

CHAOTIC POPULATION DYNAMICS FAVORS THE EVOLUTION OF DISPERSAL

Dispersal—movement between populations—is a central feature in the biology of most organisms. There is an enormous literature on the ecology and evolution of dispersal (e.g., Swingland and Greenwood 1986). Many theoretical studies have explored factors favoring the evolution of dispersal, including competition among kin and inbreeding effects (e.g., Hamilton and May 1977; Comins 1982; Frank 1986; Taylor 1988; Wiener and Feldman 1991), the influences of extrinsically generated, spatiotemporal heterogeneity (Gadgil 1971; Roff 1975; Metz et al. 1983; Levin et al. 1984; Cohen and Levin 1991), and the interplay of within-population and between-population selection (Kuno 1981; Olivieri et al. 1995).

It has been demonstrated (Hastings 1983; Holt 1985) that if individuals disperse at fixed per capita rates between sites with local density dependence, then, without temporal heterogeneity, spatial heterogeneity in abundance alone is unable to select for dispersal (see also Liberman and Feldman 1989). The reason is that if habitats vary in carrying capacity, K , there is an asymmetric flow of individuals from high- K to low- K patches (Holt 1985). Such flow, in turn, reduces density in high- K patches (increasing fitness there) while increasing density in low- K patches (depressing fitness there). Because dispersal is basically moving individuals down gradients in fitness, on average, dispersal is disfavored in spatially (but not temporally) heterogeneous environments. These theoretical results highlight the importance of temporal heterogeneity in favoring dispersal. In a metapopulation of open patches, if the rank order of fitness among patches varies through time, dispersal can be selectively advantageous (Bull et al. 1987). Dispersal in effect provides an evolutionary strategy that permits individuals to exploit spatiotemporal variation in fitness. The theoretical expectation of a relation between temporal variability and dispersal matches some data from natural populations (Roff 1990).

We previously examined a simple two-patch, discrete-generation model in which individuals dispersed at constant rates between two patches and experienced density dependence in each patch (McPeck and Holt 1992). We showed that temporal variation in density-independent growth rates, partially uncorrelated across patches, favored dispersal. Moreover, a polymorphism in dispersal rates could be stably maintained if the two patches were heterogeneous (with different carrying capacities). Other authors have also shown that dispersal polymorphisms may be maintained in temporally and spatially heterogeneous environments (Frank 1986; Cohen and Levin 1991; Karlson and Taylor 1992).

In this note, we demonstrate that chaotic population dynamics in otherwise

constant (but patchy) environments favors dispersal and that chaotic populations tend to evolve toward evolutionarily stable states with a mixture of dispersal rates when patches differ in K .

Increasing evidence suggests that many natural populations exhibit chaotic dynamics (e.g., May 1976; Schaffer and Kot 1985; Sugihara et al. 1990; Tilman and Wedin 1991; Turchin and Taylor 1992; Hastings et al. 1993; Ellner and Turchin 1995). A signature of chaos is sensitive dependence on initial conditions (Ruelle 1989)—trajectories with slightly different initial conditions diverge (i.e., have positive Lyapunov exponents) (Hastings et al. 1993). Chaotic trajectories in simple population dynamic models portray populations that sometimes rise above carrying capacity, and sometimes fall below, in a seemingly random fashion when viewed over long enough time scales (e.g., May and Oster 1976).

Given density dependence, fluctuations in population size are experienced by individuals as fluctuations in fitness, described, for instance, by temporal variance in per capita growth rates (an appropriate measure of fitness for clonal organisms, and a reasonable approximation in many other cases) (Charlesworth 1994). Chaos is a potent generator of temporal variation in fitness. Previous theoretical treatments of the selective conditions favoring dispersal in heterogeneous environments (Gadgil 1971; Balkau and Feldman 1973; Roff 1975; Asmussen 1983; Metz et al. 1983; Levin et al. 1984; Bull et al. 1987; Liberman and Feldman 1989; Cohen and Levin 1991; McPeck and Holt 1992; Olivieri et al. 1995) have assumed that extrinsic environmental variation provides the requisite spatiotemporal variance in fitness. The basic point we make here is that chaotic dynamics can also generate the fitness variation needed to favor dispersal, in the absence of these external driving forces.

