Population dynamics and evolutionary processes: the manifold roles of habitat selection

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Summary

Any character that has a substantial effect on a species' distribution and abundance can exert a variety of indirect effects on evolutionary processes. It is suggested that an organism's capacity for habitat selection is just such a character. Habitat selection can constrain the selective environment experienced by a population. Habitat selection can also indirectly influence the relative importance of natural selection, drift, and gene flow, through its effect on population size and growth rate. In many circumstances (but not all), habitat selection increases population size and growth rate, and thereby makes selection in a local environment more effective than drift and gene flow.

Keywords: Population dynamics, gene flow, evolutionary theory, habitat selection, effective population size.

Introduction

Although all characters of an organism may be grist for the evolutionary mill, surely some characters are more important in evolution than others. In particular, characters that have a substantial impact on the distribution and abundance of a species – i.e. those characters comprising that species' ecological phenotype (Parsons, 1983) – should have a profound influence on evolutionary processes. In this paper, I argue that optimal habitat selection may be just such a key component of a species' ecological phenotype.

In thinking about the evolutionary role of any character, it is useful to distinguish three causal chains relating it to natural selection. First, the character may be directly molded by selection. As a familiar example, body size may determine mortality or fecundity rates, and hence the mean body size of a population should reflect selection on body size, *per se* (e.g. Karn and Penrose, 1951). In like manner, the behavioral traits that allow an organism to choose among habitats so as to maximize its inclusive fitness should also be subject to selection. Second, the character may indirectly influence the evolution by natural selection of other characters, and do so in two distinct ways: through genetic correlations the character may constrain the *response* of other characters to selection, whereas through phenotypic channels the character may constrain the *action* of selection on other characters (e.g. the magnitude or direction of the selective differential). Although genetic correlations among characters are doubtless of great potential significance in evolutionary dynamics (Lande, 1979), it is difficult to predict when such correlations are likely to be important in the absence of a detailed understanding of the developmental machinery generating them. By contrast, it is often clear how the state of one character may guide the direction of selection acting on other characters (i.e. fitness epistasis at the phenotype level). For example, body size may determine the risk of predation. If small-bodied individuals are relatively

vulnerable to predation, then in a population with small average body size, body color may be selected for crypsis, whereas in a population with large average body size and low predation risk, selection on body color might instead reflect thermoregulatory needs or sexual selection. Similarly, I will argue below that habitat selection biases the array of environmental states a population experiences; this can constrain the direction of phenotypic evolution for traits related to the ability to exploit particular habitats. And finally, the character may play a central role in determining the dynamic properties of a species' populations – their mean abundances, the magnitude of fluctuations in population size, patterns of response to disturbance, etc. These demographic attributes in turn influence the efficacy of selection across the entire genome, relative to countervailing evolutionary forces such as drift and gene flow. A principal theme of this paper is that habitat selection can have a major effect on population dynamics, and hence indirectly on the likely importance of genetic drift and gene flow as evolutionary processes.

The paper is constructed as follows. First, I contrast two views on how populaton dynamics might be related to evolutionary processes. I then review some standard results from population genetic theory on the relation between population size and, in turn: drift; the precision and rate of natural selection; and the importance of gene flow. This is followed by a summary of the theory of optimal habitat selection and an examination of the effect of habitat selection on population size and growth rate. I tie these strands of thought together to argue that habitat selection should often (but not always) reduce the importance of genetic drift and gene flow as constraints on the evolution of local adaptation. I finally consider briefly how habitat selection channels phenotypic evolution toward increasing specialization.

Perspectives on population dynamics and evolution

In classic population genetics theory, the mean size of a population and its pattern of fluctuations around that mean are largely taken as given, a fixed backdrop against which the evolutionary play of a species unfolds (e.g. see quote in Appendix). A central focus of this classical theory has been on the interplay of various evolutionary forces, and in particular on the importance of genetic drift relative to natural selection (Crow and Kimura, 1970; Kimura, 1983).

By contrast, evolutionary ecologists have taken as principal goals understanding, on the one hand, how selection influences those phenotypic characters that strongly affect population size and growth rates, and, on the other, how population dynamics provides a kind of template for adaptive evolution. These concerns echo the viewpoint of classic ecological genetics (reviewed in Ford, 1974), which tended to emphasize the study of traits that could affect distribution and abundance (e.g. protective coloration). The literature of our field is replete with discussions of the evolution of foraging behaviors, anti-predator adaptations, reproductive 'effort', spacing systems, and other characters manifestly important in determining the dynamic behavior and average abundance of populations (for review see Emlen, 1984). As noted by Gould and Lewontin (1979), evolutionary ecologists have focused on the role of natural selection in character evolution. This emphasis is, in my opinion, perfectly reasonable, at least as a starting point. But also it would be useful for evolutionary ecologists to assay the potential of non-selective evolutionary processes to thwart adaptive evolution if for no other reason than to suggest explanations for observed or suspected deviations from predicted optimal phenotypes.

To some extent, the difference between the views on the relation between population dynamics and evolution expressed by Kimura and Ohta (1971) and the standard stance of evolutionary ecologists corresponds to differences in the kinds of characters that interest them (molecular variants for the former, versus major morphological, physiological and behavioral characters for the latter). This difference in perspective also matches the dichotomy between Ronald Fisher's

and Sewall Wright's views of adaptive evolution (Fisher, 1958; Wright, 1977), which depends on differing ecological assumptions (Provine, 1985). Fisher tended to assume that population sizes are large enough that drift can be ignored, except in populations so small that extinction is virtually inescapable; adaptations thus arise by mass selection on a locus-by-locus basis. Wright, by contrast, in his 'shifting balance theory' emphasizes that many species are rare, and that even species with large total numbers of individuals are made up of numerous populations providing partially independent arenas of evolution. The effective size of these local populations may often be small enough, particularly in light of the fluctuations in numbers observed in many species, for local populations to drift occasionally from one adaptive peak to another one with higher fitness. The species as a whole is then transformed by selective diffusion. In Wright's words 'A deme in which the set of gene frequencies comes under control of a fitness peak superior to those controlling the sets at neighboring demes tends to produce a greater surplus population and, by excess dispersion, systematically shifts the neighboring demes until they all move autonomously to control by the same fitness peak' (Wright, 1977, p. 455). The characters in question in the shifting balance model thus must have a substantial effect on local population size. In the Fisherian world-view, which emphasizes selection, population dynamics is important only insofar as it affects the relative selective values of alternative alleles or phenotypes. This may be incorporated into Wright's model as well, but in addition, population dynamics sets the relative importance of drift and selection within populations, and is involved in the process of selective diffusion (asymmetric dispersal) between populations.

