MODELS FOR PERIPHERAL POPULATIONS:
THE ROLE OF IMMIGRATION

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The movement of organisms over space has manifold consequences for both the ecology (Levin, 1976; McMurtrie, 1978) and genetics (Endler, 1977; Karlin, 1982) of populations. In this paper I examine how the rate of immigration influences the size, stability and genetic composition of a peripheral population. I contrast two classes of discrete-generation population models. (Comparable continuous-time models have been discussed elsewhere (Holt, 1983).) In the first, immigrants are genetically identical to residents, whereas in the second, immigrants differ at a haploid locus and are less fit in the local environment. For both we can ask how the rate of immigration affects equilibrial population density, N^*, local stability, and the pattern of fluctuations around N^* in unstable populations. For the genetic model we must also determine conditions for the persistence of a polymorphism. The study of the maintenance of pockets of local adaptation in the face of gene flow is a classical problem in population genetic theory (Haldane, 1930; Nagylaki, 1977). Here I place this problem into an ecological context. If selection coefficients are functions of population density, and immigration can change population size, I show that we cannot understand the ecological consequences of immigration without also understanding the genetic consequences.

Peripheral populations may exist at a species' geographical border or in marginal habitats within a species' range. Such populations are important in the study of factors limiting species' distributions (Krebs, 1978), and as crucibles for speciation (Mayr, 1963). I assume that non-peripheral populations collectively comprise a "bath" (Levin, 1976) from which immigrants are drawn. If relative to the bath a peripheral population is small in size, its population dynamics and genetic composition may be strongly perturbed by immigration, yet it may exert negligible reciprocal effects on the bath.

The first, purely ecological model is for a peripheral population with non-overlapping generations in a constant environment. If there is no immigration, the dynamics are described by the recursion $N_{t+1} = G(N_t)$. I assume that $G(0) = 0$, that there exist a unique positive equilibrium $N^* = G(N^*) \equiv K$, (the carrying capacity) and at most a single critical point N_c, $0 < N_c < K$, and that $dG/dN \leq 1$ for $N > N_c$. Geometrically, the growth function $G(N)$ may either rise monotonically with N or have a "hump". Each generation $\hat{I}$ immigrants enter the population. If we census immediately after immigration, the population model is $N_{t+1} = G(N_t) + \hat{I} \equiv F(N_t)$. Prout (1980) has cautioned that a full understanding of the implications of discrete-generation models requires a careful specification of the census stage being used. By censusing after rather than just before immigration, we highlight

the similarity between the effects of immigration in discrete-time and continuous-time models (Holt, 1983). The stability properties of discrete-time growth models have received considerable attention in the literature of mathematical ecology (May and Oster, 1976; Guckenheimer et. al., 1977). The map $F(N)$ is locally stable with monotonic or oscillatory convergence to N^* if $|\lambda| < 1$, where $\lambda \equiv dF/dN|_*$. If unstable, the population exhibits stable limit cycles or 'chaotic' behaviour around N^*. How does population size and stability vary with $\hat{I}$? Since $dN^*/d\hat{I} = (1 - dG/dN|_*)^{-1} = (1 - \lambda)^{-1} > 0$, an increase in the rate of immigration always increases equilibrial density. The effect of immigration on population stability depends upon the shape of $G(N)$. Since $d\lambda/d\hat{I} = (d^2G/dN^2)|_*(dN^*/d\hat{I})$, immigration may destabilize populations with growth curves convex at N^*, and, conversely, stabilize populations with concave growth curves. As examples of these disparate effects, consider two familiar discrete-time versions of logistic growth: the linear-logistic, $N_{t+1} = N_t(1 + r(1-N_t/K)) + \hat{I}$, and the exponential-logistic, $N_{t+1} = N_t \exp(r(1-N_t/K)) + \hat{I}$. The dynamics of some natural populations are reasonably described by the latter model (Hassell, 1978). At $\hat{I} = 0$ the two models have similar stability properties (May and Oster, 1976). Figure 1 compares their stability domains as a function of $\hat{I}$. The infeasible region in Figure 1B exists because $G(N) < 0$ if $N > K(1+r)/r$ - a biological absurdity. A simple modification of the linear-logistic is to let $N_{t+1} = \hat{I}$ wherever $G(N) < 0$. With this change, the population persists stably at $N^* = \hat{I}$ when $\hat{I}/K > (1+r)/r$. At lower $\hat{I}$, $\lambda = 1 - r(1+4\hat{I}/Kr)^{\frac{1}{2}}$, and the population is locally unstable if $(4-r^2)/4r < \hat{I}/K < (1+r)/r$. The influence of immigration upon population stability is hence model-dependent. In the modified linear-logistic, immigration may destabilize a peripheral population, although population stability re-emerges at very high rates of immigration. By contrast, in the exponential-logistic a small influx of immigrants may suffice to produce point or cyclic stability. Little is known about the shapes of growth curves and the magnitudes of growth parameters characterizing natural peripheral populations. $\hat{I}$ could exceed K if a peripheral population is at one end of a steep spatial gradient in density. Whether r is high or low should depend on the mechanisms responsible for low density. If K is low because of high rates of density-independent mortality, so too should r be low, and the peripheral population should be dynamically stable in a stable environment. Conversely, r may be high even though K is low. For example, in MacArthur's resource-consumer model, if resources equilibrate rapidly the consumer follows a logistic-like growth model (Schaffer, 1981). The expression for K is proportional to resource productivity, and K may be low even though r, which depends upon the maximal standing crop of the resource, is high.

