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THE EVOLUTION OF DISPERSAL IN SPATIALLY AND TEMPORALLY VARYING ENVIRONMENTS

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Abstract.—Using a simple two-patch model, we examine how patterns of spatial and temporal variation in carrying capacities affect natural selection on dispersal. The size of the population in each patch is regulated separately, according to a discrete-generation logistic equation, and individuals disperse from each patch at propensities determined by their genotype. We consider genotypes that express the same dispersal propensities in both patches and genotypes that express patch-specific disperal propensities. Contrary to previous analyses, our results show that some level of dispersal is favored by selection under almost all regimes of habitat variability, including a spatially varying and temporally constant environment. Furthermore, two very different polymorphisms are favored under different conditions. When carrying capacities vary spatially but not temporally, any number of genotypes with patch-specific dispersal propensities in ratios inversely proportional to the ratio of the carrying capacities can coexist. This result extends previous analyses to show that dispersal is favored in such an environment if individuals can alter dispersal propensities in response to environmental cues. In contrast, when carrying capacities vary both spatially and temporally but differ in mean or variance, a polymorphism of only two genotypes (a high-dispersal and a no-dispersal genotype) is favored when the only genotypes possible are ones expressing the same dispersal propensity in both patches. However, this dimorphism can be invaded and replaced by one genotype with a particular combination of patch-specific dispersal propensities in a ratio also inversely proportional to the ratio of the average population sizes. We discuss a number of testable predictions this model suggests about the amounts of phenotypic and genetic variation in dispersal characters that are expected both within and between populations, and the degree to which the expression of phenotypic characters affecting dispersal propensity should be sensitive to environmental conditions. The model also suggests novel mechanisms for coexistence between competing species in varying environments.

The fitness of an organism is determined jointly by its phenotype and the environment it experiences; the term *environment* here encompasses the full panoply of factors that can influence birth and death rates. Because the environment varies across space and through time, fitness likewise will vary in space and time. Dispersal, the movement of individuals between populations, modifies the array of ecological conditions that a genotype may experience (Templeton and Rothman 1981) and can be viewed as an example of a bet-hedging strategy (Seger and

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Brockmann 1987; Phillipi and Seger 1989). The outcome of natural selection on dispersal characters should thus reflect the spatiotemporal variability of the environment.

Dispersal can also influence local population size and stability (Vance 1980; Holt 1985) and thereby alter the selectively relevant environment. Given that fitnesses are density-dependent, the flux of dispersers into and out of a population should affect realized fitnesses in that population. Therefore, a full analysis of the evolution of dispersal must simultaneously examine spatiotemporal variation in ecological conditions and the demographic consequences of dispersal on population size.

Previous workers have identified several circumstances favoring dispersal (for a detailed review see Johnson and Gaines 1990). Competitive interactions among relatives can favor a nonzero dispersal rate between patches, even in a spatially and temporally constant environment (Hamilton and May 1977; Comins et al. 1980; Comins 1982; Motro 1982a, 1982b, 1983; Frank 1986). Asymmetrical competitive interactions (e.g., dominance relations among individuals) can promote dispersal in a temporally constant but spatially varying environment (Pulliam 1988). However, if interactions occur mainly among nonkin and no asymmetrical competitive interactions exist, previous studies suggest that a combination of spatial and temporal variation is needed for nonzero dispersal rates to be favored (Gadgil 1971; Roff 1975; Levin et al. 1984). Population genetic models of selection in multipatch environments indicate that if allelic fitnesses are temporally constant but different alleles are favored in different patches, alleles for reduced dispersal can always invade (see, e.g., Balkau and Feldman 1973; Teague 1977; Asmussen 1983; Liberman and Feldman 1989). Ecological models also suggest that individuals should not disperse in spatially varying but temporally constant environments (Hastings 1983; Holt 1985).

Animals and plants exhibit a broad spectrum of dispersal strategies. The simplest dispersal strategy is for individuals to disperse at constant per capita rates, regardless of the environment: an unconditional dispersal strategy. This has been the kind of dispersal strategy examined in most previous analyses of the evolution of dispersal. At the other extreme, an organism could have a highly flexible dispersal rule, which is sensitive to habitat type, local population size, and other predictors of local fitness: a conditional dispersal strategy.

In this article, we consider the evolution of a simple conditional strategy, in which the per capita dispersal rate of a given genotype depends solely on habitat type (but not density, etc.)—a simple form of phenotypic plasticity. Our focus is on how spatial and temporal variation in population sizes influences the evolution of dispersal, given that local fitnesses are density-dependent, and on comparing the success of unconditional and conditional dispersal strategies. In contrast to previous studies, our results indicate that dispersal can be favored even in spatially varying but temporally constant environments. Moreover, substantially different types of dispersal polymorphisms can develop under different regimes of spatial and temporal variation. A novel prediction to emerge is that an inverse correlation across space should exist between local population abundance and local dispersal rate.

