

Spatial scale and the cost of density-dependent habitat selection

DOUGLAS W. MORRIS

Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland, A1B 3X9, Canada

Summary

Habitat selection costs depend upon the scale of habitat. At the fine-grained microhabitat scale, cost is linked to optimal foraging, and habitat selection should be abandoned even though fitness is greater in one microhabitat than in another. At the coarse-grained macrohabitat scale, cost is linked to emigration, and habitat selection should often be maintained even though fitness may be less in the 'preferred' macrohabitat than in others. Macrohabitat selection cost is easily incorporated into habitat selection theory and can be tested by linear regression techniques on isodars (lines of every point at which the fitness of individuals in one habitat equals that of individuals in another). The results of one recent survey of white-footed mice living in different macrohabitats are consistent with the predictions of emigration cost.

Keywords: Dispersal, emigration cost, fitness, habitat selection, isodar, macrohabitat, microhabitat, migration, scale.

Introduction

Current theories of habitat selection, originating with that of Fretwell and Lucas (1970), assume that habitats should be chosen according to their relative evolutionary benefits and costs. Individuals should abandon habitat selection whenever the expected fitness rewards of different habitat choices are equal. The cost of habitat selection has been incorporated into these evolutionary models as the time individuals lose while moving through microhabitat patches in place of the benefits of active foraging in those or more rewarding patches (Rosenzweig, 1974, 1981, 1985; Charnov, 1976). An implicit assumption of these models is that the profits of foraging can be readily converted into the evolutionary currency of fitness. If this assumption holds, foraging models should effectively represent the allocation of time and energy by individuals among small-scale patches.

It is not clear how foraging models can be applied to larger-scale macrohabitat patches within which a given individual may spend most or all of its lifetime but which, nevertheless, constitute a major component of the habitat mosaic exploited by most species (Morris, 1987a). At the coarse-grained macrohabitat scale, it is probably best to think of habitat selection as a colonization process which can be modelled by the relative rewards and costs of emigration. This paper evaluates the evolutionary costs and benefits of emigration as a complementary theory to that described for fine-grained microhabitat selection. It develops the relationship between the cost of macrohabitat selection and the Fretwell–Lucas–Rosenzweig theory, and shows how census data can be used to detect emigration cost.

Foraging and emigration costs

The ideal-free distribution of Fretwell and Lucas (1970) left the scale of habitat undefined, assumed that habitat selection was without cost, and that fitness rewards within a habitat

generally declined with increased population density. With increased density, fitness in a preferred habitat would decline until it equalled the expected fitness in a second habitat. At this density, individuals would reap equivalent fitness rewards in both habitats, and both should be occupied. At any given population size, the habitat distribution of individuals would specify an ideal-free distribution if average fitness was the same among habitats.

Rosenzweig (1974) expanded the theory to include searching and foraging costs of fine-grained searchers as they moved among patches of microhabitat. His conclusions, verified implicitly by Charnov (1976), showed that habitat selection should be abandoned whenever fitness in the better patch is reduced to the fitness in the poorer patch multiplied by a ratio of search and utilization times:

$$\ln W_{BI} = \ln W_{AI} (1 + t_{mI}/t_{bI}) \quad (1)$$

where W_{BI} is the fitness of species I in patch type B, t_{mI} is the time required to discover two patches (one each of types B and A), and t_{bI} is the time an individual of species I spends exploiting patch type B (Rosenzweig, 1974, 1981; Rosenzweig and Abramsky, 1986). Provided the discovery time is greater than zero, individuals should abandon habitat selection even though fitness in the better patch exceeds that in the poorer patch.

The cost of macrohabitat selection is fundamentally different from that for microhabitats. At the scale of microhabitat, fine-grained foragers are moving among patches and the cost of habitat selection is encapsulated by the time travelling through or around sub-optimal patches in favor of finding and exploiting better ones (Fig. 1). At the scale of macrohabitat, the cost of habitat selection is the loss in fitness during emigration to a new location.

Microhabitat selection deals with individual foraging cost once a particular macrohabitat has been selected. For many species it is unlikely to vary substantially among age or other phenotypic classes. Macrohabitat selection deals with dispersal decisions, and is likely to have significant age and phenotypic biases.