Population dynamics, drift, and gene flow

The ecological phenotype of a species influences the dynamic properties of its local populations, including their average abundances, distributions among local habitats, patterns of temporal fluctuations in density, the role of dispersal relative to local birth and death rates, and the probabilities of local extinction and recolonization. Habitat selection, through its effect on these dynamic properties of populations, can influence (albeit indirectly) each of the central components of evolutionary change: the rate of origin of evolutionary novelties by mutation (if mutation rates are constant per locus, per individual, then the overall rate of introduction of mutations into a population increases with population size), and subsequent changes in the gene pool resulting from natural selection, drift, and gene flow.

Selection, drift, and population size

There is considerable diversity of opinion among evolutionists regarding the relation of population size to evolutionary rates. For instance, Ohta (1972) and Stanley (1979, pp. 47–51) have argued that phenotypic evolution should be slower in larger populations. Yet if the rate-limiting factor in adaptive evolution is the existence of constraints on the origin and maintenance of adaptive genetic variation, rather than any particular feature of the selective regime itself, adaptive evolution should often be faster and act with more precision in larger populations. Bradshaw (1983) has argued that 'genostasis' – the limitation of evolution in some ecologically significant characters by the lack of appropriate genetic variation – may indeed be the common condition in most species (see also Schaffer and Rosenzweig, 1978; Rosenzweig *et al.*, 1987).

A large population can both maintain more genetic variation (against loss to drift) and generate more new variation (via mutation) than can a small population. In the absence of selection, in each generation a fraction $1/2N_e$ of heterozygosity is lost to sampling drift. N_e is the variance effective population size (Crow and Kimura, 1971). Because evolution requires variation, the potential rate of evolution by natural selection should be faster in larger populations.

This is borne out by several models of selection and mutation. If at a single locus, unique advantageous mutants with a constant selective advantage s appear at a rate v per generation, the rate of gene substitution per generation is $4N_e sv$ (Kimura and Ohta, 1971). In directional selection on a quantitative trait influenced by numerous loci, each of minor effect, the total selective advance per generation resulting from the fixation of new mutations is asymptotically proportional to N_e (Hill, 1982). With strong selection and recurrent mutation at a single locus, the length of time a favorable allele is found in a 'boundary layer' of low frequency (where its dynamics are governed by the slow processes of mutation and drift) varies inversely with population size, implying that 'the rate of evolution is directly proportional to population size' (Gillespie, 1983, p. 707). Moreover, under stabilizing selection on a quantitative character, the probability that a population will deviate by a given amount from the optimum phenotype decreases rapidly with increasing value of N_e (Lande, 1976).

The principal way in which large local population sizes can slow adaptive evolution is embodied in Wright's shifting balance theory. In a fixed adaptive landscape, transitions between alternative, selective equilibria are most likely in populations of intermediate size, which can occasionally wander from a given adaptive peak by drift (unlike large populations) and yet not be rapidly depleted of the requisite genetic variation, also by drift (unlike small populations) (Wright, 1977, p. 450). Yet even in this theory, there are two ways in which an increase in population size can hasten adaptive evolution. First, at a fixed local density, the number of local populations is proportional to the total number of individuals comprising a species. Transitions between alternative selective peaks are unlikely in any single population (Wright, 1977), but become increasingly likely the more local populations are encompassed by a species (Newman *et al.*, 1985). So the rate of adaptive evolution should increase with a species' total population size. Second, if drift is caused by fluctuating selection pressures rather than sampling in finite populations, the likelihood of a peak shift need not diminish and may even be greater at larger local population sizes (Wright, 1977).

Effective population size

The effective sizes of most natural populations are almost always less than their average census sizes (Nei and Graur, 1984). Two ubiquitous reasons for this are temporal variation in population size, and within-population variance in fecundity (Kimura and Crow, 1963; Begon, 1977). The variance effective size of a population governs the importance of random gene frequency drift (see Ewens, 1982 for discussion of other measures of effective population size). Wright (1977) showed that the harmonic mean of population size

$$N_{\mathrm{h}} = \left(\frac{1}{t} \sum_{i=1}^{t} \frac{1}{N(i)} \right)^{-1} \tag{1}$$

(where $N(i)$ = population size in generation i) provides an excellent approximation to the rate of loss of heterozygosity in fluctuating populations (Nei *et al.*, 1975; Motro and Thomson, 1982 discuss some limitations of the harmonic mean approximation; it fails only with long population cycles and very sharp bottlenecks). For example, if a population spends a fraction of p of generations at N_{low}, and the remainder at a high density, we can write

$$N_{\mathrm{h}} \leqslant N_{\mathrm{low}}/p \tag{2}$$

The effective size of a population thus reflects both the magnitude of population lows, and the amount of time a population is at or near these low densities. Heywood (1986) has shown that

incorporating variance in fecundity leads to the following approximate expression for N_c in a fluctuating population:

$$N_c = N_h \{Q(1 + F) + 1\}^{-1}, \tag{3}$$

where N_h is the harmonic mean population size, Q is the coefficient of variation in adult fecundity (contribution to gamete pool), and F is the arithmetic mean of a measure of departure from Hardy–Weinberg proportions (with random mating in generation i, $F_i = -1/(2N_i-1)$) (Kimura and Crow, 1963)). Habitat selection can thus modify the effective size of a population through its effect on either the population size of a stable population, or on the rates of increase following a bottleneck in unstable populations, or on the variance in adult fecundity.

Selection and gene flow

Population size and fluctuations are also important in determing the relative strengths of gene flow and selection in a local environment. Many authors have observed that gene flow may be particularly important as a constraint on selection in low density populations, such as at the edge of a species range (e.g. Haldane, 1930; Mayr, 1954; Antonovics, 1968; Georghiou and Taylor, 1977; Comins, 1977; Endler, 1977; Nagylaki, 1978; Holt, 1983; Slatkin, 1985; May and Dodson, 1986). It seems less widely appreciated that population fluctuations also tend to magnify the effects of gene flow.

A criterion for the persistence of an allele in the face of gene flow developed by Nagylaki (1977, 1979) can be used to examine the effects of low or variable population size. Assume that at a single locus allele 1 is locally favored (i.e. the relative fitnesses of the three genotypes are constants such that w_{11} and $w_{12} > w_{22}$), and all immigrants are homozygous for allele 2. In each generation there is a bout of viability selection followed by immigration of adults. If in generation t there are $N(t)$ adults remaining after selection and $I(t)$ immigrants, the migration rate $m(t)$ is defined by $I(t)/(I(t)+N(t))$. The quantity $e(t) = 1 - m(t)$ is the fraction of breeding adults recruited locally rather than by immigration. Nagylaki (1979, p. 166) shows that allele 1 when rare can increase over T generations provided

$$\prod_{t=0}^{t=T-1} e(t) > (w_{22}/w_{12})^T. \tag{4}$$

Nagylaki does not explicitly consider the effect of local population density, but this effect is implicit in the parameter $e(t)$. If $N(t)$ and $I(t)$ are constant at N^* and I^*, persistence requires that $N^*/(N^*+I^*) > w_{22}/w_{12}$. The selective edge needed to retain a locally advantageous allele is thus reduced if population size is large relative to immigration.