THE MODEL

For simplicity, consider an asexual species with discrete generations occupying two patches coupled by dispersal. The total population is comprised of a number of genotypes that differ only in their propensity to move between patches. We label each genotype by its propensity to disperse. The life cycle consists of two consecutive stages: population growth and regulation within each patch, and dispersal between patches. Let $n_{i,k}(t)$ be the number of individuals of genotype k ($k = 1, 2, \ldots, d - 1, d$) in patch i ($i = 1, 2$) at the beginning of generation t; the total population size in patch i is $N_i(t) = \Sigma\, n_{i,k}(t)$. Following population regulation but before dispersal, the total population size in patch i is given by the exponential-logistic model (Moran 1950; Ricker 1954; Cook 1965; May and Oster 1976)

$$N_i'(t) = \exp(r_i(t) \cdot \{1 - [N_i(t)/K_i(t)]\}) \cdot N_i(t), \tag{1}$$

where $r_i(t)$ and $K_i(t)$ are, respectively, the intrinsic growth rate and the carrying capacity in patch i at time t. Because all genotypes are assumed to be identical within patches, the proportions of genotypes in patch i before and after population regulation are the same. Variation in population size is driven by spatial and temporal variation in carrying capacities, and because fitnesses are density-dependent, this induces spatial and temporal variation in fitness.

The life cycle is completed by dispersal. The proportion of individuals of a given genotype born in patch i that disperses to patch j each generation is assumed to be a constant, m_{ij} ($i, j = 1, 2: 0 \le m_{ij} \le 1$). No individuals die during dispersal. For genotypes with unconditional dispersal strategies, $m_{12} = m_{21}$, whereas for genotypes with conditional dispersal strategies, $m_{12} \ne m_{21}$. In the Appendix, we outline the effects of altering these assumptions about dispersal.

In our numerical studies of the evolutionary dynamics of this system, population sizes are recorded as real numbers to a precision of 20 significant digits to reduce sampling error. Initial population size in each patch is set equal to the mean carrying capacity of that patch.

We consider four distinct patterns of spatial and temporal variation in carrying capacities (Chesson 1985): a spatially and temporally constant environment, that is, $K_1(t) = K_2(t) = k$; a temporally varying but spatially constant environment, that is, $K_1(t) = K_2(t) = k(t)$, where $k(t)$ is drawn from a normal distribution; a spatially varying but temporally constant environment, that is, $K_1(t) = k_1$ and $K_2(t) = k_2$ where $k_1 \ne k_2$; and a spatially and temporally varying environment, that is, $K_1(t) = k_1(t)$ and $K_2(t) = k_2(t)$, where $k_1(t)$ and $k_2(t)$ are drawn each generation from a bivariate normal distribution. We alter the distributions of $k_1(t)$ and $k_2(t)$ in mean and variance. We also vary the degree of within-generation correlation between $k_1(t)$ and $k_2(t)$ by drawing $k_1(t)$ and $k_2(t)$ each generation from a bivariate distribution with a specified correlation but without serial autocorrelations. We examine only the range of variation in carrying capacities in which the population in a patch will not be driven totally extinct (i.e., variances for which the probability of $k_i(t) < 0$ is extremely small). Therefore, selection on dispersal caused by outright population extinction is not part of our study. Uniform, nor-

mal, and lognormal distributions of carrying capacity all give qualitatively similar results, so we present only results using a normal distribution for $k_i(t)$.

For each set of environmental conditions, we assume that the population is initially comprised of 21 genotypes with unconditional dispersal strategies that span the range of potential dispersal propensities (0%–100%) in 5% intervals. (The 0% genotype is approximated with a 0.1% dispersal propensity, hereafter referred to as the ~0% genotype, given that it is biologically unreasonable to assume that dispersal is completely impossible.) All genotypes are initially equally abundant in each patch. After many (>10,000) generations we ask whether one genotype is near fixation or whether the population is converging toward a polymorphic equilibrium. We then run new simulations in which the successful dispersal types compete pairwise against the full range of clones.

Having determined the evolutionarily stable state of the population and given the implicit constraint that dispersal is an unconditional strategy, we then introduce, pairwise, the full range of genotypes with conditional dispersal strategies. Under many conditions, a large set of genotypes with conditional dispersal strategies can coexist with the successful genotypes having unconditional dispersal strategies. Furthermore, some subset can often completely displace all other genotypes. We identify both the set that can coexist with successful genotypes having unconditional dispersal strategies and the subset that will drive all others extinct.

RESULTS

We first summarize those modifications in the model and parameter combinations that have no qualitative effects on the outcomes. In model 1, spatial and temporal variation in $r_i(t)$ over ranges precluding chaotic dynamics ($r_i(t) < 2.692$) have no qualitative effect on the results, and so $r_1(t) = r_2(t) = 1.00$ in all the analyses described below (elsewhere we will describe the consequences of chaotic population dynamics for the evolution of dispersal). Using density-dependent models different from equation (1) does not affect the qualitative outcome, nor does changing the temporal ordering of dispersal and population regulation. Finally, we never observed a case in which the outcome depends on initial conditions. Our principal findings, summarized in table 1, are described more fully in the following sections.

Spatially and Temporally Constant Environment

Many genotypes can coexist at neutral equilibria with spatially and temporally constant carrying capacities. For the set of genotypes with unconditional dispersal strategies at this neutrally stable equilibrium, each genotype has equal relative frequencies in the two patches. Altering the relative frequencies of genotypes causes the system to come to another equilibrium, but no genotype is excluded.