Dispersal will evolve as an evolutionarily stable strategy only if the average fitness of emigrants is equal to that of non-emigrants. This will occur only if emigrating individuals, on average, make the correct cost-benefit analysis of habitat quality in terms of fitness rewards. Dispersing individuals should stop travelling and settle in a habitat whenever their fitness by doing so (minus emigration cost) is greater than what they could have attained by not dispersing in the first place.

Earlier, I evaluated age-specific dispersal strategies by considering the relative benefits and costs of emigration in terms of reproductive value (Morris, 1982). Such a treatment allowed the incorporation of age-specific fecundity and survival probabilities of different macrohabitats as well as survival probabilities of individuals during migration. Without cost, macrohabitat selection in patch H by an individual aged x should be abandoned whenever:

$$V_{xD}/V_{xH} > 1 \quad (2)$$

where V_{xD} is the expected reproductive value of the individual after dispersal to D, and V_{xH} is the expected value by not dispersing from macrohabitat H. Emigration takes time, and the optimal individual needs to assess its relative rewards in D after emigration, relative to what it could have gained in H without moving.

With cost, individuals should emigrate to a new macrohabitat whenever:

$$V_{(x+t)D}/\{V_{(x+t)H} + |V_{xH} - V_{(x+t)H}|\} > 1 \quad (3)$$

where t is the duration of dispersal, and the absolute value term is the dispersal threshold (Morris, 1982) which represents the positive difference in reproductive value of emigrants relative to non-emigrants caused by reduced survival and lost opportunities for reproduction

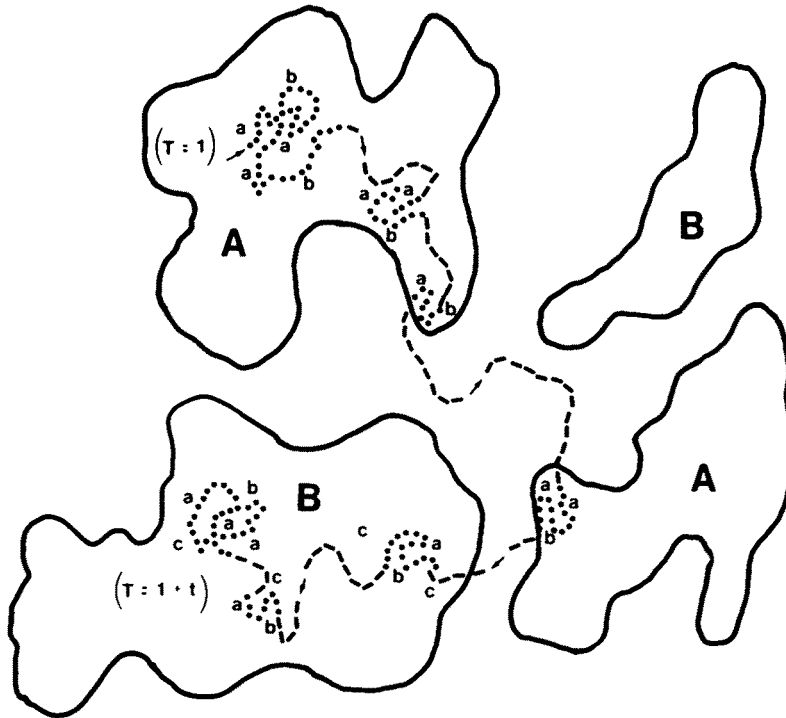


Figure 1. Habitat selection on different spatial scales in a patchy environment. Upper case symbols refer to macrohabitat patches, lower case refer to microhabitats at actual foraging sites. Dotted lines represent a typical foraging episode by an a specialist within its original (time $T = 1$) and new (time $T = 1+t$) home ranges and other foraging bouts during migration. Foraging cost is the amount of time spent searching b patches which could be used to forage there or elsewhere. Dashed lines represent dispersal to a new home range. Emigration cost is the time spent searching for a new home range within the same or different macrohabitats (after Rosenzweig, 1981).

during t . Individuals should abandon macrohabitat selection only when fitness in a better patch (H) is depressed at least as much as the dispersal threshold below that in a poorer patch (D).