Vandermeer (1982) remarks that a highly chaotic population will be rare much of the time - after a population crash, several generations must pass before numbers suffice to overshoot K once again. A constant flow of immigrants reduces the time
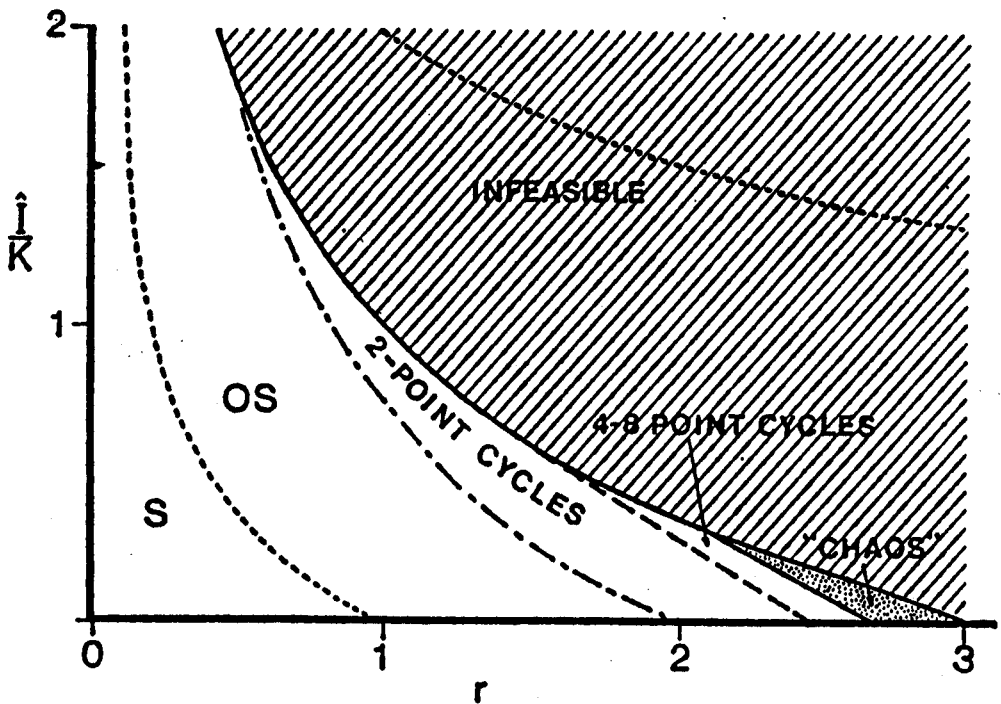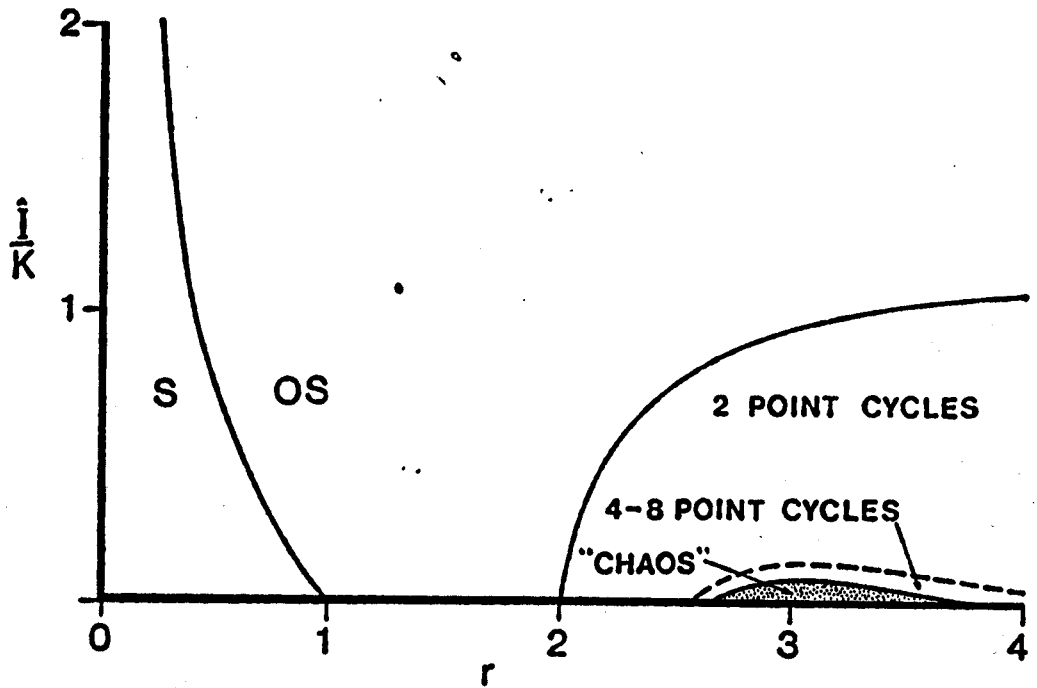
Figure 1 Stability regions for the exponential-logistic (a) and linear-logistic (b)