When one genotype with conditional dispersal strategies or many genotypes that all have greater dispersal propensities from the same patch (i.e., all with $m_{ij} < m_{ji}$) are introduced into populations dominated by a set of unconditional dispersal

TABLE 1

SUMMARY OF THE MAJOR RESULTS FROM THE STUDY

	VARIANCES	
MEANS	Zero	Greater than Zero
Equal	Usually no selection	Correlation = 1.0—usually no selection
		Correlation < 1.0—$m_{12} = m_{21} = 0.50$
Unequal	Unconditional—$m_{12} = m_{21} = 0.00$	Unconditional—dimorphism
	Conditional—continuous polymorphism ($m_{12} = (K_2/K_1)m_{21})$	Conditional—one genotype with $(m_{12}/m_{21}) = (\overline{K}_2/\overline{K}_1)$

NOTE.—The body of the table gives the major outcomes of selection in the types of environment specified by the means and variances of the carrying capacities. Outcomes beside the term Unconditional are those resulting when only genotypes with unconditional dispersal strategies are considered. Outcomes beside the term Conditional are those resulting when both conditional and unconditional dispersal genotypes are considered.

strategies at equilibrium, the genotypes with conditional dispersal strategies always go extinct. The reason is that biased dispersal pushes the population size in one patch perpetually above K and the other perpetually below K. However, genotypes with conditional dispersal strategies coexist with each other and with genotypes having unconditional strategies if two or more genotypes are introduced, such that some clones have $m_{12} < m_{21}$ while others have $m_{12} > m_{21}$. Again, the system comes to a neutrally stable equilibrium, with equal numbers of individuals leaving both patches each generation.

Temporally Varying but Spatially Constant Environment

The above results are unchanged when Ks vary through time but remain uniform across space, that is, $K_1(t) = K_2(t) = k(t)$.

Spatially Varying but Temporally Constant Environment

When the carrying capacities of the two patches vary spatially but not temporally and only genotypes with unconditional dispersal strategies are present, selection drives the population toward the lowest accessible propensity (i.e., $m_{12} = m_{21} \approx 0.0$). Increasing the difference between K_1 and K_2 increases the rate at which this genotype approaches fixation.

A genotype with conditional dispersal strategies can invade populations fixed for a genotype having unconditional dispersal strategies near zero, if the invader satisfies the inequality

$$m_{12}/m_{21} \geq K_2/K_1 \tag{2}$$

(fig. 1A). Furthermore, if genotypes with dispersal propensities satisfying the equality in equation (2) are present, all other genotypes not satisfying this equality go extinct. Any number of genotypes satisfying this equality can coexist in the equilibrium, with each genotype having equal relative frequencies in the two patches. This line of equilibrium passes through the origin (i.e., $m_{12} = m_{21} = 0.00$) and has a slope inversely proportional to the ratio of the carrying capacities ($m_{12} = (K_2/K_1)m_{21}$) (fig. 1A). This equilibrium line can be derived analytically for a continuous-time version of this model by including conditional dispersal strategies in the model examined by Holt (1985). Successful genotypes have high dispersal propensities from the low-K patch and low dispersal propensities from the high-K patch.

The equilibrium line for this polymorphism reflects the fact that an incremental change in population size in the low-K patch tends to have greater impact on fitness than does an equal change in the high-K patch. Consider the fitness consequences of dispersal when both patches are at their carrying capacities. Figure 1B presents the average fitnesses of the full range of genotypes, each respectively at fixation. Genotypes above the equilibrium line disperse relatively more individuals to the low-K patch each generation (i.e., $m_{12}K_1 > m_{21}K_2$), which causes the population in the high-K patch to be below and the population in the low-K patch to be above their respective carrying capacities. (Hastings [1983] first pointed this out for $m_{12} = m_{21}$; see also Holt 1985 and Cohen and Levin 1991.) Reduced dispersal into the low-K patch is thus favored; most dispersers are moving into
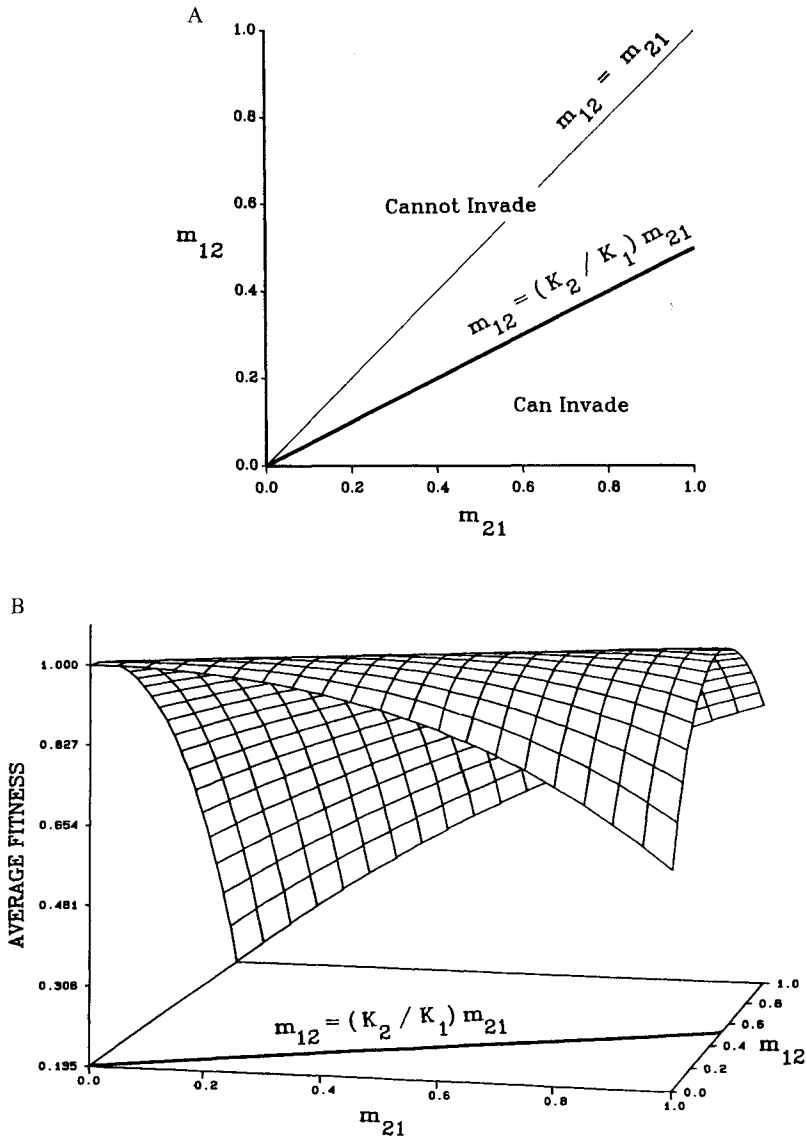
Fig. 1.—The success of genotypes when the carrying capacities of the two patches vary spatially but not temporally. In all simulations used to generate this figure, $K_1 = 100$ and $K_2 = 50$. A, The genotypes with conditional dispersal strategies that can invade populations of the ~0% genotype ($m_{12} = m_{21} = 0.001$). All simulations begin with the ~0% genotype at a relative frequency of 0.99 in both patches and the invading genotype at 0.01 in both patches. All genotypes below the equilibrium line (labeled $m_{12} = (K_2/K_1)m_{12}$) increase in frequency and come to an equilibrium with both genotypes coexisting. All genotypes above this line cannot invade. Any genotype on this equilibrium line will invade and drive extinct any combination of genotypes not on the line. Any number of genotypes having dispersal propensities along this line will coexist. B, The average fitness of genotypes when each is at fixation in the two patches under these conditions. The equilibrium line is given in the m_{12}, m_{21} plane.