Local population fluctuations tend to magnify the importance of gene flow. If different populations fluctuate asynchronously, and immigrants are drawn from a number of populations, N should vary more than I. Variation in N will thus lead to variation in local recruitment to the breeding pool ($e(t)$). Let $\bar{e}$ and e_g denote the arithmetic and geometric means of $e(t)$ over T generations. Expression (4) can be compactly written as $e_g > w_{22}/w_{12}$. Because $\bar{e} > e_g$ (unless there is zero variance in $e(t)$), fluctuations in N make it more difficult for the locally favored allele to persist. For instance, if a population spends a fraction μ of generations at a low density N', with local recruitment e', and the remainder at high densities (so $e(t) \approx 1$), the condition for persistence is $(e')^\mu > w_{22}/w_{12}$. A population which takes a long time to recover from a perturbation to low densities (i.e. high μ) is thus more likely to lose locally superior alleles to gene flow, relative to populations which rebound rapidly in numbers.

Slatkin (1977, 1985, 1987) has argued that gene flow may be particularly important in 'weedy'

species with frequent extinction and recolonization of local populations. Such species are at one end of a spectrum of increasing demographic instability. Empirical estimates of dispersal rates coupled with theoretical studies of the migration–selection balance (Endler, 1977) suggest that gene flow is not very effective at preventing local adaptation when it couples established, stable populations of equal size. The argument sketched above indicates that an increase in population instability (as measured, say, by the coefficient of variation in log N) should enhance the importance of gene flow relative to selection, even if populations do not fluctuate to the point of extinction. Moreover, the likelihood of extinction may often be correlated with the magnitude of population fluctuations (Leigh, 1981).

To summarise the above remarks, in populations that are large and constant in numbers, natural selection should act with more precision in honing adaptations to local environments, compared to smaller and more variable populations, because (1) drift is less likely to produce deviations from the selective optimum, (2) a greater store of genetic variation may be maintained or generated via mutations, (3) the 'waiting time' to the appearance of favorable mutants is shorter, and (4) gene flow is less likely to inhibit selection. The most important exception to this generalization is when selective advance requires populations to move between adaptive peaks; this is not likely to be important in the evolution of any single population but may be essential to understanding long-term evolution in some species comprised of an ensemble of many loosely coupled populations. (However, the rate of this shifting balance mode of adaptive evolution should also increase with the number of local populations comprising the species (the size of a 'metapopulation')). Habitat selection through its effect on local population dynamics may substantially affect the importance of non-selective evolutionary mechanisms.

A precis of optimal habitat selection theory

The original aim of the ecological theory of habitat selection (Fretwell, 1972; Rosenzweig, 1974, 1979, 1981, 1985; Charnov, 1976; Whitham, 1980) was to predict the spatial distribution of a population in which individuals choose habitats so as to maximize individual fitness. Because fitness is often density-dependent, both within and between species, the evolutionarily stable distribution of a population among habitats should reflect its intraspecific and interspecific competitive milieu. The genetic consequences of habitat selection that have been explored most thoroughly in the literature are its potential for enhancing the likelihood of stable genetic polymorphisms (Taylor, 1976; Hedrick, 1986; Garcia-Dorado, 1986), and its role in sympatric speciation (Rice, this issue; Bush, 1975). Other ecological and genetical consequences of habitat selection have only begun to be explored.

Fretwell (1972) put forth a simple, useful model for predicting an optimal habitat distribution. Let $F_i(N_i)$ be a measure of fitness for an animal that restricts its activities to habitat i when that habitat contains N_i conspecifics. For simplicity we will consider just two habitats ($i = 1, 2$). If there is competition for resources or other sources of negative density-dependence, F_i declines monotonically with N_i. The simplest case of habitat selection occurs if individuals can move among habitats with negligible costs or interference from conspecifics. If for given values of N_1 and N_2, $F_1(N_1) < F_2(N_2)$, it obviously pays individuals to move from habitat 1 to habitat 2. Hence, for the population to be in behavioral equilibrium, it must be the case that either $F_1(N_1) = F_2(N_2)$, or all individuals will be found in just one patch (i.e. in habitat 1, if $F_1(N_1) > F_2(0)$). The basic prediction of habitat selection theory is simply that individuals are distributed such that expected fitnesses are equal among all occupied habitats. The carrying capacity of a patch K_i is defined to be that density of individuals at which births just match deaths, or $F_i(K_i) = 1$. It follows that under optimal habitat selection, each habitat equilibrates at its respective carrying capacity.

Habitat selection and population abundance

Elsewhere (Holt, 1985) I have shown that optimal habitat selection may either increase, decrease, or leave unchanged the total number of individuals in a population, compared with an otherwise similar population in which individuals utilize habitats at random. The models discussed there were for populations with continuously overlapping generations. Here I show that similar results hold for populations with discrete generations (the usual structure for population genetic models).

In models for populations with discrete generations, the temporal ordering of demographic events is important (Prout, 1980). I will assume the following order of life-history events: (1) birth in a habitat patch, (2) maturation to adulthood in that patch, (3) movement of adults among patches, and (4) reproduction of adults within patches. We census the population at the time of birth. I will assume that the fecundity of an adult depends on its natal habitat, rather than on the habitat to which it moves. Changing this assumption alters the detailed character of the model but does not affect the qualitative effects to be described.

Were there no movement among patches, the standard recursion – $N_i(t+1) = N_i(t)F_i(N_i(t))$, where $F_i(N_i(t))$ is the expected number of offspring for an individual born into habitat i – would describe the population dynamics of habitat i. However, if a fraction E of adults leave their natal habitat to move to the other habitat, the recursion describing the dynamics in the two coupled patches is

$$N_1(t+1) = (1-E)N_1(t)F_1(N_1(t)) + EN_2(t)F_2(N_2(t)) \tag{5a}$$

$$N_2(t+1) = EN_1(t)F_1(N_1(t)) + (1-E)N_2(t)F_2(N_2(t)) \tag{5b}$$

A newborn in patch 1 can expect to leave $(1-E)F_1(N_1)$ offspring in patch 1, and $EF_1(N_1)$ offspring in patch 2. This model of discrete population growth in two coupled habitats can display the usual rich array of dynamic behaviors, with transitions from monotonic and oscillatory convergence to a stable point equilibrium, then to limit cycles, and ultimately to chaotic behaviors, as one increases the intrinsic growth rates of each patch and strengthens the intensity of density dependence near K (May, 1976). A full analysis of this model will not be attempted here. Instead, I will choose parameter values which ensure local dynamic stability.

