

On the evolutionary stability of sink populations

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Summary

The evolution of adaptive behaviours can influence population dynamics. Conversely, population dynamics can affect both the rate and direction of adaptive evolution. This paper examines reasons why sink populations – populations maintained by immigration, preventing local extinction – might persist in the habitat repertoire of a species over evolutionary time-scales. Two such reasons correspond to standard explanations for deviations from an ideal free habitat distribution: organisms may not be free to settle in whichever habitat has the highest potential fitness, and may be constrained by costs, perceptual limitations, or mode of dispersal in the acuity of their habitat selectivity. Here, I argue that a third general reason for persistent sink populations is provided by unstable population dynamics in source habitats. I present a simple model illustrating how use of a sink habitat may be selectively advantageous, when a source population has unstable dynamics (which necessarily reflects temporal variation in local fitnesses). Species with unstable local dynamics in high-quality habitats should be selected to utilize a broader range of habitats than species with stable local dynamics, and in particular in some circumstances should utilize sink habitats. This observation has implications for the direction of niche evolution, and the likelihood of niche conservatism.

Keywords: habitat breadth; niche conservatism; source–sink dynamics

Introduction

Dispersal influences many fundamental phenomena of population ecology, from species' spatial distributions, to patterns of temporal fluctuations in numbers, to the evolution of specialization. One consequence of dispersal that has sparked considerable interest in recent years is that dispersal in a heterogeneous landscape may sustain 'sink' populations in habitats with environmental conditions outside a species' niche (Holt, 1985, 1993; Pulliam, 1988, 1996; Pulliam and Danielson, 1991; Dias, 1996). In this paper, by definition a 'sink habitat' has death rates exceeding birth rates at all densities; a 'sink population' will be a population occupying such a habitat. A population found in a sink habitat in effect heads deterministically towards extinction; it is held from extinction only because of recurrent immigration from source populations in habitats where births exceed deaths.

There is an increasing wealth of well-documented examples of sink populations, from a wide range of taxa and biomes (Dias, 1996; Pulliam, 1996). Sink populations exist because individuals disperse from habitats where mean fitness exceeds unity (sources) into habitats where mean fitness is less than unity (sinks). On the face of it, such movement would appear to be selectively disadvantageous. If organisms fit the requirements for an ideal free distribution (IFD; Fretwell, 1972) – which are that organisms can freely select habitats, without cost, settling within whichever habitat provides the highest fitness rewards, and in addition populations achieve a demographic equilibrium – at equilibrium each distinct habitat should equilibrate at its respective carrying capacity (see, e.g. Holt, 1985; Rosenzweig, 1985). Because a sink habitat has a carrying capacity of zero, this suggests that no individuals should occupy sink habitats, at all. Thus, the very existence of sink

populations automatically seems to pose an evolutionary puzzle. As Robert MacArthur once asked (with his usual prescience), 'Why would any individual ever migrate to a less favorable area? Why not stay put if it is better at home?' (MacArthur, 1972, p. 150).

I suggest there are three basic reasons why a sink population might be evolutionarily stable, at least with respect to the evolution of dispersal and optimal habitat selection (Holt, 1996a,b, deals with the complementary issue of evolutionary stability with respect to local adaptive evolution). Sink populations may arise because the assumptions of the IFD do not hold, either organisms are (1) not 'free' or (2) not 'ideal'. Because the literature on optimal habitat selection has dealt with these causes of deviation from an IFD (albeit without specific reference to source-sink dynamics), here I only briefly touch on them, and concentrate instead on a third reason. I argue that sink populations may be expected to occur whenever (3) source populations have sufficiently unstable local population dynamics. I present a simple model illustrating how population instability in source habitats promotes the evolution of dispersal strategies incorporating sink habitats within the habitat range of a species. The model illustrates a phenomenon that characterizes a much broader range of models. In the Discussion, I comment on the implications of habitat selection and dispersal for population dynamics (Chesson and Rosenzweig, 1991) and touch on how the results presented here bear on general evolutionary issues.