the low-K patch with detrimental fitness consequences, and this is not offset by the fitness gains obtained by individuals moving into the high-K patch (fig. 1B). Conversely, genotypes below the equilibrium line disperse relatively more individuals to the high-K patch each generation ($m_{12}K_1 < m_{21}K_2$), which causes the population in the high-K patch to be above and the population in the low-K patch to be below their respective carrying capacities. Here, the majority of dispersers are also moving into a patch with detrimental fitness consequences. However, higher fitnesses can be gained by dispersing more individuals into the low-K patch because of the greater fitness rewards there relative to the fitness costs in the high-K patch. Therefore, increased dispersal into the low-K patch is favored (fig. 1B). Concordant with changes in the relative frequencies of the dispersal strategies, population sizes will shift in each patch. All dispersal strategies along the equilibrium line (the ridge of the adaptive surface) have equal fitness, because equal numbers of individuals move into and out of both patches each generation (i.e., $m_{12}K_1 = m_{21}K_2$ for all genotypes on the equilibrium line), and each patch is demographically balanced with the number of individuals in a patch equaling the local carrying capacity. These considerations suggest that the ESS of the population should be along this line.

Spatially and Temporally Varying Environment

Ks with equal means and variances.—When the carrying capacities of the two patches vary both spatially and temporally in an uncorrelated fashion and with equal means and variances, the genotype with $m_{12} = m_{21} = 0.50$ is always favored. A dispersal propensity of 0.5 is favored because population sizes in both patches have equal probabilities in any given generation of being above K while the other patch is below K.

Even small amounts of temporal variation favor dispersal in such an environment. To assess the generality of this result, we ran simulations with various degrees of correlation between the Ks and different amounts of variance in the Ks. Neither of these alter the outcome of selection, but both do affect the strength of selection. Making the correlation between the carrying capacities of the two patches more negative causes the genotype with $m_{12} = m_{21} = 0.50$ to approach fixation more quickly (fig. 2A); a negative correlation increases the intensity of selection on dispersal by increasing the probability that one patch is above while the other patch is below K. (Only in the limit of a perfect positive correlation between the carrying capacities is there no selection on dispersal.) Similarly, increasing variance in the Ks also leads to more rapid fixation (fig. 2B); increased variance magnifies the average fitness gains and decrements of dispersal when populations are respectively below and above their Ks. (Only in the limit of no variance in carrying capacities is there no selection on dispersal.)