I shall now contrast a population in which individuals optimally select habitats with a population in which individuals move among habitats indiscriminately. Let $N_T = N_1 + N_2$. At $E = 1/2$ (i.e. a uniform division of progeny between the habitats), $N_1 = N_2 = N_T/2$, and

$$N_T(t+1) = N_T(t)\{F_1(N_T/2) + F_2(N_T/2)\}/2 \tag{6}$$

The quantity in brackets divided by 2 is just the average finite growth rate over both patches. The equilibrial population size N_T^* is found from $F_1(N_T^*/2) + F_2(N_T^*/2) = 2$.

As a rule, N_T^* will differ from the equilibrial population size achieved under optimal habitat selection. An optimal habitat selector should distribute its offspring so as to maximize its total fitness. If the clutch size of an individual is small relative to the number of individuals in a given habitat, at the time of birth the distribution of individuals across the two habitats should be such that $F_1(N_1) = F_2(N_2)$; if this is not possible, the adults should adjust their movements such that all offspring will be born in the habitat providing higher expected fitness. The habitat that has higher fitness at low densities is labelled habitat 1 (i.e. $F_1(0) > F_2(0)$). At first, the population should be restricted to habitat 1 and grow according to $N_T(t+1) = N_T(t)F_1(N_T(t))$. In generation t', if $F_1(N_T(t')) < F_2(N_2)$, some individuals should switch to habitat 2 (Fretwell, 1972). Henceforth, as the population grows, the number of individuals in each habitat in generation t should be constrained such that $F_1(N_1) = F_2(N_T - N_2)$, and the population's growth will be described by

$N_T(t+1) = N_1(t)F_1(t) + N_2(t)F_2(t) = N_T(t)F_1(N_1(t))$. The population equilibrates at $K_1 + K_2$.

The population with a uniform habitat distribution may achieve either a higher or a lower abundance than $K_1 + K_2$. Fig. 1 shows a simple graphical method for determining which outcome occurs. Following Fretwell (1972), we plot F_1 against N_1 for each patch. In the figure, patch 2 is a sink; the population there cannot be sustained without immigration. Given optimal habitat selection, all individuals will reside in patch 1, leaving patch 2 empty. With a uniform progeny distribution between the two habitats, individuals experience the average growth rate; the population equilibrates when the number in each patch is such that its rate of increase in patch 1 just matches its rate of decrease in patch 2. In Figure 1a, habitat selection increases population size; in Figure 1b, habitat selection decreases population size.

For an algorithmic example, assume that the population in patch 1 grows according to $F_1(N_1) = R_1/(1+aN_1^b)$ (see, e.g., Begon and Mortimer, 1981) and that patch 2 declines at a constant rate $F_2(N_2) = R_2 < 1$. Given optimal habitat selection, no individuals will be in patch 2, and patch 1 equilibrates at

$$N_{opt}^* = \left\{ \frac{R_1 - 1}{a} \right\}^{1/b} \tag{7}$$

With a uniform distribution, the equilibrial abundance for both patches combined is

$$N_{uni}^* = 2 \left\{ \frac{1}{a} \left(\frac{R_1 + R_2 - 2}{2 - R_2} \right) \right\}^{1/b} \tag{8}$$

The population with optimal habitat selection persists if $R_1 > 1$, whereas the population with a uniform distribution requires that $R_1 + R_2 > 2$, which is a more stringent criterion. Habitat selection thus enhances population persistence by shielding individuals from exposure to low-quality habitats.

Habitat selection increases the total population size maintained at equilibrium if $R_2 < 2/(1+R_1)$, and otherwise decreases population size. The effect of habitat selection is to increase population size if both R_1 and R_2 are low. This effect is reversed at high R_1. We can conclude that if the environment in general is unfavorable with low maximal growth rates even in the best available habitat, then habitat selection tends to increase population size and may even be necessary for the population to exist at all. However, if growth rates are high in favorable habitats, the 'spillover' of individuals into less favorable habitats may allow populations with a suboptimal pattern of habitat utilization to maintain a larger total number of individuals than found in a population with optimal habitat selection.

Habitat selection and population growth rate

Optimal habitat selection does not as a rule maximize population growth rates. In generation t, the partitioning of the total population size $N_T(t)$ into the two habitats (i.e. N_1 and $N_2 = N_T - N_1$) that maximizes the total population size at generation $t+1$ is found by fixing N_T at some constant value and solving

$$\frac{\partial}{\partial N_1} (N_1 F_1(N_1) + N_2 F_2(N_2)) = 0, \tag{9}$$

or

$$F_1(N_1) - F_2(N_2) + N_1 \frac{\partial F_1}{\partial N^1} - N_2 \frac{\partial F_2}{\partial N_2} = 0. \tag{10}$$
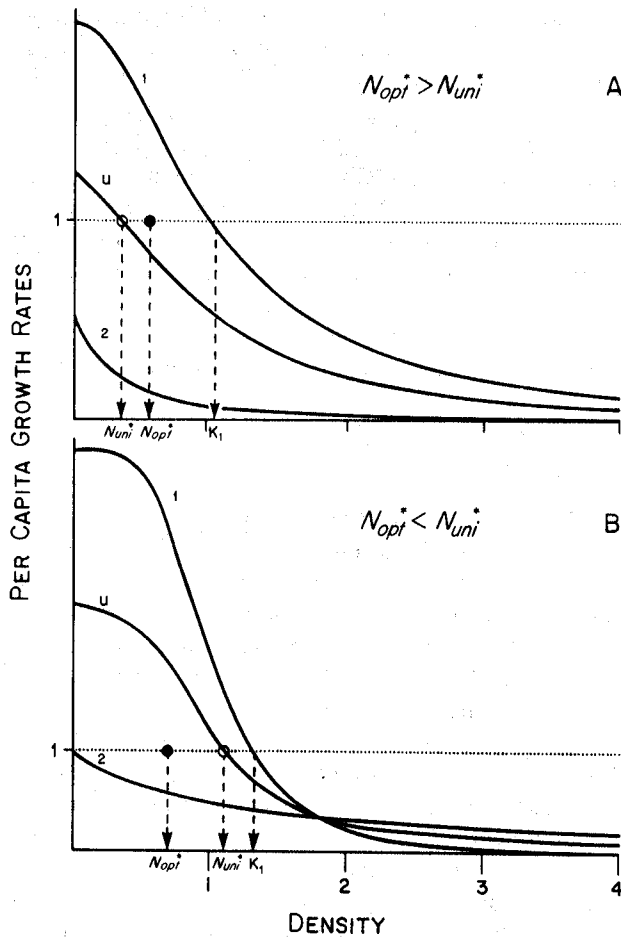
Figure 1. Density-dependent growth functions. The lines denoted 1 and 2 are per capita growth rates in each of two habitat types. The lines denoted u are average growth rates when individuals use the habitats indiscriminately, with zero movement costs. In both cases shown, habitat 2 is a sink; the population cannot persist there with immigration. Given optimal habitat selection, all individuals will choose to reside in habitat 1, which will equilibrate at its carrying capacity. The solid dot is the average density over both habitat (assumed to be equal in area). The open dot marks the average density given indiscriminate habitat use. In 1A, optimal habitat selection increases population size; in 1B, by contrast, optimal habitat selection decreases population size. (Population size here is the summed number of individuals over both habitats combined.)