Evolutionary reasons for persistent sinks

1. *Sinks may persist because organisms are not 'free'*. Fretwell (1972) contrasted the IFD with the 'ideal despotic distribution'. Basically, if individuals defend territories or engage in interference competition, and have dominance hierarchies, then low-ranking individuals may find it advantageous to leave a high-quality habitat and settle in a lower-quality habitat, even if their absolute fitness there is less than unity (viz., the lower-quality habitat is a sink).

The source-sink model of Pulliam (1988) provides a straightforward formalization of this idea (see also Holt, 1993). One assumes that in the source, a fixed number of breeding sites are available. If the population exceeds this number, the excess individuals are forced into a second habitat, where their death rate exceeds their birth rate. At demographic equilibrium, the reproductive surplus in the source sustains the sink population.

This spatial structure can be evolutionarily stable, provided two conditions hold. First, individuals in the sink must achieve a reproductive success exceeding that they would have enjoyed had they stayed in the source (taking into account both resource pre-emption and interference by residents in the source). This condition for evolutionarily persistent sinks requires either variance among individuals in competitive ability, or site pre-emption (Pulliam and Danielson, 1991). Secondly, emigration to sink habitats should be an ESS only if there is also sufficient reverse migration from sink to source, so that individuals in the sink can expect to have descendants in the source (Bull *et al.*, 1987; Morris, 1991).

2. *Sinks may persist because organisms are not 'ideal'*. Constraints upon or costs of movement may lead to a non-ideal distribution (van Baalen and Sabelis, 1993) and persistent sink populations. Many empirical studies of patch use reveal that poorer patches are used relatively more, and better patches relatively less, than expected in an IFD (Sutherland *et al.*, 1988; Kennedy and Gray, 1993). Abrahams (1986) observed that perceptual constraints may lead to an inability to discriminate among habitats, and an overuse of poorer habitats. Many mechanisms of dispersal are necessarily imprecise and will often place organisms into inappropriate habitats. For instance, species which rely upon wind or water currents for dispersal are likely to suffer considerable losses of dispersers settling into poor habitats, where the species may occur as sink populations (Morris, 1991). The sink population in a sand dune annual plant described by Keddy (1981) provides an

excellent example of a sink population in a species dependent upon wind dispersal. Strong winds off the ocean strip seeds from the productive strand habitat and deposit them in the dune interior, sustaining a dense population, despite deaths exceeding births in that habitat. Organisms which ride the wind cannot escape the fact that the wind is a wastrel.

In contrast to reason (1) above, sinks which exist because organisms are constrained in their dispersal biology may obviously be evolutionarily persistent, even if there is no reciprocal dispersal from sinks back to sources. Moreover, in systems with strong density dependence and competition among kin, dispersal may be evolutionarily stable, even if a large fraction of dispersers disappear from the breeding population (Hamilton and May, 1977); these lost emigrants may well sustain sink populations, without back-emigration.

3. *Sinks may persist because of unstable population dynamics in source habitats.* Few, if any, natural populations attain and stay at a local, unchanging equilibrium in population size. Instead, local populations show considerable variability in abundance over time, reflecting temporal variation in local demographic parameters, and thus local growth rates (Pimm, 1991). In a closed population in a given habitat, variation in population size necessarily expresses temporal variance in individual absolute fitnesses. Here, I present a simple model suggesting that unstable dynamics in a source population can promote the evolution of dispersal, favouring the sustained existence of sink populations. The basic idea is quite simple. Utilization of a sink habitat can be selectively advantageous, provided (a) there are some generations in the source when fitness there is temporarily less than in the sink, and (b) individuals that disperse into the sink can leave descendants which successfully disperse back into the source.

