal into a population depend upon whether or not immigrants differ genetically from residents. In the study of species' borders, in particular, it should be realized that ecological and genetical phenomena may be inextricably entangled.

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APPENDIX

THE DISCRETE LOGISTIC MODEL

Without immigration, the single nontrivial equilibrium is $N^* = K$, and the stability-setting eigenvalue is $\lambda = 1-r$. N converges asymptotically to K if $r < 2$. Stable limit cycles occur when $2 < r < 2.828$, whereas for $2.828 < r \leq 3$ the population exists in a chaotic regime in which the long-term behavior of any particular population depends upon its initial conditions; the behavior may be either periodic or aperiodic (May and Oster, 1976). Given $r > 3$, the model can predict negative densities; to preclude this biological absurdity we require that $r \leq 3$. In like manner, as I increases we would like to ensure that population production G(N) is never negative. For the discrete logistic, a population minimum occurs during the generation immediately following a maximum. The maximum value of $N(t + 1)$ occurs at the critical point $(N(t) = (K(1 + r)/2$ of (3), so $\max N(t+1) = \frac{K(1+r)^2}{4r} + I$. If we require that $G(\max N) \geq 0$, we find that the ratio I/N is bound by the following expression:

$$\frac{I}{K} \leq \frac{1}{2} + \frac{3}{4r} - \frac{r}{4}.$$

This bound on I/K is the dotted line of Figure 2. We can avoid the annoying possibility of negative densities by simply setting $N(t+1) = I$ whenever $G(N)$ is a negative quantity, which occurs whenever

$$N(t) > K\ \left(\frac{1+r}{r}\right).$$

For this modified discrete logistic, the dashed line in the Figure is an *upper* bound on the parameter values that allow fluctuating densities.

Let $Y = (1 + 4I/rK)^{1/2}$. Then $N^* = K(1+Y)/2$, and the eigenvalue is $\lambda = 1 - rY$.

As N^* increases with increasing I, λ decreases. The maximum r consistent with local stability is

$$r = 2((I^2/K^2 + 1)^{1/2} - I/K).$$

THE STABILITY OF THE CONTINUOUS-TIME HAPLOID MODEL (6)

The two eigenvalues are

$$\lambda = [a \pm (a^2 - 4\phi_1 N_2 \frac{d\phi_2}{dN})^{1/2}]/2,$$

where

$$a = \phi_1 + N_1\frac{d\phi_1}{dN} + N_2\frac{d\phi_2}{dN}.$$

Since the quantities

$$\phi_1,\ \frac{d\phi_1}{dN},\ \text{and}\ \frac{d\phi_2}{dN}$$

are all negative at $N = K_2$, $a < 0$. This implies that $\mathrm{Re}(\lambda) < 0$. Moreover, straightforward manipulations show that the separatrix

$$a^2 - 4\phi_1 N_2 \frac{d\phi_2}{dN}$$

is positive, so (N^*, p^*) is a stable node. The per capita growth rates of type 1 and 2 were assumed to be negatively density-dependent at all densities. Applying Theorem (2) of Hastings (1978) we find that the equilibrium is globally stable. The critical assumption required for this result is that the fitness of both types depends only upon the total density of the population.

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