Dispersal cost for pre-reproductive individuals incorporates only survival costs, whereas for older animals it may also include lost fecundity. Consequently, most emigrants should be either young individuals which have not yet attained maximum reproductive value, or older individuals whose residual reproductive value is low (see Morris, 1982). All other things being equal, t should increase with increased distance between macrohabitat patches.

Relation to the Fretwell–Lucas theory

The emigration cost of macrohabitat selection can be easily joined to the Fretwell–Lucas model of density-dependent habitat selection. Consider two similar macrohabitats which differ only in productivity. The effect of increased density on fitness should be similar in both habitats such that the feedback of density on fitness (the fitness–density functions) can be assumed to be represented by parallel negatively sloped straight lines (Fig. 2a; Morris, in review, a). If individuals

select habitats on the basis of fitness rewards, the distribution of individuals should be adjusted such that:

$$W_i = W_j - C_{i \rightarrow j} \quad (4)$$

where W_i is the fitness in habitat i , and $C_{i \rightarrow j}$ is the cost of dispersal from i to j (equals the dispersal threshold) which was assumed to be zero in the original Fretwell–Lucas model.

Fitness-density functions can be modelled as:

$$W_1 = B_1 - bN_1 \quad (5)$$

where W_1 is the fitness in habitat 1, B_1 is the basic fitness in habitat 1 at zero density, and bN_1 is the linear relation between fitness and density in habitat 1. Similarly, for habitat 2:

$$W_2 = B_2 - bN_2$$

At any given fitness:

$$N_1 = (B_1 - W_1)/b \quad (6)$$

and:

$$N_2 = (B_2 - W_2)/b$$

If there is no emigration cost, individuals should colonize both habitats when $W_1 = W_2$, that is, when:

$$B_1 - bN_1 = B_2 - bN_2$$

and the density in habitat 1 relative to that in habitat 2 is given as:

$$N_1 = N_2 + (1/b) (B_1 - B_2) \quad (7)$$

N_1 will be some constant value greater than N_2 when both habitats are occupied and fitness is equal (Fig. 2a). At fitness W_d , for example, the expected density in habitat 1 is D_1 , and that in habitat 2 is D_2 . Note that this general prediction holds whether or not the relation between fitness and density is linear because equation (7) becomes:

$$N_1 = N_2 + \{1/g(N)\} \{B_1 - B_2\}$$

where $g(N)$ is any other fitness-density function.

With emigration cost, however, individuals should leave habitat 1 in favor of habitat 2 only when the fitness in 2 exceeds that in 1 by a value at least equal to the cost of emigration. Suppose first that cost is independent of density. Then the perceived quality of habitat 2 to potential colonists is given by:

$$W_2 = (B_2 - C_{1 \rightarrow 2}) - bN_2 \quad (8)$$

and the expected densities in the two habitats are:

$$N_1 = N_2 + (1/b) (B_1 - B_2 + C_{1 \rightarrow 2}) \quad (9)$$

Density-independent emigration cost results in a consistent fitness depression in less preferred habitats. The dotted line in Fig. 2b shows the expected cost-induced fitness depression in habitat 2 with emigration cost. At fitness W_d , emigration from habitat 1 at density D_1 should now occur only when the density in habitat 2 $< D_4$.

A fixed density-independent cost may seem counter intuitive at first. Density-independent cost implicitly assumes that the duration of dispersal is also independent of density. According to