In patchy systems with chaos but no dispersal, subpopulations on different patches with slightly different initial conditions will diverge as their population trajectories unfold in time. Given a sufficiently long time series, the rank order of fitness among patches should vary, even if the environment is physically constant. Based on this verbal argument, we conjectured that chaotic dynamics in a patchy environment should favor the evolution of dispersal. To examine this conjecture, we have studied a wide range of dynamic models for patchy populations with nonoverlapping generations. In this note, we use one exemplar model to illustrate the basic effect.

For simplicity, assume clonal genetic variation. In patch j in generation t , clone i has density $N_{ij}(t)$. Clones differ only in a fixed dispersal rate, e_i , defined as the fraction of individuals dispersing from their natal patch each generation. Assume realized fitness in patch j , $W_j(N_{Tj}[t])$, is identical for individuals of all clones and depends functionally on the summed abundances $N_{Tj}(t)$ of all clones in patch j (i.e., density dependence is spatially localized). Without dispersal, the per capita growth rate for clone i in patch j is $W_j(N_{Tj}[t])$, and its dynamics are governed by the usual recursion:

$$N_{ij}(t + 1) = W_j(t)N_{ij}(t).$$

Given dispersal, a fraction m of dispersers survive to enter their nonnatal patch (the quantity $1 - m$ is a measure of the "cost of dispersal"). For two clones in

two coupled patches, we assume the dynamics can be described by a model (see McPeck and Holt 1992), which for clone 1 is as follows:

$$N_{11}(t+1) = (1 - e_1)W_1[N_{T1}(t)]N_{11}(t) + me_1W_2[N_{T2}(t)]N_{12}(t),$$

and

$$N_{12}(t+1) = (1 - e_1)W_2[N_{T2}(t)]N_{12}(t) + me_1W_1[N_{T1}(t)]N_{11}(t).$$

Similar equations describe clone 2 or, more generally, clone i (recall N_{Tj} is summed abundance of all clones in patch j). The above model assumes that reproduction and density dependence precede dispersal, the census immediately follows dispersal, costs of dispersal for a clone are experienced entirely by those individuals who actually disperse, and population densities are sufficiently high that they can be represented by continuous state variables (local densities) rather than discrete integers. The last assumption implies that when a given clone is sufficiently rare, it does not experience significant density dependence from itself but only from the more common clone, which in turn reduces the importance of kin interactions (as in, e.g., Hamilton and May 1977; Taylor 1988) versus ecological mechanisms in the evolution of dispersal (Holt 1985).

For illustrative purposes, we here use the functional form $W_j = \exp(r_j[1 - \sum N_{ij}/K_j])$ (the Ricker model; May and Oster 1976), generalized to multiple clonal genotypes, to describe local population growth in patch j (without dispersal). The quantity N_{ij} is the abundance of clone j in patch i , and the parameters r_j and K_j are, respectively, the intrinsic rate of increase and the carrying capacity of patch j (which we assume to be the same for all clones). (Other density-dependent submodels describing within-patch growth lead to qualitatively similar conclusions to those reported here; B. D. Holt and M. A. McPeck, unpublished data.) In an isolated patch, if $0 < r_j < 2$, the population stabilizes at K ; for $2 < r_j < 2.69$, it exhibits stable limit cycle behavior; for $2.69 < r_j$, the dynamics are chaotic (May and Oster 1976).

Consider the implications of dispersal in the absence of direct dispersal costs (i.e., let $m = 1$). Because clones have identical realized fitness within patches, evolution in our model is driven solely by how dispersal modulates interpatch variation in fitness. Dispersal influences clonal fitness in three ways. First, dispersal has a demographic effect on fitness: because of density dependence, by changing within-patch densities via immigration and emigration, dispersal modifies patch-specific fitnesses (Nakano 1981; Holt 1985). Second, because of such density dependence, the rate of dispersal indirectly influences the spatiotemporal correlation structure in local fitnesses. Third, the magnitude of dispersal for a given clone determines how that clone averages among spatially variable local fitnesses to determine its overall global fitness (a kind of "bet hedging"; Seger and Brockmann 1987). All three of these effects enter in determining how dispersal will evolve.