Ks with different means but equal variances.—If the mean carrying capacities of the two patches differ, the genotype with $m_{12} = m_{21} = 0.50$ is no longer favored. When only sets of genotypes having unconditional dispersal strategies are considered, populations evolve toward a persistent polymorphism consisting of ~0% ($m_{12} = m_{21} = 0.001$) and 60% ($m_{12} = m_{21} = 0.60$) dispersal genotypes (table 2). The ~0% genotype is more common in the higher-mean carrying-
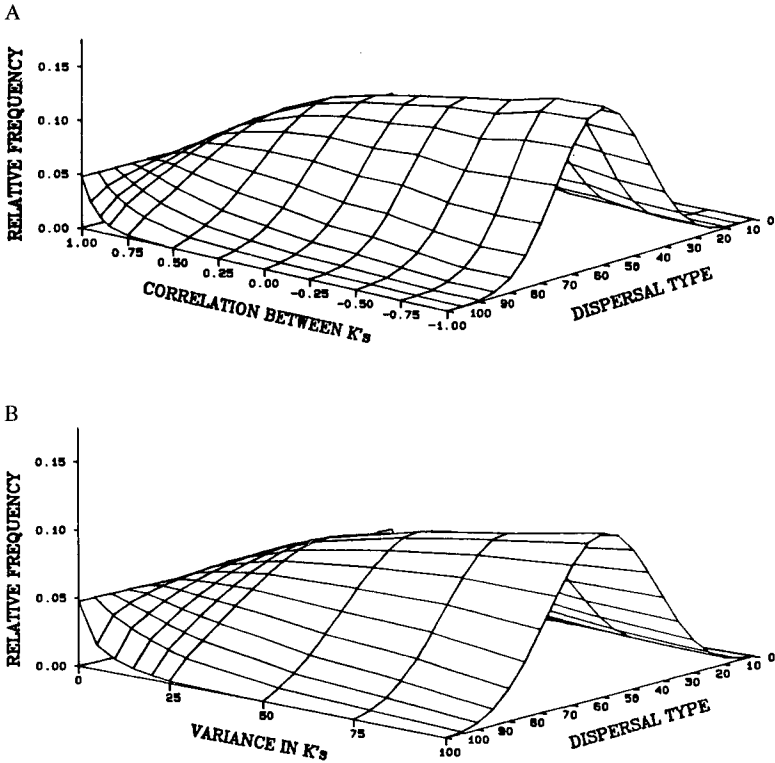
Fig. 2.—The consequences of altering the correlations between and the variances of the carrying capacities of two patches that have the same mean carrying capacities. *A*, The relative frequencies of the 21 genotypes with unconditional dispersal strategies after 5,000 generations for simulations using different correlations between the carrying capacities. In these simulations both patches have carrying-capacity means of 100.0, variances of 100.0, and the specified correlation each generation. *B*, The relative frequencies of the 21 genotypes with unconditional dispersal strategies after 5,000 generations for simulations using different variances in the carrying capacities. Both patches have carrying-capacity means of 100.0 and correlations of 0.0. The two patches have the same variances in any given simulation. The means of 100 simulation runs for each correlation and each variance are presented.

capacity patch, and the 60% genotype is more common in the lower-mean carrying-capacity patch (table 2). Increasing the difference in mean Ks between the two patches increases the relative abundances of the low-dispersal clone (table 2).

A broad range of genotypes having conditional dispersal strategies can invade this polymorphism. An example is presented in figure 3. Most genotypes with $m_{12} < m_{21}$ can invade the polymorphism (assuming $\overline{K}_1 > \overline{K}_2$, where $\overline{K}_i$ is the mean K for patch i); of those with $m_{12} < m_{21}$, only a small range of genotypes with very low or very high dispersal propensities cannot invade the polymorphism (e.g., fig. 3), and these ranges increase as the difference between the mean carrying capacities increase. In contrast, almost all genotypes with $m_{12} > m_{21}$ cannot

TABLE 2

THE RELATIVE FREQUENCIES OF THE ~0% AND 60% GENOTYPES IN POLYMORPHISMS AND THE GENOTYPE WITH CONDITIONAL DISPERSAL STRATEGIES THAT DISPLACED ALL OTHERS WHEN THE CARRYING CAPACITIES OF THE TWO PATCHES VARIED BOTH SPATIALLY AND TEMPORALLY BUT DIFFERED IN MEAN VALUE

MEAN Ks		RELATIVE FREQUENCY IN POLYMORPHISM*				MOST SUCCESSFUL GENOTYPE†	
		PATCH 1		PATCH 2			
1	2	~0%	60%	~0%	60%	m_{12}	m_{21}
100	98	.02	.98	0	1.00	.49	.50
100	95	.06	.94	.01	.99	.48	.50
100	90	.11	.89	.02	.98	.45	.50
100	75	.27	.73	.04	.96	.41	.56
100	50	.50	.50	.06	.94	.34	.68

NOTE.—Carrying capacity variances = 100.0 and correlations = 0.00 for all simulations considered in this table. The mean carrying capacities are given in the first two columns of the table.
* The relative frequencies of the ~0% and 60% genotypes in the polymorphism when only genotypes having unconditional disperal strategies are considered.
† The dispersal propensities of the genotype with conditional dispersal strategies that would go to fixation under these conditions.

invade the polymorphism; only a very small range of genotypes with m_{12} only slightly larger than m_{21} and with both near 0.65 can invade (e.g., fig. 3), and this range decreases as the difference between the mean carrying capacities increases.

Of those genotypes that can invade the polymorphism, one drives all others extinct (table 2). The ratio of the dispersal propensities of this evolutionarily stable strategy (ESS) is inversely proportional to the ratio of the mean carrying capacities of the two patches (i.e., $m_{21}/m_{12} = \overline{K}_1/\overline{K}_2$). A similar relation describes the line of equilibrium in spatially varying but temporally constant environments (eq. [2]; fig. 1). However, with temporal variation imposed on persistent (average) spatial variation, the population becomes monomorphic for a particular conditional dispersal strategy. Increasing the variances of the Ks or making the correlation between the Ks more negative does not alter which is the winning strategy, for a given difference in the mean Ks, but does increase the rate at which this strategy approaches fixation. When the successful genotype is fixed, dispersal has no effect on local population density, which on the average equals $\overline{K}_i$.