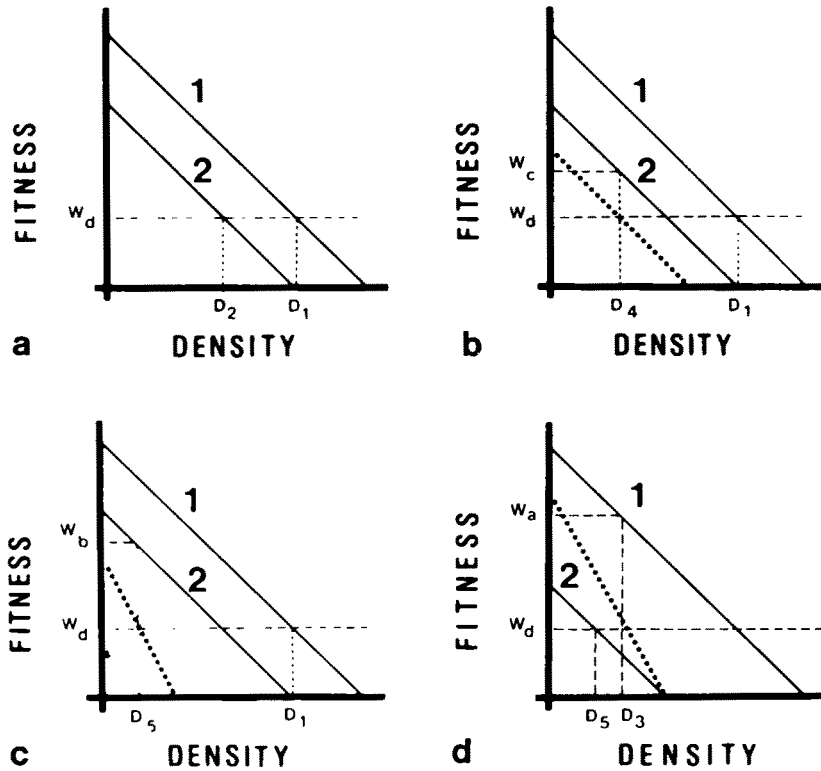


Figure 2. The effect of emigration cost on the Fretwell–Lucas density-dependent habitat selection theory for two habitats. Dotted lines are the perceived quality of a second habitat by emigrating individuals. Dashed lines indicate expected and realized fitness as well as colonizing densities in the two habitats. (a) The ideal-free distribution with no cost. At fitness W_d the expected density in habitat 1 is D_1 , that in 2 is D_2 . (b) The ideal-free distribution with density-independent cost. At fitness W_d the density in 2 is now D_4 . (c) The ideal-free distribution with density-dependent cost (curves diverging; migration is toward a poorer habitat). At fitness W_d the density in 2 is D_5 . (d) The ideal-free distribution with density-dependent cost (curves converging; migration is toward a better habitat). At fitness W_d the density in 1 is D_3 . In b, c and d the realized age-specific fitness of successful colonists and their descendants (W_c , W_b and W_a respectively) is much greater than the expected fitness of individuals remaining in the source habitat. For these three cases, the *per capita* population growth rate in the second habitat will exceed that in the source habitat and reduce the rewards of emigration.

Fretwell and Lucas (1970), fitness should decline with density. Thus, as population density increases, the absolute fitness rewards per unit time are reduced, and so too should be the cost of emigration (migration time constant; reproductive value declines with density). Yet this is the same reason why the relative costs of emigration may be constant. True, individuals lose less by emigration at high density, but they also gain less by staying at home. To see this, let the density-dependent fitness for an individual aged x in habitat 1 be estimated as:

$$V_{x1} = B'_{x1} - b'N_1 \tag{10}$$

where B'_{x1} represents the basic reproductive value of an individual aged x in habitat 1. It is very

likely that a wide range of age classes experience the same degree of density-dependent feedback on reproductive value. Thus, for an individual aged $x + t$:

$$V_{(x+t)1} = B'_{(x+t)1} - b'N_1 \quad (11)$$

From equation (3) we see that migration to habitat 2 is cost-effective if and only if:

$$V_{(x+t)2} > V_{(x+t)1} + |V_{x1} - V_{(x+t)1}| \quad (12)$$

Substituting equation (11) into (12):

$$\begin{aligned} B'_{(x+t)2} - b'N_2 &> [B'_{(x+t)1} - b'N_1] \\ &+ |(B'_{x1} - b'N_1) - (B'_{(x+t)1} - b'N_1)| \end{aligned} \quad (13)$$

then:

$$B'_{(x+t)2} - b'N_2 > |B'_{(x+t)1} - b'N_1| + |B'_{x1} - B'_{(x+t)1}|$$

and setting the right hand term equal to cost and generalizing:

$$V_{(x+t)i} > V_{(x+t)j} - C_{i \rightarrow j} \quad (14)$$

which is of the same form as equation (4). The relative cost of emigration is independent of population density.