Figure 1 (continued) The lines demarcating zones of monotonic convergence (s), oscillatory convergence to N^* (os), and two-point cycles were found using the methods outlined in May and Oster (1976). The regions marked "chaos" are those in which numerical simulations produced cycles of period > 8 and seemingly aperiodic behavior. The region in (b) marked "infeasible" contains parameter values which necessarily give rise to negative N for the unmodified linear-logistic. The region above the dotted line, $\hat{I}/K = (1+r)/r$, is stable in the modified linear-logistic.

elapsing between successive overshoots. This effect seems to account for the creation of cycles out of chaos in the exponential-logistic model. It also partially explains the non-monotonic relation between the time-average of density over τ generations ($\langle N \rangle \triangleq (\Sigma N(i))/\tau$) and $\hat{I}$ found in fluctuating populations and illustrated in Figure 2. The behaviour of decreasing $\langle N \rangle$ with increasing $\hat{I}$ contrasts with the monotonic increase of N^* with $\hat{I}$ expected in populations at a stable point equilibrium.

The dependence of the size of stable populations upon $\hat{I}$ does not hold if immigrants differ genetically from residents. To sharpen the contrast between the genetic and non-genetic cases, consider a haploid model where all immigrants contain allele 1, but allele 2 is selectively favored in the peripheral population. Populations are censused just afer immigration. If g_i is the absolute selective value of type i, the model is

$$N_1(t+1) = N_1(t)g_1 + \hat{I}, \quad N_2(t+1) = N_2(t)g_2. \tag{1}$$

$N_i g_i$ corresponds to the growth function G. The carrying capacities are defined by $g_i(K_i) = 1$. An equivalent representation is

$$\Delta p = \frac{pq(g_1 - g_2) + q\hat{I}/N}{\bar{g} + \hat{I}/N}, \quad \Delta N = N(\bar{g}-1) + \hat{I}$$