Given optimal habitat selection, $F_1(N_1) = F_2(N_2)$ when both habitats are occupied. For this optimal distribution to maximise the rate of growth of the population, it must be the case that

$$N_1 \, \partial F_1/\partial N_1 = N_2 \, \partial F_2/\partial N_2. \tag{11}$$

This will not usually be true. However, if densities are low enough, optimal habitat selection does maximize the overall population growth rate $N_1F_1 + N_2F_2$. The within-habitat growth rates F_i in this case are constants: any use of a suboptimal habitat clearly reduces population growth, and the population grows most rapidly when all individuals choose the habitat with higher F_i.

To understand better why optimal habitat selection does not necessarily maximize population growth rates, consider a population which initially has an optimal distribution such that $N_1 > N_2$, and

$$F_1(N_1) = F_2(N_2) = \lambda_0 \tag{12}$$

λ_0 is the finite rate of increase for the subpopulation in each habitat as well as for the overall population. If we introduce a small component of non-selective or random movement, there will be a net displacement of a few individuals from habitat 1 to habitat 2; the average rate of increase for the population changes by an amount proportional to

$$- N_1 \, \partial F_1 / \partial N_1 + N_2 \, \partial F_2 / \partial N_2. \tag{13}$$

With $N_1 > N_2$ and $\partial F_i / \partial N_i < 0$, this quantity is positive unless

$$\left| \frac{\partial F_2}{\partial N_2} \right| >> \left| \frac{\partial F_1}{\partial N_1} \right|, \tag{14}$$

which states that density dependence must be considerably stronger in the lower-quality habitat. This condition may often be true (see Travis and Trexler, 1986 for an example), but there is no reason to expect it always to hold. With a non-selective component of movement, the number of individuals in the high-K habitat declines, and the individuals remaining enjoy an increase in fitness, while the number of individuals in the low-K habitat increases, with a corresponding decrease in their fitness. Simply because there are more individuals to start with in the high-K habitat, the net effect on the population growth rate of a small deviation from an optimal distribution tends to be biased by the increased fitness of individuals in the high-density habitat; this leads to an increase in total population growth rate.

We can summarize the above observations as follows. If population numbers are low, optimal habitat selection invariably increases the overall rate of population increase. A population of habitat selectors can thus more quickly rebound from disturbances that greatly reduce population size, compared to populations with a significant component of random habitat use. However, when population size is large habitat selection may either decrease or increase the rate of population increase.

Habitat selection and effective population size

The equilibrial size predicted by the above models for a population in a stable environment is not quite identical to the genetically relevant effective population size. I assumed that fitness depended on the number of newborn individuals occupying a habitat, so I censused juveniles in each habitat. The effective size of a population, however, is its number of breeding adults, corrected for variance in fecundity. The models discussed above can be re-analysed with adults as the census stage. The results of such an analysis parallel the results presented above: habitat selection may either increase, decrease, or leave unchanged the effective size of a population, compared to a population in which individuals use habitats indiscriminately.

The expected fitness of a newborn individual may be written as $F_i(N_i) = S_i M_i$, where S_i is the probability of surviving to the adult stage, and M_i is the fecundity of an adult in habitat i. Competition among immatures can conceivably reduce both survivorship and adult fecundity (e.g. through effects on the body size of developing individuals). Given optimal habitat selection, $S_1/S_2 = M_2/M_1$. Let us assume that fecundity but not survivorship is density-dependent. If survivorship is equal in the two habitats, with optimal habitat selection the population is

distributed such that expected fecundities are also equal. In other words, habitat selection tends to reduce spatial variance in fecundity, thus increasing the effective population size (see equation 1). If survivorship differs in the two habitats however, then at equilibrium there may still exist some variance in fecundity. Mueller *et al.* (1985) and Heywood (1986) report substantial fecundity variance in populations of *Euphydras editha* and annual plants. Much of this may reflect differences in microhabitat quality.

The effect of optimal habitat selection on the effective size of equilibrial populations is thus somewhat equivocal. In harsh environments, optimal habitat selection should typically increase effective population size. But in benign environments where fitnesses are not too low in the suboptimal habitat, and density-dependence is stronger in the optimal habitat, habitat selection may actually reduce effective population size. However, when populations experience bottlenecks due to catastrophic disturbances, habitat selection will greatly increase the rate of increase from low abundances. Because the effective size of a population is particularly sensitive to the length of time it remains near lows in abundance, habitat selection behavior in a population which experiences occasional or frequent disturbances should almost always increase its effective population size, and thereby diminish the importance of drift relative to selection.

Habitat selection and gene flow

We earlier observed that gene flow acts most potently as a deterrent to selection when population numbers are low relative to the flux of immigrants (e.g. in peripheral populations). In those circumstances where habitat selection increases population size, it thereby reduces the importance of gene flow. Just as with genetic drift, the effects of gene flow are also greatly magnified if population size fluctuates, so that the population experiences some periods of low abundance and high relative immigration rates. Because habitat selection increases the rate of increase of a population depressed well below its equilibrial density, habitat selection tends to vitiate the swamping effects of gene flow in populations that occasionally or periodically suffer sharp reductions in abundance.

There is another reason to expect gene flow to be less important because of habitat selection, at least in stable environments. In a species fixed for behaviors permitting optimal habitat selection, the number of immigrants flowing into a typical population should be less than if individuals were to move among habitats in a less selective fashion. In a stable environment, most populations will be at or near carrying capacity, so that fitnesses should be approximately unity across space. Individuals will not be selected to disperse unless their expected fitness elsewhere exceeds their expected fitness in the habitat into which they are born. This will not be the case if average fitnesses everywhere are near unity. Formal arguments presented in Hastings (1983) and Holt (1985) show that even if there are no costs to dispersal, *per se*, dispersal in temporally stable environments is selected against (barring kin effects and interference).