Before presenting the model, it is helpful to be precise about what is meant by 'source habitat' and 'sink habitat', given unstable population dynamics. Consider a species with discrete generations, occupying a landscape with two distinct habitats. Habitat 1 is the source and habitat 2 is the potential sink. For a moment, assume each habitat is closed; local dynamics is driven entirely from local births and deaths. In generation t , habitat i has $N_i(t)$ individuals, each with an average fitness (= expected number of descendants in generation $t + 1$) of $W_i(N_i, t)$. The familiar recursion describing population dynamics in habitat i is:

$$N_i(t + 1) = N_i(t) W_i(N_i, t)$$

A closed population persisting in habitat 1 in a constant environment should be able to increase when rare – that is, $W_1(0) > 1$. If numbers are not to increase in an unbounded fashion, at high densities W_1 should decline with increasing N_1 , such that for some K_1 , $W_1 < 1$ if $N_1 > K_1$.

Populations may experience variation in local growth rates because of extrinsic or intrinsic reasons. The general result given below applies to both sources of variation. The example presented in Fig. 1 assumes an intrinsic source of temporal variability in fitness. As is well known, even in a constant environment, if density dependence near K_1 is sufficiently strong, the point equilibrium abundance is unstable, and the population should exhibit stable limit cycles or chaotic dynamics (May and Oster, 1976). From the perspective of an individual, unstable population dynamics expresses temporal variation in absolute fitness. A closed population which persists, fluctuating within bounds, should have a long-term geometric growth rate, W_G , equal to unity. (By 'geometric growth rate', I mean the $1/T$ th root of $\prod W_i(t)$, where T is the length of the period for species exhibiting limit cycles, or a very long time for species with chaotic dynamics, or dynamics driven stochastically by the external environment.)

By contrast, a closed population in habitat 2 which experiences $W_2(t) < 1$ each generation has a long-term geometric mean growth rate < 1 , so this population ineluctably declines to lower densities and eventually faces extinction. Habitat 2 is a sink habitat for this species, where it can only persist if there is recurrent immigration from habitat 1. In short, a source habitat is one which,

when closed to dispersal, has an expected geometric mean growth rate of unity, whereas a habitat with a growth rate less than unity each generation (and hence, a geometric mean growth rate less than unity) is assuredly a sink habitat. (Sometimes a sink habitat has $W_G < 1$, but with $W_i(t) > 1$ for some t . We do not consider such 'transient sinks' here.)

If the source population is closed to dispersal and has stable dynamics, at equilibrium the population there reaches its carrying capacity. The growth rate is thenceforth unity. Individuals clearly suffer a fitness loss if they disperse from the source habitat at equilibrium into the sink habitat. This suggests dispersal should be selected against, such that the evolutionarily stable distribution on the landscape should not include a sink population (as predicted by Hastings, 1983; Holt, 1985).

However, if the source population has unstable dynamics, in some generations the realized growth rate in the source is necessarily less than unity, and possibly considerably less. The greater the variance in fitness (i.e. the more unstable the local dynamics), the more likely it is that there will be some time periods in which individuals who disperse into the sink habitat may enjoy a short-term increase in their fitness (provided their descendants can back-immigrate into the source in future generations; see Morris, 1991), compared to individuals staying in the source habitat.

We illustrate this idea with the following model.

The model

Assume that at the beginning of generation t , there are $N(t)$ individuals. Of these, a fraction p settle in habitat 1; the remaining $1 - p$ settle into habitat 2; the quantity p can range from 0 to 1. (This assumption about dispersal permits a representation of population dynamics as a single-dimensional recursion, rather than tracking numbers separately in each habitat.) Habitat 1 is a source habitat, with a density-dependent growth rate of $W_1(N_1)$, where $N_1 = pN(t)$ is the number of individuals residing in habitat 1.

Habitat 2 is a sink habitat, with a rate of population decline of $W_2(t) < 1$. For simplicity, we examine in detail a system in which the sink fitness is fixed (i.e. density-independent; see below). Over a single generation, the recursion in numbers for the entire population, in both habitats combined, is:

$$N(t+1) = N(t)[pW_1(N_1(t)) + (1-p)W_2]$$

Following density dependence, the reproductive output of both patches congeals into a common pool, which then divides among the two habitats to initiate the next generation.