Figure 1 shows examples of characteristic patterns in evolutionary dynamics we observe when clones differing in dispersal rate (and no dispersal costs) compete against each other in numerical experiments. In the examples shown, the ordinate is the frequency of clone 1, with a high dispersal rate of $e_1 = 0.5$,

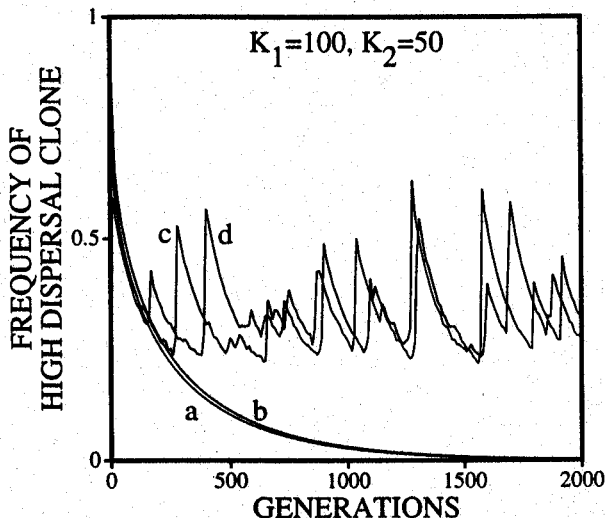


FIG. 1.—Numerical examples of the influence of chaos on the evolution of dispersal in a two-patch environment. The basic model structure is described in the text. The ordinate is the frequency of clone 1, with $e_1 = 0.5$ (high dispersal rate), competing against clone 2, with $e_2 = 0.01$ (low dispersal rate). Four examples (denoted by letters) are shown for two patches with carrying capacities of 100 and 50 and equal r_i 's. Example *a* has $r = 1$ (stable dynamics), initial frequency of clone 1, $p_0 = 0.95$. The high-dispersal clone is selectively disfavored. Example *b* has $r = 2.5$ (stable limit cycles); $p_0 = 0.95$. Dispersal is again disfavored. Example *c* has $r = 3.0$ (chaos); $p_0 = 0.95$. A polymorphism persists with both high- and low-dispersal clones. Example *d* has $r = 3.0$ (chaos); $p_0 = 0.05$. The high-dispersal clone successfully invades. The persistent dispersal polymorphism is characterized by chaotic genetic dynamics, punctuated by sharp increases and gradual declines in the frequency of the high-dispersal clone.

competing against clone 2, with a low dispersal rate of $e_2 = 0.01$. Four examples are shown for two patches with carrying capacities of 100 and 50 and equal r_i 's (i.e., both clones have equal r 's, within and between patches):

1. $r = 1$ (stable dynamics), initial frequency of clone 1 is $p_0 = 0.95$. The high-dispersal clone is selectively disfavored.

2. $r = 2.5$ (stable limit cycles); $p_0 = 0.95$. Dispersal is again disfavored; the patches fluctuate in abundance but with synchronized cycles.

3. $r = 3.0$ (chaos); $p_0 = 0.95$. A polymorphism persists with both high- and low-dispersal clones.

4. $r = 3.0$ (chaos), $p_0 = 0.05$. The high-dispersal clone successfully invades, when initially rare, but without fully displacing the low-dispersal clone. Together with example 3, this example suggests that the polymorphism is robust, since it arises from widely different initial conditions.

Two general features emerged in our simulations. First, chaotic dynamics permits a dispersing clone to invade, given an initial condition of low dispersal; in

contrast, dispersal is disadvantageous given stable or cyclic dynamics. Second, the population evolves toward a persistent polymorphic state where there is a mixture of low- and high-dispersal clones, which fluctuate in their relative frequencies. It is useful to look at these two general features more closely.

At sufficiently low intrinsic rates of increase (i.e., low r 's), the population settles into stable point or cyclic equilibria (May and Oster 1976). Given population stability, clones with relatively lower dispersal rates displace clones with higher rates, as predicted analytically (Balkau and Feldman 1973; Asmussen 1983; Hastings 1983; Holt 1985; Liberman and Feldman 1989). As noted above, the intuitive reason for dispersal to be disadvantageous in stable populations is that dispersers flow from high- K to low- K patches, indirectly increasing fitness in the former, while decreasing fitness in the latter (Hastings 1983; Holt 1985; McPeck and Holt 1992). Hence, dispersers have lower fitness, on average, than nondispersers. The evolutionarily stable state of a dynamically stable population is zero dispersal.