Habitat selection should also have subtle effects on the number of immigrants entering a given habitat patch each generation. If there is an environmental pocket with a different selective regime than found in the source area for immigrants and potential immigrants carry alleles that reduce their fitness there, they should avoid this habitat. Such avoidance enhances the probability of persistence for locally adapted alleles. Moreover, the number of individuals moving across geographical barriers (defined as regions with low expected fitness) should also be low, simply because active habitat selectors should avoid areas in which they have a low expected fitness.

We can therefore predict that habitat selection should permit natural selection to fashion more precise adaptations to local environments because of a reduction in gene flow. This reduction occurs both because habitat selection tends to increase the rate of increase from population lows,

and because individuals should not readily cross low fitness barriers or disperse into habitats in which their expected fitness is low relative to residents.

Habitat selection and constraints on the direction of phenotypic evolution

In marshalling the above arguments, I have assumed that the functional relationships between fitness, habitat type, and population density (*viz.*, the biology underlying the per capita growth curves in Fig. 1) are fixed properties of the species in a given environmental setting. This assumption allowed me to make a fair comparison of the size and dynamics of populations that differ in no respect save habitat selectivity. But natural selection should also act on the organismal characters that determine these functional relations. Over evolutionary time, non-selective and selective populations should diverge in their respective capacities to exploit the environment.

Consider evolution in haploid populations occupying a two-habitat environment. The optimal habitat selector entirely avoids habitat 2, while the non-selector uses the two habitats indiscriminately. At equilibrium, there are K_1 individuals in habitat 1, with fitness $F_1 = 1$, and no individuals in habitat 2; were there any there, they would have fitness $F_2 < 1$. In the non-selective population, individuals are equally distributed across the two habitats and experience an average fitness $(F_1' + F_2')/2 = 1$ (the primes indicate that the habitat-specific fitnesses may differ from the habitat selector due to shifts in the number of individuals in each habitat). A mutant phenotype arises in the selective population which enjoys an increment of fitness δF_1 in habitat 1, at the expense of a decrease in its potential fitness δF_2 in habitat 2; a similar mutant in the non-selective population experiences changes in fitness $\delta F_1'$ and $\delta F_2'$. The criterion for the increase in frequency of this novelty in the population with habitat selection is simply $\delta F_1 > 0$; no individuals are exposed to selection in the other habitat, so the potential reduction in fitness therein is irrelevant to the potential selective advantage of this allele. By contrast, in the non-selective population the allele increases only if

$$\delta F_1' > |\delta F_2'| \tag{15}$$

Use of the suboptimal habitat increases the selective advantage required for an allele specialized for the better habitat to increase in frequency. Habitat selection thus filters the array of locally available environment states against which mutants are continually being tested (Templeton and Rothman, 1981) and could play a key role in the survival probability of favorable mutants. Natural selection should continually refine the ability of a population to use those habitats it already selectively occupies, even at the expense of its potential ability to use other habitats not so occupied. Over time, for the habitat selector this leads to an increasing fitness differential between habitats used and those not used. This in turn increases the fitness advantage provided in the first place by habitat selection. As noted in Holt (1985), this positive feedback between the selective advantage of habitat selection and the phenotypic specialization by habitat that makes habitat selection advantageous may, over evolutionary time, lock a species into phenotypic specialization. By contrast, with suboptimal habitat use general-purpose phenotypes will tend to be favored, and selection will be biased towards whichever habitat is most frequently encountered. The net effect is to reduce the selective advantage of habitat selection. We can envisage two population syndromes: on the one hand, populations comprised of generalists found in a number of habitats with poor abilities at habitat selection, and, on the other, populations of specialists well-adapted both to occupy a particular habitat and to avoid other habitats. These ideas are also treated by Rosenzweig in his contribution to this symposium. A deeper exploration of the idea that habitat selection may provide an important historical constraint on evolution will

require a consideration of the evolution of phenotypic plasticity (Via and Lande, 1985) and dispersal (Levin *et al.*, 1984), as well as an assessment of how organismal characters determine the density-dependent growth functions characterizing each habitat type.

Habitat selection and speciation

Habitat selection may, through its effects on population dynamics, indirectly influence the relative strengths of three central forces in phyletic evolution: natural selection, drift, and gene flow. Habitat selection can also be of salient importance in certain modes of speciation. Rice, Rosenzweig, and others (this symposium, and references cited therein) have argued that habitat selection may permit rapid speciation without the geographical separation of populations. In addition to the direct importance of habitat selection in this mechanism of speciation, there may be indirect effects on the likelihood of rapid speciation during the founding of new populations. There is at present considerable disagreement about the significance of founding events for speciation. Carson and Templeton (1984, p. 128) argue that 'founder events are often a precondition for the genetic changes leading to speciation'. The two most plausible mechanisms leading to speciation via founders – genetic transilience and founder-flush – both require that a population grow rapidly after it is founded. Precise habitat selection can greatly increase the initial growth rate of a population in a spatially variegated environment, and thus should make these models of speciation more feasible.

However, Barton and Charlesworth (1984, p. 158) contend that there is 'no reason to assign special significance to founder effects'. Reproductive isolation, they suggest, may typically arise as a pleiotropic by-product of the gradual divergence of allopatric gene pools, each undergoing ordinary phyletic evolution. If this divergence requires transitions between alternative stable states in a relatively fixed adaptive landscape, the rate of divergence leading to isolation may be greatest in populations of intermediate size (small enough to experience significant drift, yet large enough to maintain a substantial pool of heritable variation). Since habitat selection tends to increase effective population size in many (but not all) circumstances, it is likely in this case to have an ambiguous effect on the rate of allopatric speciation. If by contrast geographically separated populations are characterized by different adaptive landscapes (due to differences in their physical or biotic environment), they will tend to evolve in different directions. The rate of divergence should be scaled by the rate of ordinary phyletic evolution, which, for the reasons given above, should increase with increasing effective population size. Habitat selection should in this case indirectly speed up speciation.

Conclusion

In the literature of ecology and evolution one may discern two implicit stances regarding the interplay of population dynamics and evolution. On the one hand, evolutionary ecologists focus on characters that have a major impact on population dynamics, at least in part because the average size and dynamic properties of a population in turn determine the relative selective values of alternative phenotypes in a population. This, the Fisherian view, tends to slight the potential importance of drift and gene flow as evolutionary processes. On the other hand, much of classical population genetics is concerned with the interplay of selection and various non-selective evolutionary processes; population dynamics is a vital element in this view of evolution, for it sets the relative strengths of selection, drift and gene flow. Yet for analytical convenience, it is usually assumed that evolution proceeds without much reciprocal effect on population dynamics. This may be an appropriate assumption for molecular variants, but not for the morphologi-

cal, behavioral, and physiological characters of interest to ecologists. I suggest that those characters of an organism that have a major impact on the distribution, abundance, and dynamic behavior of populations can exert a pervasive indirect effect on evolutionary processes. The ability of an organism to select its habitat in a spatially variable environment is just such a character.