Now assume clonal variation exists in p , our measure of dispersal, but that individuals are otherwise identical (so that all individuals within a given habitat experience the same realized fitness each generation). Moreover, we assume that there is no cost to habitat choice. The bracketed term in the above expression provides a fitness-generating function $W(p)$ (Vincent and Brown, 1989), which can be used to examine evolutionary dynamics in p . We ask two simple questions. If the population is initially restricted to the source habitat (i.e. $p = p' = 1$), can an alternative clone with a lower p invade and persist? If the answer is 'yes', selection on dispersal tends to retain the sink habitat within the habitat repertoire of the species. Alternatively, if the initial population encompasses both habitats, can a clone selective solely on habitat 1 invade and displace the initial clone? If so, sink populations should be evolutionarily transient phenomena.

The answers to these questions depend on several factors: the stability, or instability, of population dynamics; the magnitude of the rate of decline in the sink habitat; and the magnitude of temporal variation in fitness in the source.

Consider first stable populations. Numbers equilibrate at a constant, N^* , and at equilibrium fitness is unity: $1 = W(p) = pW_1(N_1^*) + (1-p)W_2$, where $N_1^* = N^*p$. If the initial population is fixed at $p = 1$, habitat 1 settles to its carrying capacity (so that $W_1 = 1$), and no individuals are found in habitat 2 at all. Now introduce a clone with some $p = p' < 1$, in sufficiently small numbers that the density (and thus fitness) in habitat 1 is to a good approximation unchanged. The geometric growth rate of this clone when rare is $W(p') = p'W_1(K_1) + (1-p')W_2 < 1$. Hence, any clone that utilizes the sink habitat at all tends to be eliminated when rare. Similarly, if the initial state of the population is $p < 1$, a clone with $p > p'$ will increase when rare. The ESS of the population, given stable numerical dynamics, is clearly $p = 1$, with no utilization of the sink habitat at all.

Now consider a population which, when restricted to the source habitat, experiences a 2-point stable limit cycle – that is, $N(t+2) = N(t)$. Letting $t = 0$, and using $W_1(t)$ to represent the realized fitness in habitat 1 in generation t , for an equilibrial 2-point cycle, we must have $W_1(1)W_1(2) = 1$. In one generation, the population is below K_1 and enjoys a fitness exceeding 1, but it then overshoots K_1 , leading to a realized fitness the following generation less than 1. Without loss of generality, let generation 1 denote the generation with fitness exceeding 1 (i.e. $W_1(1) > 1$).

We again introduce a clone with $p < 1$, in numbers sufficiently small that realized fitnesses and densities in habitat 1 are to a good approximation unchanged through the cycle, and ask if this clone can increase when rare. Using $W^2(p)$ to denote the net growth rate of this clone over a full cycle, we have:

$$\begin{aligned} W^2(p) &= (pW_1(1) + (1-p)W_2)(pW_1(2) + (1-p)W_2) \\ &= p^2 + (1-p)^2W_2^2 + 2p(1-p)W_2\langle W \rangle \end{aligned} \quad (1)$$

where in the last expression we use the fact that $W_1(1)W_1(2) = 1$, and define $\langle W \rangle = (W_1(1) + W_1(2))/2$ as the time-average of fitness in the source, averaged over the cycle. In a cyclic population, $\langle W \rangle > 1$, because the arithmetic mean always exceeds the geometric mean, and the latter is unity for fitness in a population with a stable limit cycle. In populations with large-amplitude cycles, because $W_1(2) = 1/W_1(1)$, to a good approximation $\langle W \rangle = W_1(1)/2$. The greater the amplitude of the cycles, the larger is $W_1(1)$, and hence $\langle W \rangle$.