The evolutionary outcome changes dramatically at higher r 's, permitting chaotic dynamics (fig. 1). The parameter conditions that give rise to chaotic population dynamics define a regime of persistent polymorphism in dispersal rates, given that patches have different K 's. This regime is characterized by chaotic genetic dynamics, in which in time series (see fig. 1) one sees gradual declines in frequency of the high-dispersal clone, punctuated by sharp increases in frequency. These episodic increases in the frequency of the high-dispersal clone increase the mean dispersal rate, which in turn tends to synchronize population dynamics in the two patches. Once the patches are synchronized, dispersal becomes disfavored (as with stable or cyclic dynamics). The frequency of the high-dispersal clone then declines, the patch dynamics become progressively uncoupled, and the shifting rank order of relative fitnesses among patches generated by chaotic dynamics once again reemerges. This dynamic by-product of a low average dispersal rate in turn provides the conditions in which dispersal is once again advantageous. The net effect is a pattern of bounded fluctuations in the frequency of dispersal.

When clones with dispersal rates ranging from completely sedentary ($e = 0$) to uniform mixing ($e = 0.5$) compete in pairwise trials, three evolutionary domains tend to emerge. An example is shown in figure 2A. In region *a* of the figure, low dispersal is favored over no dispersal, and no polymorphism is observed; in region *b*, high dispersal rates are disfavored when competing against more moderate dispersal rates, and no polymorphism is maintained. In effect, when clones that are similar to each other in dispersal compete, the system moves toward an inflection or saddle point (roughly $e = 0.125$, for the example shown with $K_1 = 100$ and $K_2 = 50$). In region *c*, clonal combinations with high and low dispersal rates (relative to the inflection point) coexist and beat out clones with intermediate dispersal rates. Similar outcomes emerge for each pair of patch-species carrying capacities we have examined, in that pairs of clones with high and low dispersal rates (relative to a saddle point, which varies with patch carrying capacities) can coexist and displace clones with intermediate dispersal rates.

The arrows in figure 2A indicate the direction of evolutionary trajectories ob-

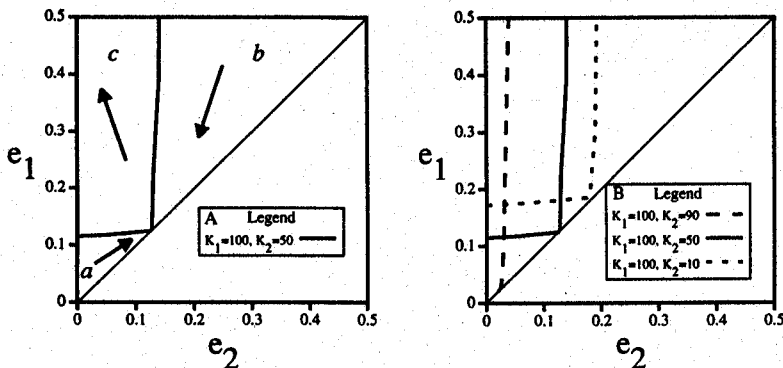


FIG. 2.—A, The outcome of pairwise and three-way trials among competing clones with dispersal rates ranging from completely sedentary ($e = 0$) to complete, uniform mixing ($e = 0.5$). The parameters used are $r_1 = r_2 = 3$, $K_1 = 100$, $K_2 = 50$. By convention, clone 1 has the higher dispersal rate. In region *a*, clone 1 displaces clone 2; that is, the population evolves toward higher dispersal. In region *b*, clone 2 displaces clone 1; that is, the population evolves toward lower dispersal. In region *c*, clones 1 and 2 persist; that is, the population evolves toward intermediate dispersal, with a polymorphism in dispersal rates. The heavy arrows indicate the direction of evolutionary change in the system if three clones compete at once. If all possible pairs of three clones have dispersal rates falling in region *a*, the one with the highest dispersal rate displaces its competitors. In region *b*, the clone with the lowest dispersal rate wins. In region *c*, the clone with intermediate dispersal rate is excluded, and a persistent polymorphism of high- and low-dispersal types emerges. B, The influence of patch-specific carrying capacity on the positions of parameter space describing monomorphism and polymorphism, in pairwise competition between clones differing only in dispersal rates. In all, $r_1 = r_2 = 3$. The boundaries between the three regions are shown for three different combinations of carrying capacities for the two patches. The solid line repeats the line in A. The advantage of dispersal weakens with increasing spatial disparity in K 's. In the limiting case of equal K 's, dispersal can successfully invade nondispersing populations; however, as discussed in the text, populations synchronize such that abundances are equal across space, and thenceforth clonal frequency remains unchanged, at levels dependent on initial abundances.