where $N = N_1 + N_2$, $p = N_1/N$, $q = 1 - p$, and $\bar{g} = pg_1 + qg_2$ (the mean fitness). Comins (1977) has discussed a related model for how immigration hampers the evolution of pesticide resistance. I now make the important simplifying assumption that the g_i are density-dependent but *not* frequency-dependent, so $g_i = g_i(N)$. In a polymorphic population, at the point equilibrium $N_2^* = N_2^* g_2(N^*)$. Hence $(N^*, p^*) = (K_2, \hat{I}/K_2(1-g_1(K_2))$. Two necessary conditions for the existence of a stable point polymorphism are 1) $K_1 < K_2$, and 2) $\hat{I} < K_2(1-g_1(K_2))$. In a stable, polymorphic population a change in $\hat{I}$ does not perturb total population size *at all*. Instead, a change in immigration rate is absorbed by a shift in gene frequency. This simple result readily generalizes to multiple alleles if the resident allele has the highest K and is not part of the immigrant pool.

As with the purely ecological model, the relation between $\hat{I}$ and local
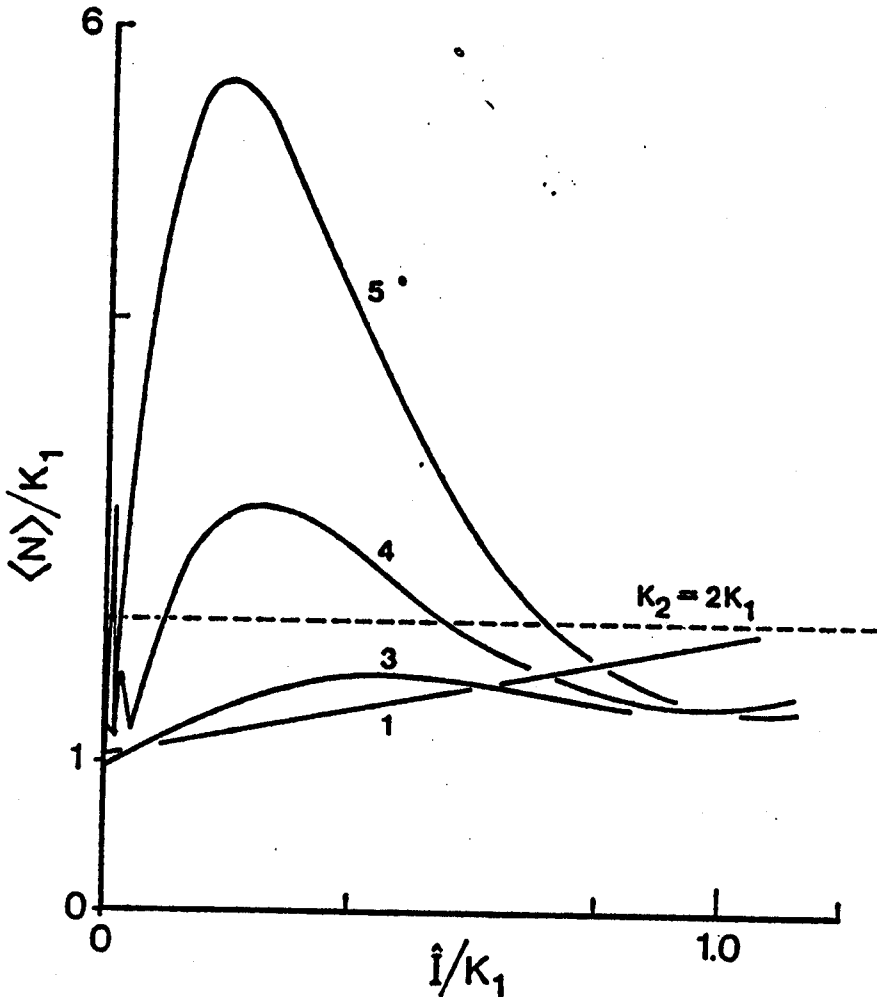
Figure 2 The time-average of density for the exponential-logistic. The solid lines
show how $\langle N \rangle$ depends upon r_1 (the number beside each line) and $\hat{I}$ in
populations monomorphic for type 1. From Figure 1, if $.1 < \hat{I}/K_1 < 1$ most
values of $r > 2$ lead to stable two-point cycles, for which $\langle N \rangle \simeq \hat{I} \rightarrow$
$G(\hat{I})/2$; the approximation is excellent for $r = 3$ if $\hat{I}/K_1 > .3$, and for
$r = 4$ and 5 if $\hat{I}/K_1 > .05$. At low $\hat{I}/K_1$ and $r_1 = 4$ or 5, $\langle N_1 \rangle$ exhibits
a complex pattern of multiple peaks as $\hat{I}/K_1$ increases; this is marked by
a "blip" in the curve for $r = 4$ near the ordinate. Polymorphism requires
$K_2 > \langle N_1 \rangle$. For example, if $K_2 = 2K_1$ the position of the broken line
relative to $\langle N_1 \rangle$ determines the persistence of allele 2; at $r = 4$ or 5
polymorphism may be less likely at intermediate levels of $\hat{I}$ than at
either low or high levels.