To determine whether a clone with a dispersal parameter p slightly less than 1 can invade, we evaluate $d/dp[W^2(p)]$ in the limit $p \rightarrow 1$. If this is negative, a clone utilizing the sink to some small degree is selectively favoured in a population originally restricted to the source habitat. After a little manipulation, the condition for this turns out to be simply:

$$W_2\langle W \rangle > 1 \quad (2)$$

All else being equal, evolution tends to favour the utilization of a sink habitat, the higher the fitness in the sink, and the greater the magnitude of population fluctuations in the source. The above condition implies $W_2 > W_1(2)$: the sink habitat, to be exploited, must offer a greater fitness reward than the source during the generation when fitness is low in the source.

The above argument assumes simply that fitness in a source habitat cycles, but does not make any assumption about the source of such temporal variation. In the example discussed below, population cycles arise because of strong density dependence. But this is not necessary; fitnesses, for instance, could cycle because of forcing by an environmental cycle. More generally, stochastic variation in fitness also favours the utilization of sink habitats. For example, if the source habitat experiences $W_1(1)$ and $W_1(2)$ with equal probability, and the long-term geometric mean fitness of the source habitat is 1, criterion (2) describes the conditions for invasion of a clone using the sink (R.D. Holt, M. McPeck and R. Gomulkiewicz, unpublished results).

The above inequality can be intuitively understood as follows. Recall that we are considering the fate of a clone which on average spends only a small amount of time in the sink, and the rest of its

time in the source. When an individual of this clone is in the source, it has a fitness equal to that of the residents. If it spends one generation in the sink, it experiences a fitness W_2 , but in the next generation its descendants will almost surely reside back in the source. There is an equal probability that these descendants will experience both the high and low points in the cycle, so their expected fitness that generation is the arithmetic mean fitness, averaged over the cycle. So over two generations, the compound quantity $W_2\langle W \rangle$ scales the increase in number of grand-offspring expected because of a small amount of exposure to the sink.

The adaptive advantage of exploiting the sink, given unstable source dynamics, can be viewed in two distinct ways. First, it is a kind of 'bet-hedging' (Seeger and Brockmann, 1987). Secondly, dispersal in space permits utilization of the sink to be adaptively favoured because of a spatial 'storage effect' (Chesson and Rosenzweig, 1991); recruitment during good years in the source can be 'stored' in the sink during bad source years.

In the case of stable source dynamics, we inferred above that the ESS for dispersal required the sink habitat to be empty. Given unstable population dynamics, it is difficult to assess in general the ESS or resultant spatial distribution in numbers. The reason is that dispersal affects population size in the source, and hence (because of density dependence) the temporal pattern of variation in fitness. Further insight requires one to assume particular functional forms for density-dependent fitness.

As a concrete example, let fitness in the source be given by the familiar Ricker equation, $W_1(N_1) = \exp[r_1(1 - N_1/K_1)]$; fitness in the sink is a density-independent constant, $W_2 = \exp[r_2] < 1$. As is well known (May and Oster 1976), the dynamics of the source population are stable if $r_1 < 2$, exhibit cycles (2 to n -point) if $2 < r_1 < 3.102$, and are chaotic for $r_1 > 3.102$. Figure 1 shows conditions for invasion by clones utilizing the sink, into populations initially restricted to a source with unstable dynamics, for both 2-point cycles ($r_1 = 2.5$) and chaotic dynamics ($r_1 = 3.5$). Increasing r_1 in this model increases the magnitude of population fluctuations in the source. The figure shows that this makes it much easier for clones utilizing the sink habitat to invade a population initially restricted to the source.

Figure 1 also indicates that many parameter combinations lead to populations with a persistent polymorphism in dispersal. The reason for this appears to be that increased dispersal into the sink lowers the maximal growth rate of the population, which thereby becomes less prone to population cycles or chaos. When the population approaches a demographic equilibrium, dispersal into the sink becomes disadvantageous. But as the population becomes increasingly confined to the source habitat, the inherent instability of the source re-emerges, setting up the conditions favouring clones which utilize the sink. Holt and McPeck (1996) explore this effect in some detail (albeit without reference to source-sink dynamics *per se*).