served when mutants of small effect arise and "test" preexisting monomorphic or polymorphic populations. If all possible pairs in a clonal triplet lie in region *a*, the clone with highest e wins; when all combinations fall in region *b*, the clone with lowest e supplants those with higher e 's; when a persistent polymorphism is feasible (region *c*), intermediate values for e are driven extinct. Given sufficient time and genetic variation, a polymorphism for dispersal (with high [e near one-half] and low [e near zero] clones coexisting) is a likely evolutionary outcome.

The particular combination of dispersal rates that can coexist in a persistent polymorphism varies with the relative carrying capacities of the two patches. Figure 2B shows a numerical example. We should emphasize that the "infection point" of the figure is not an evolutionarily stable strategy (ESS) dispersal rate but an evolutionary saddle. The system evolves toward it if all clones have either

higher or lower dispersal values; but if the clones straddle it, a polymorphism persists if one clone disperses at a higher rate, and another at a lower rate, than the saddle (with clones dispersing at intermediate rates being excluded).

The existence of this evolutionary attractor reflects two opposing forces. Without dispersal, chaos generates spatially uncorrelated variance in fitness, favoring dispersal. But high dispersal synchronizes population dynamics, producing conditions selecting against dispersal. Inspecting the patch-specific abundances of each clone (data not shown), we observe that the high-dispersal clone tends to predominate in the low- K patch, whereas the low-dispersal clone tends to predominate in the high- K patch. This partial spatial segregation permits clonal coexistence.

Because the above model describes the dynamics of asexual clonal genotypes, it can also portray competition between species. Our model shows that functionally identical species that differ solely in dispersal rates can coexist in a spatially heterogeneous landscape, if their intrinsic rates of increase are sufficiently high to generate chaotic dynamics. Differences in dispersal rate need not be correlated with differences in local competitive ability, or niche differences, for regional coexistence to be observed. The model provides one clear way in which chaotic dynamics may matter in addressing traditional questions in community ecology, such as competitive coexistence.

The specific results reported in the figures assume that dispersal has no costs (i.e., $m = 1$). Repeating the simulations, but using small dispersal costs (e.g., $m = 0.95$), leads to essentially the same outcomes as shown in figure 2A and B (R. D. Holt and M. A. McPeck, unpublished data). It is obvious that large costs to dispersal tend to disfavor dispersal. For instance, if $m = 0$, dispersal is always disfavored, regardless of the value for r . However, dispersal can be strongly favored in populations with chaos, surmounting even large dispersal costs. For instance, in the example shown in figure 1, the high-dispersal clone successfully invades a population made up of low dispersers, even if $m = 0.3$.

A limiting case of the model is for the two patches to have identical carrying capacities. In the above model, if K 's are equal, dispersal tends to synchronize dynamics in the two patches, such that abundance, and hence fitness, becomes equal in the two patches (even if abundances still vary chaotically through time). Without direct costs to dispersal, given such synchronized dynamics and spatial homogeneity, it is clear that the rate of dispersal will be a neutral trait.

However, if one starts the system with zero dispersal and chaotic dynamics, such that uncoupled patches with slightly different initial conditions follow different trajectories around the same K , numerical studies show that a high-dispersal clone can always increase when rare. As such clones increase in frequency, they have the demographic effect of synchronizing the patch dynamics, and the system becomes selectively neutral (without the dispersal clone going to fixation). Moreover, the frequency of the dispersing clone at the time neutrality is achieved varies greatly, depending on the detailed initial conditions of the populations in the two patches.

Thus, chaotic dynamics on its own, in the absence of spatial heterogeneity in carrying capacity, does favor dispersal over nondispersal when the population is largely comprised of nondispersers, but it only weakly defines the ultimate state

of the system. However, it should be noted that the neutral stability observed with two identical patches and synchronized dynamics is unlikely to be particularly relevant to natural populations, in which spatial variation in carrying capacity is the norm, not the exception.