The ecological theory of habitat selection suggests that mobile organisms in a spatially heterogeneous environment should choose to reside in those habitats providing the greatest expected fitness. Such habitat selection has several important indirect effects on evolutionary processes. One is that individuals in a population are exposed to a biased subset of the array of potential environmental states. Organisms with habitat selection in a sense define the selective regime of their population. Habitat selection can also modulate the potency of natural selection by affecting the average size of local populations, and the pattern of growth or decline for populations not at equilibrium, inasmuch as these demographic effects indirectly influence the likely importance of non-selective evolutionary factors such as drift and gene flow.

This paper has explored some of the indirect effects of habitat selection on evolution using models of populations distributed across two distinct habitat patches. The basic strategy has been to contrast a population in which individuals utilize the two habitats at random with a similar population in which individuals show an ideal free distribution (Fretwell, 1972).

In a stable population, habitat selection affects the effective population size in two ways: (1) by reducing among-individual variance in fitness, and (2) by altering the total number of individuals sustained in both patches combined. In many circumstances, habitat selection increases effective population size. Interesting exceptions may occur if density-dependence is weaker in the habitat with lower carrying capacity.

If the size of a population varies over time, either because of external perturbations or the interplay of time-lags and density-dependence, effective population size is dominated by periods of low density. Habitat selection can greatly enhance the ability of a population to rebound from disturbances, which reduces the importance of genetic bottlenecks.

Fluctuations in population size can also magnify the effects of gene flow relative to local selection. This deterministic effect is compounded by the effects of drift in finite populations. Because habitat selection tends to increase the average density of a population in a fluctuating environment, habitat selection should often moderate the swamping effects of gene flow.

We can conclude that because habitat selection as a rule increases effective population size (although with some potentially important exceptions) and decreases the effective immigration rate, habitat selection should often permit natural selection to act with more precision in honing adaptations to local environments.

Acknowledgments

Appendix

Kimura and Ohta (1971, p. 74) tellingly state that 'in the process of gene substitution in evolution, the relative proportions of genes change enormously, while the total population number remains relatively constant due to population regulating mechanisms. To a first approxi-

mation, total population number is determined by such factors as food, space and competitors, rather than the relative frequencies of alleles at a particular locus where a substitution is occurring.' It is mildly amusing to note that the chapter from which this quote is lifted is titled 'Adaptive evolution and substitutional load'. The adaptations in question must thus not appreciably affect population size! Of course, many characters of ecological relevance are quantitative in nature, and thus influenced by variation at many loci. For such characters, it is possible for individual genes to show approximate neutrality despite intense selection at the phenotypic level (see, e.g., Lynch, 1984). Regardless of the genetic architecture underlying the characters ecologists study, I feel that I would be useful for ecologists to consider the possibility that some of the non-selective processes studied in classical population genetics theory (drift, gene flow) could be important in constraining the effectiveness of adaptive evolution.

References

Antonovics, J. (1968) Evolution in closely adjacent plant populations. VI. Manifold effects of gene flow. *Heredity*, **23**, 507–24.

Barton, N. H. and Charlesworth, B. (1984) Genetic revolutions, founder events, and speciation. *Ann. Rev. Ecol. Syst.* **15**, 133–64.

Begon, M. (1977. The effective size of a natural Drosophila subobscura population. *Heredity* **38**, 13–18.

Begon, M. and Mortimer, A. (1981) *Population Ecology*. Sinauer Press, Sunderland, Mass.

Bradshaw, A. D. (1983) The importance of evolutionary ideas in ecology – and vice versa. B. Shorrocks (ed.), pp. 1–25. *Evolutionary Ecology*. Blackwells, London.

Bush, G. L. (1975) Modes of animal speciation. *Ann. Rev. Ecol. Syst.* **6**, 339–64.

Carson, H. L. and Templeton, A. R. (1984) Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Ann. Rev. Ecol. Syst.* **15**, 97–131.

Charnov, E. L. (1976) Optimal foraging: The marginal value theorem. *Theor. Pop. Biol.* **9**, 129–36.

Comins, H. N. (1977) The development of insecticide resistance in the presence of migration. *J. Theor. Biol.* **64**, 177–97.

Crow, J. F. and Kimura, M. (1970) *An Introduction to Population Genetics Theory*. Harper and Row, New York.

Diamond, J. M. (1984) 'Normal' extinctions of isolated populations. In *Extinctions* (M. H. Nilecki, ed.) pp. 191–246. University of Chicago Press, Chicago.

Emlen, J. M. (1984) *Population Biology*. Macmillan, New York.

Endler, J. A. (1977) *Geographic Variation, Speciation, and Clines*. Princeton Univ. Press, Princeton, N.J.

Endler, J. A. (1986) *Natural Selection in the Wild*. Princeton Univ. Press, Princeton, N.J.

Ewens, W. J. (1982) On the concept of effective population size. *Theor. Pop. Biol.* **21**, 373–8.

Fisher, R. A. (1958) *The Genetical Theory of Natural Selection*. Dover Publications, New York.

Ford, E. B. (1974) *Ecological Genetics*, 4th edn. Chapman & Hall, London.

Fretwell, S. D. (1972) *Populations in a Seasonal Environment*. Princeton Univ. Press: Princeton, N.J.

Garcia-Dorado, A. 1986. The effect of niche preference on polymorphism protection in a heterogeneous environment. *Evolution* **40**, 936–45.

Georghiou, G. P. and Taylor, C. E. (1977) Genetic and biological influences in the evolution of insecticide resistance. *J. Econ. Entom.* **70**, 319–23.

Gillespie, J. H. (1983) Some properties of finite populations experiencing strong selection and weak mutation. *Amer. Natur.* **121**, 691–708.

Ginzburg, L. R. (1983) *Theory of Natural Selection and Population Growth*. Benjamin-Cummings, Menlo Park, Ca.

Gould, S. J. and Lewontin, R. C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. Roy. Soc. London* (B) **205**, 581–98.

Grant, V. (1980) Gene flow and the homogeneity of species populations. *Biol. Zbl.* **99**, 157–69.

Haldane, J. B. S. (1930) A mathematical theory of natural and artificial selection. Part VI. Isolation. *Proc. Camb. Phil. Soc.* **26**, 220–30.

Hastings, A. (1983) Can spatial variation alone lead to selection for dispersal? *Theor. Pop. Biol.* **24**, 244–51.

Hedrick, P. W. (1986) Genetic polymorphism in heterogeneous environments: A decade later. *Ann. Rev. Ecol. Syst.* **17**, 535–66.