Preliminary investigations of a wider range of models (e.g. with habitat-specific dispersal rates, as in McPeck and Holt (1992), or optimal, density-dependent habitat selection (Rosenzweig, 1985), or density dependence in the sink as well as the source (Holt, 1996b)) suggest that the evolutionary persistence of sink populations is a generic feature of systems with unstable dynamics in source habitats (R.D. Holt, unpublished results). The details of dispersal biology and density dependence do matter, of course. For instance, in some systems, sink populations will always be present (e.g. if dispersal is constrained to be density-independent, at a rate fixed by clonal genotype), whereas in other systems, sink populations may arise only during periods of high density in the source habitat (e.g. if dispersal is 'ideal free', hence density-dependent). Moreover, with limited dispersal (partial mixing of patches, as in McPeck and Holt (1992) and Holt (1996a)), threshold effects may be observed, such that for a given range of temporal variation in source fitness, dispersal must exceed a certain threshold value to be favoured (R.D. Holt, M. McPeck and R. Gomulkiewicz, unpublished results). Nonetheless, the generalization that temporal variation in fitness in source habitats favours the utilization of sink habitats appears to be robust.

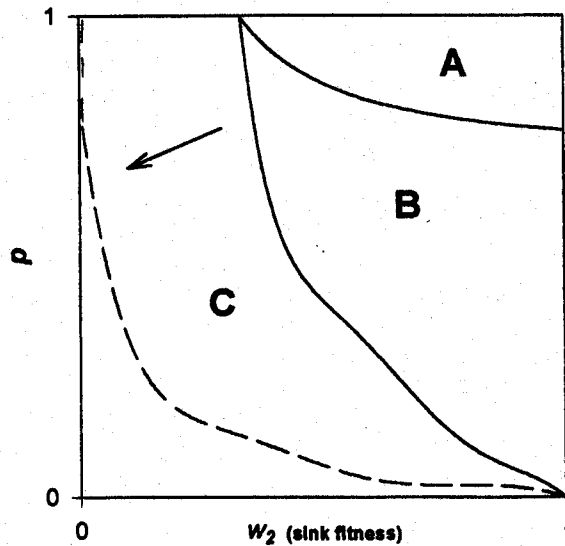


Figure 1. Conditions for invasion of a clone utilizing a sink habitat. The model is described in the text. For each combination of p (fraction of individuals of the invasive clone residing in the source) and W_2 (rate of decline in the sink habitat), the model was simulated to assess invasibility of a population that initially is restricted to the source habitat. The solid lines denote the outcome of these contests, assuming $r_1 = 2.5$ (i.e. a two-point cycle in the source). In region A, the clone utilizing the sink invades, and displaces the clone specialized to the source habitat. In region B, the two clones co-exist. In region C, the clone specialized to the source resists invasion by the clone utilizing the sink. In the former two cases, utilization of the sink is favoured by natural selection on dispersal. The dashed line shows how the demarcation between regions B and C shifts, if the source has more unstable dynamics ($r_1 = 3.5$, implying chaotic dynamics in a closed source habitat). Increasing the magnitude of population instability greatly increases the favourableness of using the sink habitat.

One limitation of the above model is that we assumed sink fitness to be density-independent. This is often a reasonable starting assumption. The basic question we have addressed is what happens in a population that is initially restricted to the source (i.e. $p = 1$), where abundances are fluctuating around K , and a clone invades which has fitness identical to the original population, but also utilizes the sink habitat to a small extent. Can this clone increase when rare? If so, the species is expected to include to some extent the sink habitat within its habitat repertoire. Initially, the invading clone will be too rare to influence the realized, density-dependent fitnesses in the source, or the sink (were there density dependence in this habitat). The above model, without sink density dependence, suffices to show that sink utilization is evolutionarily stable. A more detailed analysis is required to determine the extent of sink use at an evolutionary equilibrium; density dependence in the sink clearly can affect how much sink utilization is expected. In particular, incorporating negative density dependence in the sink tends to reduce the fraction of the population occupying the sink at an evolutionary equilibrium (R.D. Holt, unpublished results).