Ks *with different variances but equal means.*—Analogous results are obtained when the carrying capacities of the two patches have the same mean but different variances, because average population size tends to be smaller in the patch with the larger variance (Vance 1980). However, differences in variances have much smaller effects on the outcome than do differences in means. For example, when the carrying capacities of both patches have means of 100.0 but the variance is 0.0 for patch 1 and 500.0 for patch 2, the relative frequencies (combining both patches) in the resulting polymorphism (when only genotypes with $m_{12} = m_{21}$ are considered) are 0.03 for the ~0% genotype and 0.97 for the 60% type. Under
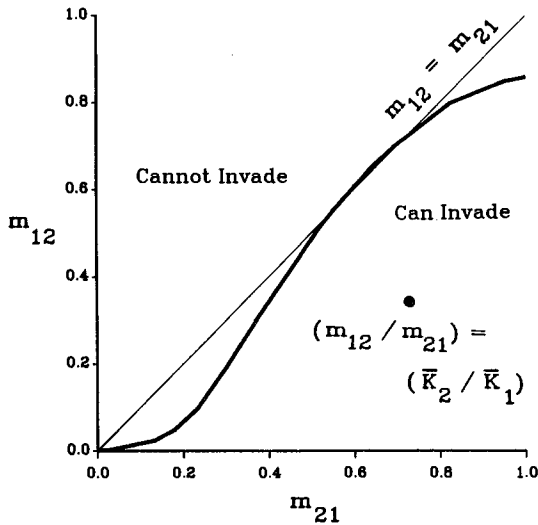
FIG. 3.—The genotypes with conditional dispersal strategies that can invade the polymorphism of genotypes (i.e., ~0% and 60% genotypes) when the carrying capacities of the two patches vary spatially and temporally but have different mean carrying capacities. In the simulations used to generate this figure, the carrying capacity for patch 1 has mean of 100, and patch 2 has mean of 50. Carrying-capacity variances are 100 for both patches. All simulations begin with a genotype having $m_{12} = m_{21} = 0.001$ at a relative frequency of 0.495 in patch 1 and 0.10 in patch 2, a genotype having $m_{12} = m_{21} = 0.60$ at a relative frequency of 0.495 in patch 1 and 0.89 in patch 2 (these are the genotypes at their polymorphic equilibrium in the two patches), and the invading genotype at 0.01 in both patches. All genotypes below the *curved, thick line* can invade the polymorphism and come to an equilibrium. Genotypes above the *curved, thick line* cannot invade the polymorphism. The genotype identified by the *closed circle* ($m_{12} = 0.34$, $m_{21} = 0.68$ under these conditions [table 2]) displaces all others and goes to fixation, regardless of initial population composition.

these same conditions, the genotype with conditional dispersal strategies that will drive all others extinct has $m_{12} = 0.49$ and $m_{21} = 0.52$.

DISCUSSION

In our model, selection for dispersal occurs whenever there is variation in fitness between patches (cf. Bull et al. 1987). Fitness differences between patches can be generated either by the external environment (expressed in our model as fluctuations in local carrying capacities) or by biases in dispersal that push local population sizes away from local carrying capacities. Selection tends to equilibrate realized fitnesses across space. Whether selection leads to monomorphism or polymorphism for dispersal is determined by an interaction between environmental conditions and the types of strategies present in the populations (unconditional or conditional).

Disperal is a neutral character if the environment is uniform across space (whether or not the environment varies in time), unless all genotypes with condi-

tional dispersal strategies have higher dispersal propensities from the same patch. This seems unlikely as a general rule, so we conclude that ecological variation affecting all patches in a region similarly (e.g., seasonal or yearly climatic changes) is irrelevant to the evolution of dispersal.

Dispersal is favored in all other regimes of spatial and temporal variation (table 1). When the means and variances of carrying capacities are equal, individuals dispersing uniformly ($m_{12} = m_{21} = 0.50$) are favored. This result is qualitatively consistent with previous studies, which assume different models of population regulation (Gadgil 1971; Roff 1975; Levin et al. 1984) and different methods for generating variability in ecological conditions (e.g., local extinctions: Van Valen 1971; Comins et al. 1980; Comins 1982).

We also find that dispersal between patches can be favored in a spatially varying but temporally constant environment, if organisms can express conditional dispersal strategies. By contrast, previous studies have considered only unconditional dispersal strategies and conclude that zero dispersal is the ESS (e.g., Balkau and Feldman 1971; Teague 1977; Asmussen 1983; Hastings 1983; Holt 1985; Liberman and Feldman 1989). Without temporal heterogeneity, the population can consist of any mix of strategies along the equilibrium line such that the ratio of the conditional dispersal propensities is inversely proportional to the ratio of local carrying capacities (eq. [2]; fig. 1). Cohen and Levin (1991) also find that in spatially heterogeneous environments no one fixed dispersal rate may be evolutionarily stable but rather many dispersal types can invade and coexist. Our model suggests that the coexisting dispersal types are a nonrandom subset of the possible types.

Our model also predicts two extremes of dispersal polymorphism; these polymorphisms only arise in spatially heterogeneous environments. A continuum of dispersal strategies, discussed in the previous paragraph, is expected if carrying capacities vary spatially but not temporally. However, a polymorphism of two discrete dispersal types with unconditional dispersal strategies can exist when carrying capacities vary spatially and temporally and have different means or variances. The expression of dispersal characters by individuals in the continuous polymorphism should be sensitive to environmental conditions associated with different patch types (i.e., a conditional strategy), whereas the expression of dispersal characters in the dimorphism should show little sensitivity to environmental conditions (i.e., an unconditional strategy). Also, species displaying these two polymorphisms should differ greatly in population structure. The phenotypic and genetic variation for dispersal characters in a species with a continuous polymorphism should be large within patches but small between patches. In contrast, the phenotypic and genetic variation for dispersal characters in a species having a dimorphism should be small within patches but large between patches.

The dimorphism is vulnerable to invasion by phenotypically plastic genotypes, and given the complete range of potential variation in local dispersal propensities, the population evolves toward a monomorphism of a single conditional dispersal strategy. A species with this phenotypically plastic dispersal strategy will superficially resemble a species having the dimorphism. This type of species can be discriminated from the dimorphism by noting that a species of this phenotypically

plastic type should have little genetic variation in dispersal characters both within and between populations, and expression of these characters should be sensitive to environmental conditions.