stability is more complex. In one limiting case it can be shown that an increase in $\hat{I}$ is necessarily stabilizing. If immigrants are much less fit than residents $(K_1 << K_2)$, near $N^* = K_2$, $G_1 \simeq 0$ and $dG_1/dN \simeq 0$. The stability-setting eigenvalue is $\lambda = 1 + N_2^* dg_2/dN|_*$. As $\hat{I}$ increases, N_2^* decreases. For both the modified linear- and exponential-logistic models, $\lambda = 1 - N_2^* r_2/K_2$. Since $N_2^* \simeq K_2 - \hat{I}$, the peripheral population is stable if $r_2 < 2(1-\hat{I}/K_2)^{-1}$. The maximum r_2 consistent with local stability increases with $\hat{I}$. Numerical studies suggest that as a general rule decreasing the fitness of immigrants relative to residents tends to enhance the stabilizing influence of immigration.

It is difficult to characterize fully conditions for the persistence of polymorphisms in cyclic or chaotic peripheral populations. In a cyclic population with a persistent polymorphism, let τ be the period of one cycle in N. Since allele 2 persists, $N_2(\tau)/N_2(0) = 1 = \prod_{i=0}^{\hat{\tau}} g_2(N(i))$, or $<\ln(g_2)> = 0$. In the exponential-logistic, $g_2 = \exp(r_2(1-N/K_2))$, and $<\ln(g_2)> = r_2(1-<N>/K_2) = 0$, or $<N> = K_2$. For this model, average population size in a cyclic, polymorphic population is independent of $\hat{I}$. To persist, allele 2 must be able to increase when rare. If $N_2(0)$ is sufficiently small, the population will be essentially monomorphic for allele 1 $(N(t) \simeq N_1(t))$ and may cycle at a period τ'. For allele 2 to increase, we require $N_2(\tau') > N_2(0)$, or $<\ln(g_2)> > 0$. With the exponential-logistic, this is $K_2 > <N> \simeq <N_1>$ where $<N_1>$ depends upon $\hat{I}$ as shown in Figure 2. Numerical studies suggest that the heuristic condition for persistence, $K_2 > <N_1>$, is valid in populations with long cycles or seemingly aperiodic behavior. This condition, in conjunction with the figure, leads to two conclusions. First, for $\hat{I}/K \lesssim .75$, as r_1 increases it becomes progressively more difficult to maintain a polymorphism. Second, at high r_1 an increase in $\hat{I}$ may *increase* the likelihood of polymorphism; this is impossible in a stable population.

The ecological significance of immigration into a peripheral population thus depends upon the existence of local genetic differentiation. In turn, the maintenance of pockets of local adaptation reflects local ecological processes. In particular, overcompensatory, density-dependent growth processes may make it difficult for local adaptations to persist. For a particular model we have seen that dynamic instability through its effect on $<N>$ may magnify the swamping effect of gene flow. Although this phenomenon does not occur in all discrete-time population models, it does occur in many commonly used models. Moreover, a cyclic or chaotic population repeatedly forces itself through bottlenecks of low density. A rate of immigration that is small in absolute numbers may actually be large relative to the number of residents then present. Locally adapted alleles may be low by drift during each bottleneck; this stochastic effect compounds the deterministic effect of instability. If local adaptation is requisite for speciation in peripheral isolates, speciation may be less likely in dynamically unstable (high r) than in stable (low r) peripheral populations. One key to a better understanding

of patterns of speciation may thus be provided by the study of the ecological factors responsible for the existence of species borders and the shapes of growth curves in peripheral populations. ＼

Acknowledgements

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