Changing assumptions about individual behaviour also influences the likelihood of persistent polymorphisms in dispersal (as in McPeck and Holt, 1992). Standing back from particular assumptions about the details of dispersal, density dependence and individual plasticity, however, the expectation that unstable population dynamics in source habitats promotes the evolutionary persistence of sink populations in heterogeneous landscapes appears to be robust.

Discussion

These results suggest that utilization of sink habitats makes evolutionary sense, provided source populations have unstable dynamics, with occasional incursions to fitnesses less than fitness in the sink. Let me conclude by pointing out the relevance of these results to broader issues in ecology and evolutionary biology.

The evolution of adaptive behaviour often has significant implications for population dynamics (e.g. Chesson and Rosenzweig, 1991; Abrams, 1996). The particular model depicted in Fig. 1 provides a simple example of how natural selection can destabilize population dynamics. At sufficiently low values of p , enough individuals experience the low fitness of the sink each generation for the population to be stable in its numerical dynamics. Natural selection in this case favours higher values for p , concentrating individuals into the source, which has higher maximal growth rates. Because of the time-lag inherent in discrete generation dynamics, an indirect consequence of selection on dispersal in this system may be a destabilization of population dynamics, leading to cyclic or chaotic dynamics. Indeed, the evolution of optimal behaviours can often erode sources of population stability in ecological models (e.g. van Baalen and Sabelis, 1993). This seems to have been ignored in recent debates about whether natural selection might ever indirectly lead to chaotic dynamics.

Given stable population dynamics, optimal habitat selection tends to restrict species to habitats to which they are already adapted (Holt, 1985, 1996a; Rosenzweig, 1985, 1987). Adaptive evolution, then, is automatically focused towards the maintenance and improvement of adaptation to these habitats, but is impotent at directly favouring improvement for habitats that are not utilized (Holt, 1996b). With unstable population dynamics in favourable habitats, we have seen that natural selection can favour the utilization of a wider range of habitats, including sink habitats that, on their own, cannot support the species. By virtue of individuals being exposed to the conditions in these habitats, these conditions automatically become selectively relevant. This makes it more likely that species will remain habitat generalists.

More broadly, I suggest that the character of population dynamics (*viz.*, stable *vs* unstable) may have important implications for whether one observes niche conservatism, or instead niche evolution, in species occupying spatially heterogeneous environments, via the indirect effect of such dynamics on the evolution of dispersal and optimal habitat utilization strategies. My qualitative prediction is that species with locally unstable population dynamics should tend to evolve generalized adaptation across many habitats, rather than specialization to any particular one. Assessing the robustness of this prediction is a task for future work.

As a historical note, it is intriguing that a resolution of the puzzle posed by MacArthur regarding migration may, in the end, require an appreciation of the interplay of spatial and temporal heterogeneity in the environment, and the subtleties inherent in defining fitness in variable environments. This is a combination of forces and issues MacArthur clearly recognized to be important in explaining delayed germination in annual plants in the desert (see MacArthur, 1972, pp. 165–168). I like to imagine that he would be pleased by our growing recognition of the underlying conceptual unity of seemingly disparate problems in evolutionary ecology (see also Holt, 1996a).