Dispersal polymorphisms are found in many plants and animals (seed dimorphisms in plants: see, e.g., Koller and Roth 1964; Baker and O'Dowd 1982; Venable and Levin 1985a, 1985b; wing dimorphisms in insects: reviewed in Harrison 1980; Roff 1986; continuous seed polymorphisms: Venable et al. 1987; continuous wing polymorphisms in insects: Desender 1989). It is difficult to relate these intriguing examples in detail to our model because key data are typically unavailable. For example, wingless and winged morphs of a lygaeid bug (*Horvathiolus gibbicollis*) breed true over a range of environmental conditions in the laboratory and thus may represent a truly dimorphic species, but only anecdotal evidence concerning habitat stability and the level of a population differentiation is available (Solbreck 1986). The expression of dispersal characters is often not inflexible but rather is influenced by environmental factors in a number of apparently dimorphic species (Harrison 1980; Roff 1986). Thus, many of these species may not be truly dimorphic, since substantial variation in dispersal characters within each defined morph is often present (Walker and Sivenski 1986). Perhaps, these species illustrate how a phenotypically plastic genotype tends to supplant a dispersal dimorphism. By focusing attention on the relationships among key variables, our model suggests a framework for future work on these polymorphisms.

Species may not conform perfectly to the predictions of this model because the evolution of dispersal characters is often influenced by the evolution of other characters. For example, dispersal characters are often correlated with characters for living in a seasonal environment, such as dormancy and diapause (Dingle 1978; Vepsäläinen 1978; Venable and Lawlor 1980; Levin et al. 1984; Venable 1985), and with other life-history parameters, such as growth rate and fecundity (Roff 1984, 1986; Zera and Rankin 1989). Such relationships could greatly shift the outcome of evolution away from that expected when only selection on dispersal is operating.

A striking, empirically testable prediction to emerge is that local population sizes and the proportions of local populations that disperse should be negatively correlated if populations are at both their evolutionary and demographic equilibria and if fitnesses are density-dependent. In other words, individual turnover because of dispersal should be greatest in low-density populations. This is true regardless of whether one considers unconditional or conditional dispersal strategies. The strength of this relationship should also increase with increasing differences in local carrying capacities.

Our results complement those obtained by Pulliam (1988), who considers a model in which individuals actively select which habitat to occupy and must choose between habitats that can maintain populations without immigration (source habitats) and habitats in which populations can only be maintained by continual immigration (sink habitats). Individuals breeding in source habitats produce more offspring than necessary to replace themselves (fitness > 1.0), but individuals breeding in sink habitats do not produce enough offspring to replace

themselves (fitness < 1.0). In both Pulliam's (1988) and our models large segments of populations in "good" habitats (source habitats or high carrying-capacity habitats) will not disperse, while many individuals in "bad" habitats (sink habitats or low carrying-capacity habitats) will disperse each generation. Evaluating whether the habitat-specific demographic rates found in bad habitats can support a population without continual immigration is required to separate these two models (Pulliam 1988).

Dispersal and Species Coexistence

Because our model deals with asexual genotypes, it can also be interpreted as a model of competition between two or more species that are identical except in their propensity to disperse. Monomorphism corresponds to competitive exclusion. In keeping with previous work on ecological variability and species coexistence (Chesson 1985, 1986), we find that temporal variation by itself does not necessarily foster coexistence. However, coupling spatial and temporal variation can permit coexistence if each species expresses unconditional dispersal strategies. Under these conditions, a low-dispersing species dominates high carrying-capacity patches, whereas a high-dispersing species dominates low carrying-capacity patches (table 2). A useful rule of thumb for stable coexistence in deterministic models of interspecific competition is that each species must exert density dependence more strongly on itself than on its competitor. In our system under these conditions, each species is numerically dominant in a different patch. Therefore, each species experiences competition from its own kind more than from the other, which is consistent with the rule of thumb. In many discussions of the role of dispersal in community ecology (e.g., in successional dynamics), a trade-off is assumed between dispersal and competitive ability so that dispersal allows one species to seek out temporary refuges from a superior competitor. However, our model does not assume this because all individuals are competitively identical within patches. An open question for future work with multiple-patch models is to determine how many species that differ only in dispersal behavior can coexist (see Kishimoto 1990).

Adaptation and Dispersal

Although our model does not address how adaptations affecting within-patch fitnesses and those affecting dispersal might coevolve, it is reasonable to expect some important relationships (cf. Levins 1964). If large, consistent differences in ecological conditions exist between patches and the environment is temporally constant, different adaptations are likely to be favored in different patches. A species in which individuals are well adapted to one patch type will have a high carrying capacity in that patch type but a low carrying capacity in the other. This scenario also selects for the evolution of low dispersal rates out of the patch type to which the species is well adapted (high K patches) and high dispersal rates out of patch types to which the species is not well adapted (low K patches) if the species can express conditional dispersal strategies, or for no dispersal between patches if the species can express only unconditional dispersal strategies (this study and references cited above). In the limit of no dispersal, selection takes

place independently within the two patches. With conditional dispersal strategies, by contrast, selection is likely to be biased toward the high-K patch.