Heywood, J. S. (1986) The effect of plant size variation on genetic drift in a population of annuals. *Amer. Natur.* **127**, 851–61.

Hill, W. G. (1982) Rates of change in quantitative traits from fixation of new mutations. *Proc. Natl. Acad. Sci.* USA **79**, 142–5.

Holt, R. D. (1983) Models for peripheral populations: The role of immigration. In *Population Biology* (H. I. Freedman and C. Strobeck, eds), Lecture Notes in Biomathematics, Vol. 52, pp. 25–32. Springer-Verlag, New York.

Holt, R. D. (1985) Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.* **28**, 181–208.

Karn, M. N. and Penrose, L. S. (1951) Birth weight and gestation time in relation to maternal age, parity, and infant survival. *Annals Eugen.* **16**, 147–64.

Kimura, J. and Crow, J. F. (1963) The measurement of effective population numbers. *Evolution* **17**, 279–88.

Kimura, J. and Ohta, T. (1971) *Theoretical Aspects of Population Genetics*. Princeton University Press: Princeton, N.J.

Lande, R. (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution* **30**, 314–34.

Lande, R. (1979) Quantitative genetic analysis of multivariate evolution, applied to brain–body size allometry. *Evolution*, **33**, 402–16.

Leigh, E. G. (1981) The average lifetime of a population in a varying environment. *J. Theor. Biol.* **90**, 213–39.

Levin, S., Cohen, D. and Hastings, A. (1984) Dispersal strategies in patchy environments. *Theor. Pop. Biol.* **26**, 165–91.

Lynch, M. (1984) The selective valve of alleles underlying polygenic traits. *Genetics* **108**, 1021–33.

May, R. M. (1976) Simple mathematical models with very complicated dynamics. *Nature* **261**, 459–467.

May, R. M. and Dodson, A. P. (1986) Population dynamics and the rate of evolution of pesticide resistance. In *Pesticide Resistance: Strategies and Tactics for Management*, pp. 170–93. National Academy Press, Washington, D.C.

Maynard Smith, J. (1983) The genetics of stasis and punctuation. *Ann. Rev. Genet.* **17**, 11–25.

Mayr, E. (1954) Change of genetic environment and evolution. In *Evolution as a Process* (J. Huxley, A. C. Hardy and E. B. Ford, eds) pp. 157–80. Allen and Unwin, London.

Motro, U. and Thomson, G. (1982) On heterozygosity and the effective size of populations subject to size changes. *Evolution* **36**, 1059–66.

Mueller, L. D., Wilcox, B. A., Ehrlich, P. A., Heckel, D. G. and Murphy, D. D.(1985) A direct assessment of the role of genetic drift in determining allele frequency variation in populations of *Euphydryas editha*. *Genetics* **110**, 495–511.

Nagylaki, T. 1975. Conditions for the existence of clines. *Genetics* **80**, 595–615.

Nagylaki, T. (1977) *Selection in One- and Two-Locus Systems*. Springer-Verlag, New York.

Nagylaki, T. (1978) Clines with asymmetric migration. *Genetics* **88**, 813–27.

Nagylaki, T. (1979) The island model with stochastic migration. *Genetics* **91**, 163–76.

Nei, M., Maruyama, T. and Chakraberty, R. (1975) The bottleneck effect and genetic variability in populations. *Evolution* **29**, 1–10.

Nei, M. and Grauer, D. (1984) Extent of protein polymorphism and the neutral mutation theory. *Evol. Biol.* **17**, 73–118.

Newman, C. M., Cohen, J. E. and Kipnis, C. (1985) Neo-darwinian evolution implies punctuated equilibria. *Nature* **315**, 400–1.

Ohta, R. (1972) Population size and rate of evolution. *J. Mol. Evol.* **1**, 305–14.

Parsons, P. A. (1983) *The Evolutionary Biology of Colonizing Species*. Cambridge University Press, Cambridge.

Provine, W. B. (1985). The R.A. Fisher–Sewall Wright controversy and its influence upon modern evolutionary biology. *Oxford Surveys in Evol. Biol.* **2**, 197–19.

Rosenzweig, M. L. (1974) On the evolution of habitat selection. *Pr. First Internat. Cong. Ecol.* pp. 401–4. Center for Agricultural Publishing and Documentation, Wageningen, Netherlands.

Rosenzweig, M. L. (1985) Some theoretical aspects of habitat selection. In *Habitat Selection in Birds* (M. Cody, ed.), pp. 517–40. Academic Press, New York.

Rosenzweig, M. L., Brown, S. and Vincent, T. L. (1987) Red Queens and ESS: the coevolution of evolutionary rates. *Evol. Ecol.* **1**, 59–96.

Schaffer, W. M. and Rosenzweig, M. L. (1978) Homage to the Red Queen I. Coevolution of predators and their victims. *Theor. Pop. Biol.* **9**, 135–57.

Slatkin, M. (1977) Gene flow and genetric drift in a species subject to frequent local extinctions. *Theor. Pop. Biol.* **12**, 253–62.

Slatkin, M. (1985) Gene flow in natural populations. *Ann. Rev. Ecol. Syst.* **16**, 393–430.

Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science* **236**, 787–92.

Stanley, S. M. (1979) *Macroevolution: Pattern and Process*. W. H. Freeman, San Francisco.

Taylor, C. E. (1976) Genetic variation in heterogeneous environments. *Genetics* **83**, 887–94.

Templeton, A. R. and Rothman, E. D. (1981) Evolution in fine-grained environments. II. Habitat selection as a homeostatic mechanism. *Theor. Pop. Biol.* **19**, 326–40.

Travis, J. and Trexler, J. C. (1986) Interactions among factors affecting growth, development and survivorship in experimental populations of *Bufo terrestris* (Anura: Bofonidae). *Oecologia* **69**, 110–16.

Via, S. and Lande, R. (1985) Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution* **39**, 505–22.

Wallace, B. (1959) Influence of genetic systems on geographic distribution. *Cold Spring Harbor Symp. Quant. Biol.* **24**, 193–204.

Wallace, B. (1975) Hard and soft selection revisited. *Evolution* **29**, 465–73.

Whitham, T. G. (1980) The theory of habitat selection: Examined and extended using Pemphigus aphids. *Amer. Natur.* **115**, 449–66.

Whittaker, R. H. (1967) Gradient analysis of vegetation. *Biol. Rev.* **42**, 207–64.

Wright, S. (1977) *Evolution and the Genetics of Populations. Vol. 3. Experimental Results and Evolutionary Deductions*. University of Chicago Press, Chicago.

Wright, S. (1982) The shifting balance theory and macroevolution. *Ann. Rev. Genet.* **16**, 1–19.