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References

- Abrahams, M.V. (1986) Patch choice under perceptual constraints: A cause for deviations from an ideal free distribution. *Behav. Ecol. Sociobiol.* **19**, 409–415.
- Abrams, P.A. (1996) Dynamics and interactions in food webs with adaptive foragers. In *Food Webs: Integration of Patterns and Dynamics* (G.A. Polis and K.O. Winemiller, eds), pp. 113–121. Chapman & Hall, London.
- Bull, J.J., Thompson, C., Ng, D. and Moore, R. (1987) A model for natural selection of genetic migration. *Am. Nat.* **129**, 143–157.
- Chesson, P. and Rosenzweig, M. (1991) Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* **72**, 1187–1195.
- Dias, P.C. (1996) Sources and sinks in population biology. *Trends Ecol. Evol.* **11**, 326–330.
- Fretwell, S.D. (1972) *Populations in a Seasonal Environment*. Princeton University Press, Princeton, NJ.
- Hamilton, W.D. and May, R.M. (1977) Dispersal in stable habitats. *Nature* **269**, 578–581.
- Hastings, A. (1983) Can spatial variation alone lead to selection for dispersal? *Theor. Pop. Biol.* **24**, 244–251.
- Holt, R.D. (1985) Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Pop. Biol.* **28**, 181–208.
- Holt, R.D. (1993) Ecology at the mesoscale: The influence of regional processes on local communities. In *Species Diversity in Ecological Communities* (R. Ricklefs and D. Schluter, eds), pp. 77–88. University of Chicago Press, Chicago, IL.
- Holt, R.D. (1996a) Demographic constraints in evolution: Towards unifying the evolutionary theories of senescence and niche conservatism. *Evol. Ecol.* **10**, 1–11.
- Holt, R.D. (1996b) Adaptive evolution in source–sink environments: Direct and indirect effects of density-dependence on niche evolution. *Oikos* **75**, 182–192.
- Holt, R.D. and McPeck, M.A. (1996) Chaotic population dynamics favors the evolution of dispersal. *Am. Nat.* **148**, 709–718.
- Keddy, P.A. (1981) Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *J. Ecol.* **69**, 615–630.
- Kennedy, M. and Gary, R. (1993) Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. *Oikos* **68**, 158–166.
- MacArthur, R.H. (1972) *Geographical Ecology*. Harper and Row, New York.
- May, R.M. and Oster, G.F. (1976) Bifurcations and dynamic complexity in simple ecological models. *Am. Nat.* **110**, 573–599.
- McPeck, M.A. and Holt, R.D. (1992) The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027.
- Morris, D.W. (1991) On the evolutionary stability of dispersal to sink habitats. *Am. Nat.* **137**, 907–911.
- Pimm, S.L. (1991) *The Balance of Nature?* University of Chicago Press, Chicago, IL.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *Am. Nat.* **132**, 652–661.
- Pulliam, H.R. (1996) Sources and sinks: Empirical evidence and population consequences. In *Population Dynamics in Ecological Space and Time* (O.E. Rhodes Jr, R.K. Chesser and M.H. Smith, eds), pp. 45–70. University of Chicago Press, Chicago, IL.
- Pulliam, H.R. and Danielson, B.J. (1991) Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *Am. Nat.* **137**, S50–S66.
- Rosenzweig, M.L. (1985) Some theoretical aspects of habitat selection. In *Habitat Selection in Birds* (M. Cody, ed.), pp. 517–540. Academic Press, New York.
- Rosenzweig, M.L. (1987) Habitat selection as a source of biological diversity. *Evol. Ecol.* **1**, 315–330.
- Seger, J. and Brockmann, H.J. (1987) What is bet-hedging? *Oxford Surv. Evol. Biol.* **4**, 182–211.
- Sutherland, W.J., Townsend, C.R. and Patmore, J.M. (1988) A test of the ideal free distribution with unequal competitors. *Behav. Ecol. Sociobiol.* **23**, 51–53.
- van Baalen, M. and Sabelis, M.W. (1993) Coevolution of patch selection strategies of predator and prey and the consequences for ecological stability. *Am. Nat.* **142**, 646–670.
- Vincent, T.L. and Brown, J.S. (1989) The evolutionary response of systems to a changing environment. *Appl. Math. Comput.* **32**, 185–206.