Conversely, when the ecological conditions in patches fluctuate in time and space and the ranges of fluctuations for the patches broadly overlap, generalist adaptations that are successful over the range of ecological conditions experienced in the patches should be favored (Levins 1968; MacArthur 1972; Felsenstein 1979). These ecological conditions also favor high dispersal propensities. Under these conditions, selection favors similar adaptations in each patch and dispersal of these adaptations to every patch, which causes population differentiation to be much less likely.

From this preliminary consideration, a correlation appears to exist between the mechanisms affecting population differentiation in morphological, physiological, and behavioral characters determining ecological performance (i.e., fitness) within different patches and the evolution of characters affecting gene flow between patches (Holt 1987); the dispersal rates that most facilitate adaptive evolution under different ecological conditions (Levins 1964) appear to be the dispersal rates that will usually evolve. Obviously, models that incorporate more explicit ecological and genetic assumptions are needed to address the ecological and evolutionary interplay between the adaptations favored under different ecological conditions and the spread of genes that code for these adaptations throughout the range of a species. Such models will provide a basis for coupling evolutionary theories of adaptation and population differentiation (see, e.g., Wright's [1977] shifting balance theory) to ecological theories of population dynamics and species coexistence.

APPENDIX

EVOLUTION ASSUMING ALTERNATIVE DISPERSAL SYNDROMES

We consider two other dispersal syndromes besides the two-patch, stepping-stone model discussed in the body of this article (hereafter referred to as syndrome 1). Syndrome 2 is one in which dispersers from both patches first enter a dispersal pool, and individuals in this pool are then redistributed equally to the two patches. Here (and in the third syndrome described below) the proportion of individuals of a genotype that disperse from patch i into the dispersal pool (p) will be denoted by m_{ip} ($i = 1, 2$: $0 \leq m_{ip} \leq 1$). This syndrome can be thought of as representing the conditions in which the two patches cover equal areas, and so dispersers leaving the dispersal pool have equal chances of entering either

patch. We consider genotypes with $m_{1p} = m_{2p}$ and with $m_{1p} \neq m_{2p}$. Syndrome 3 is one in which dispersers from both patches first enter a dispersal pool, and individuals in this pool are then redistributed to the two patches in proportion to their carrying capacities. This syndrome can be thought of as representing the conditions in which the areas covered by the two patches are proportional to their carrying capacities, and so dispersers leaving the dispersal pool find the two patches in proportion to their carrying capacities. We examine these three dispersal syndromes because we feel they bracket a large range of the potential syndromes. The three syndromes usually have similar consequences for the evolution of dispersal, but under some conditions the different dispersal syndromes cause substantial differences in the outcome of selection. We highlight these differences here.

SPATIAL AND TEMPORALLY CONSTANT ENVIRONMENT

Analyses using each of the three dispersal syndromes give similar results under these conditions. See the Results section.

TEMPORALLY VARYING BUT SPATIALLY CONSTANT ENVIRONMENT

Analyses using each of the three dispersal syndromes give similar results under these conditions. See the Results section.

SPATIALLY VARYING BUT TEMPORALLY CONSTANT ENVIRONMENT

Results of analyses using the dispersal syndrome in which dispersers leaving the dispersal pool enter the two patches with equal frequency (syndrome 2) are similar to results of analyses using the direct dispersal syndrome (syndrome 1).

In contrast, results of analyses using the dispersal syndrome in which dispersers leaving the dispersal pool enter the two patches in proportion to the patches' carrying capacities (syndrome 3) are strikingly different. No selection on dispersal propensities occurs with this dispersal syndrome under these conditions. Because dispersers are redistributed to the two patches in proportion to the carrying capacities each generation, population sizes and consequently fitnesses in the two patches are usually not altered by dispersal. Consequently, dispersal is a neutral character under most combinations of dispersal propensities.

SPATIALLY AND TEMPORALLY VARYING ENVIRONMENT

When the carrying capacities of the two patches vary both spatially and temporally and their means and variances are equal, the genotype with $m_{1p} = m_{2p} = 1.00$ is always favored for both dispersal syndromes 2 and 3. Remember that the genotype with $m_{12} = m_{21} = 0.50$ is always favored with the direct dispersal syndrome (syndrome 1) because of the equal probabilities of fitness gains and losses in each patch. Complete dispersal into the dispersal pool is favored under these conditions because dispersers are redistributed back to the two patches in roughly equal frequencies each generation for both syndromes (always in equal frequencies for syndrome 2 and on the average for syndrome 3). As an example, consider the genotype with $m_{1p} = m_{2p} = 0.50$. Half of the individuals of this type move into the dispersal pool, but on the average half of those individuals are returned. Therefore, the actual dispersal proportion of individuals that move to the other patch is 0.25. The only genotype that can achieve an actual dispersal proportion of 0.50 is the type having $m_{12} = m_{21} = 1.00$.

When the carrying capacities vary both spatially and temporally and have different means, polymorphisms are also favored using dispersal syndromes 2 and 3 when only types with unconditional dispersal strategies are considered. However, genotypes with $m_{1p} = m_{2p} = 0.001$ and $m_{1p} = m_{2p} = 1.00$ are maintained in polymorphisms under both dispersal syndromes. The ranges of genotypes with conditional dispersal strategies that can invade polymorphisms under these two dispersal syndromes are similar to the ranges that can invade polymorphisms under the direct dispersal syndrome (e.g., fig. 3). The genotype with conditional dispersal strategies that can drive all others extinct for a given

set of conditions under syndrome 2 has dispersal propensities similar to the most success-
ful type under syndrome 1 (e.g., table 2). Apparently, no genotype with conditional dis-
persal strategies is uniformly superior to all others for a given set of conditions under
syndrome 3.

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