Other factors, however, suggest that emigration cost is unlikely to be independent of population density. Increased crowding may frequently be accompanied, for example, by reduced growth rates, shifts toward smaller body size, reduced energy reserves and increased stress-related disorders. Phenotypes possessing these traits can be expected to suffer increased mortality risks during and following emigration, and perhaps reduced fecundity. This means that the dispersal threshold should increase with increasing population density and:

$$W_2 = B_2 - bN_2 - f(N)(C_{1 \rightarrow 2}) \quad (15)$$

where $f(N)$ is the density-dependent increase in emigration cost. Assuming for simplicity that this function is also linear, it has the effect of rotating the habitat 2 fitness-density function clockwise. The clockwise rotation generates divergent slopes of the fitness-density functions, and thereby further reduces the expected density in the second habitat (Fig. 2c).

Successional changes, population dynamics, stepping stone effects and a variety of historical and chance events will create a patchwork of habitats of variable quality. Many of these will be of lower quality than the habitats from which emigrants originate, some will be of higher quality. Density-dependent emigration cost acts to lower the intercept and rotate the slope of fitness-density curves of all habitats to which individuals might migrate regardless of the habitats' basic quality. Average fitness of individuals dispersing to higher quality habitats equals that of non-dispersers only if the density in the better habitat corresponds to points along the cost curve (Fig. 2d), which converges on the fitness-density curve of the poorer habitat.

Emigration cost leads to an interesting paradox. Once individuals arrive in a second habitat, actual age-specific fitness exceeds that of individuals in the source habitat (the expected life-time contribution of emigrants and non-emigrants is the same). Other things being equal, the *per capita* population growth rate in the second habitat would necessarily exceed that in the source habitat, and the dispersal threshold would be quickly closed by reproduction of the successful colonists and their descendants (Fig. 2b, 2c and 2d). Differences in habitat quality which initially favored dispersal are rapidly equilibrated by the greater reproductive success of the colonists. Dispersal is a speculative life history, and we can predict that macrohabitat dispersal can be

maintained only by temporal and spatial variation in habitat quality. Furthermore, an optimum dispersal strategy is likely to include pulsed emigrations which correspond to the temporal and spatial mosaic of habitat quality.

If the two habitats are of similar quality, the perceived fitness in the better habitat may actually cross over the fitness–density curve in the poorer habitat. Cross overs are particularly interesting because they enable a counter-intuitive reversal of population densities (Fig. 3). The density in the better habitat is exceeded by that in the poorer habitat. This will be a transient effect, however, because rapid population growth in the better habitat will quickly allow it to establish itself as the habitat with the greatest density. Cross overs can certainly occur, but they may seldom be discovered. Holt (1985) has also treated fitness–density curves which cross over.

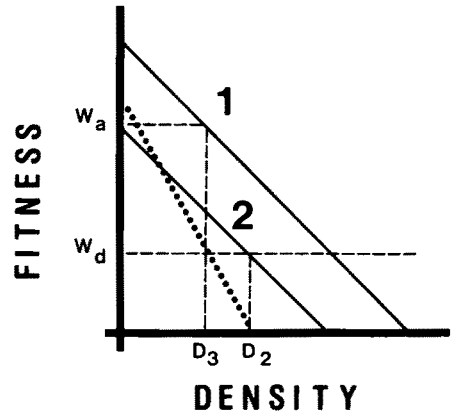
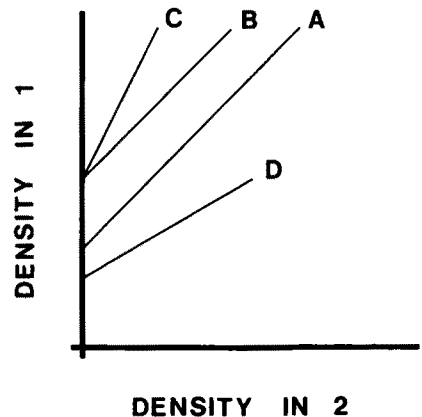


Figure 3. An example of how emigration cost can lead to cross overs and a temporary reversal of population density between rich and poor habitats. The plot is the same as Fig. 2d except that quantitative differences between habitats are reduced. At fitness W_a , the density in habitat 2 (D_2) exceeds that in habitat 1 (D_3).