The following simple heuristic argument helps explain why chaos favors dispersal. In the absence of dispersal, populations in different patches will have independent population histories. Given deterministic dynamics, each population should persist with bounded fluctuations. Such persistence implies that in each patch, the long-term geometric growth rate (local fitness) is unity, with variation through time around unity in realized fitnesses. Imagine that all patches can be described by the same frequency distribution in realized fitnesses (the argument is heuristic, because we do not provide a formal proof for this assumption). Introduce a clone that disperses uniformly across all patches, without any dispersal costs. The growth rate of this dispersal clone when it is rare (too rare to affect local densities) will be an arithmetic average of the realized fitnesses in each patch. Because the arithmetic average of a distribution always exceeds the geometric average, this clone should increase each generation. Thus, clones that disperse should always be able to invade a nondispersing, chaotic population. (A similar argument was developed more formally in Metz et al. 1983 for populations experiencing externally forced temporal heterogeneity in local growth rates.)

Our results complement earlier theoretical analyses of the role of extrinsically driven environmental variability in the evolution of dispersal (see previously cited references). We have explored a variety of different models with localized density dependence and chaotic dynamics. These include changing the order of dispersal and density dependence in the life cycle, using alternative functional forms for density dependence, increasing the number of patches, employing global versus localized dispersal in spatially explicit patch arrays, blending random environmental variation with chaos, and permitting dispersal rates to be patch dependent (M. A. McPeck and R. D. Holt, unpublished data). The basic message that chaotic dynamics promotes selection for dispersal seems to be robust to all such changes. These changes in model structure should, of course, be quantitatively important, in particular in determining the precise conditions leading to persistent polymorphisms (as in McPeck and Holt 1992), but they do not affect the force of the conclusion that chaotic dynamics favor dispersal in patchy environments.

Recent demonstrations (Allen et al. 1993; Holt 1993) that chaotic dynamics can promote the global persistence of metapopulations with weak dispersal point out the importance of moderate dispersal rates for species' persistence. Our results suggest that an incidental (but welcome) by-product of evolution toward low average dispersal rates, bounded away from zero, may be enhanced persistence for populations experiencing chaotic dynamics. Turning this around, we see that the ubiquity of dispersal in natural populations may be a signature of pervasive spatiotemporal variation in fitness arising from either external environmental variation or chaotic dynamics, or both.

Our results highlight one potential evolutionary implication of chaotic population dynamics. For some evolutionary questions, chaos may prove to have little effect on the direction of evolution (e.g., as in the evolution of competitive ability;

Godfray et al. 1992). By contrast, chaotic dynamics can crucially modulate the evolution of any trait whose dynamics is sensitive to the existence and structure of spatiotemporal variance in fitness. Dispersal is paradigmatic of such traits; others include sex and diapause.

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LITERATURE CITED

- Allen, J. C., W. M. Schaffer, and D. Rosko. 1993. Chaos reduces species extinction by amplifying local population noise. *Nature (London)* 364:229-232.
- Asmussen, A. M. 1983. Evolution of dispersal in density regulated populations: a haploid model. *Theoretical Population Biology* 23:281-299.
- Balkau, B. J., and M. W. Feldman. 1973. Selection for migration modification. *Genetics* 74:171-174.
- Bull, J. J., C. Thompson, D. Dg, and R. Moore. 1987. A model for natural selection of genetic migration. *American Naturalist* 129:143-157.
- Charlesworth, B. 1994. *Evolution in age-structured populations*. 2d ed. Cambridge University Press, Cambridge.
- Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. *Theoretical Population Biology* 39:63-99.
- Comins, N. H. 1982. Evolutionarily stable strategies for localized dispersal in two dimensions. *Journal of Theoretical Biology* 94:579-606.
- Ellner, S., and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. *American Naturalist* 145:343-375.
- Frank, A. S. 1986. Dispersal polymorphisms in subdivided populations. *Journal of Theoretical Biology* 122:303-309.
- Gadgil, M. 1971. Dispersal: population consequences and evolution. *Ecology* 52:253-261.
- Godfray, H. C. J., L. M. Cook, and M. P. Hassell. 1992. Population dynamics, natural selection and chaos. Pages 55-86 in R. J. Berry, T. J. Crawford, and G. M. Hewitt, eds. *Genes in ecology*. Blackwell, London.
- Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. *Nature (London)* 269:578-581.
- Hastings, A. 1983. Can spatial variation alone lead to selection dispersal? *Theoretical Population Biology* 24:244-251.
- Hastings, A., C. L. Hom, S. Ellner, P. Turchin, and H. C. J. Godfray. 1993. Chaos in ecology: is mother nature a strange attractor? *Annual Review of Ecology and Systematics* 24:133.
- Holt, R. D. 1985. Population dynamics in two-patch environments: some anomalous consequences of an optimal habitat distribution. *Theoretical Population Biology* 28:181-208.
- . 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77-88 in R. Ricklefs and D. Schluter, eds. *Species diversity in ecological communities*. University of Chicago Press, Chicago.
- Karlsen, H. R., and M. H. Taylor. 1992. Mixed dispersal strategies and clonal spreading of risk: predictions from a branching process model. *Theoretical Population Biology* 42:218-233.
- Kuno, E. 1981. Dispersal and the persistence of populations in unstable habitats: a theoretical note. *Oecologia (Berlin)* 49:123-126.
- Levin, A. S., D. Cohen, and A. Hastings. 1984. Dispersal strategies in patchy environments. *Theoretical Population Biology* 26:165-191.
- Lieberman, U., and M. W. Feldman. 1989. The reduction principle for genetic modifiers of the migra-

- tion rate. Pages 111–137 in M. W. Feldman, ed. *Mathematical evolutionary theory*. Princeton University Press, Princeton, N.J.
- May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature (London)* 261:459–467.
- May, R. M., and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. *American Naturalist* 110:573–599.
- McPeck, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Metz, J. A. J., T. J. deJong, and P. G. L. G. Klinkhamer. 1983. What are the advantages of dispersing? a paper by Kuno explained and extended. *Oecologia (Berlin)* 57:166–169.
- Nakano, T. 1981. Population regulation by dispersal over patchy environments. I. Regulation by the threshold dispersal. *Researches on Population Ecology (Kyoto)* 23:1–18.
- Olivieri, I., Y. Michalakis, and P.-H. Gouyon. 1995. Metapopulation genetics and the evolution of dispersal. *American Naturalist* 146:202–228.
- Roff, D. A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. *Oecologia (Berlin)* 19:217–237.
- . 1990. The evolution of flightlessness in insects. *Ecological Monographs* 60:389–421.
- Ruelle, D. 1989. *Chaotic evolution and strange attractors*. Cambridge University Press, Cambridge.
- Schaffer, W. M., and M. Kot. 1986. Chaos in ecological systems: the coals that Newcastle forgot. *Trends in Ecology & Evolution* 1:58–63.
- Seger, J., and H. J. Brockmann. 1987. What is bet-hedging? *Oxford Surveys in Evolutionary Biology* 4:182–211.
- Sugihara, G., B. Grenfell, and R. M. May. 1990. Distinguishing error from chaos in ecological time series. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 330:235–251.
- Swingland, I. R., and P. J. Greenwood, eds. 1986. *The ecology of animal movement*. Oxford University Press, Oxford.
- Taylor, P. D. 1988. An inclusive fitness model for dispersal of offspring. *Journal of Theoretical Biology* 130:363–378.
- Tilman, D., and D. Wedin. 1991. Oscillations and chaos in the dynamics of a perennial grass. *Nature (London)* 353:653–655.
- Turchin, P., and A. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73:289–305.
- Wiener, P., and M. W. Feldman. 1991. The evolution of dispersal in a model of mixed selfing and random mating. *Evolution* 45:1717–1725.

ROBERT D. HOLT*

MUSEUM OF NATURAL HISTORY AND
DEPARTMENT OF SYSTEMATICS AND ECOLOGY
UNIVERSITY OF KANSAS
LAWRENCE, KANSAS 66045

MARK A. McPEEK

DEPARTMENT OF BIOLOGICAL SCIENCES
DARTMOUTH COLLEGE
HANOVER, NEW HAMPSHIRE 03755

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* To whom correspondence should be addressed; E-mail: predator@kuhub.cc.ukans.edu.