The detection of emigration cost

How can we detect the presence of emigration cost between habitats? One indirect way would be to measure the intercept and slope differences in the fitness–density relations between habitats. These relations can be represented graphically as isodars, lines at every point of which the fitness of individuals in habitat 1 equals that of individuals in habitat 2 (Fig. 4). Isodars capture the essence of density-dependent fitness reduction between habitats (Morris, in review, a).

Figure 4. Isodars plotted for the four scenarios of emigration cost in Fig. 2. A – No emigration cost, basic fitness in habitat 1 exceeds that in habitat 2, fitness–density curves are parallel and the isodar slope = 1.0. B – Density-independent emigration cost, habitat 1 is perceived as having a constant increased fitness advantage over habitat 2, fitness–density curves are still parallel and the isodar slope = 1.0. C – Density-dependent emigration cost, habitat 1 is perceived to increase in quality relative to habitat 2 in a density-dependent fashion, fitness–density curves are divergent and the isodar slope > 1.0. D – Density-dependent emigration cost, habitat 1 is perceived to decrease in quality relative to habitat 2 in a density-dependent fashion, fitness–density curves are convergent and the isodar slope < 1.0.



On isodar graphs, absolute differences in habitat quality (fitness) are given by the intercepts of the isodars on the density axis of the better habitat. The slope of the isodar portrays the relationship between the degree of density-dependence in fitness between the two habitats (Morris, in review, a). Parallel fitness–density curves give isodar slopes equal to 1.0; divergent curves give slopes greater than 1.0, and convergent curves give slopes less than 1.0 (Fig. 4). These properties are easily measured by linear regression.

To construct isodars of the fitness–density functions in Fig. 2, draw sets of horizontal lines and plot the densities which correspond to the intersections of each of these with the habitat-specific fitness–density curves (points of equal fitness) on a graph of N_1 versus N_2 . Fig. 4 shows the results of such a plot for each of the four cost scenarios depicted in Fig. 2. Notice that each of these can be distinguished by intercept and/or slope differences. Thus, density-independent cost and no emigration cost curves for parallel fitness–density functions both result in isodar slopes of 1.0, but the N_1 intercept changes with cost. Similarly, when emigration cost is density-dependent, and the direction of movement is toward habitats of lower quality, the isodar slope is greater than 1.0; when emigration is toward habitats of greater quality, the isodar slope is less than 1.0. The removal of emigration cost will often result in changes to both the slope and intercept of the appropriate isodar.

Cross overs complicate the isodar analysis. Above the cross over, fitness–density curves converge, and we might correctly conclude that emigration was toward a habitat of higher quality. Below the cross over, fitness–density curves diverge, and we might incorrectly assume that migration was toward a habitat of lesser quality. In both cases, the isodar analysis would detect emigration cost. Subsequent analyses of divergent curves would reveal the correct direction of migration (see below).

Morris (in press) showed that non-parallel slopes can also be detected in expanding populations by plotting replicated estimates of population density for two macrohabitats simultaneously on a single graph. This is very similar to isodar analysis, and if the fitness–density slopes diverge, such a plot should give a linear regression with a slope significantly greater than 1.0. Density plots of an expanding population of white-footed mice (*Peromyscus leucopus*) revealed divergent slopes between high (forest and scrub) and low density (old-field) macrohabitats.

Habitats may often differ in their density-dependent fitness rewards (Morris, in press, in review, a) and it is not enough simply to evaluate slope and intercept differences between habitats to detect the cost of macrohabitat selection. Divergent slopes should occur, for example, whenever the efficiency of resource extraction in the richer habitat exceeds that of the poorer habitat. More resources can be gained per unit density in the better habitat, and this leads to increased fitness. Convergent slopes occur when individuals are more efficient in the poorer habitat. Similarly, if habitats differ in absolute quality, isodar intercepts will reflect those differences.

There are at least four ways to overcome this limitation. Monitoring the movement of individuals would appear to be the simplest, but if this really was easy we wouldn't need isodars to evaluate dispersal between habitats. A second and more realistic alternative is to census habitats at two or more intervals, during which differential population growth rates between habitats will lead to changes in their relative densities. If the degree of divergent, convergent or cross over regulation has been influenced by density-dependent emigration costs, differential growth rates which close dispersal thresholds will reduce the slope of cost curves. This in turn will result in isodar slopes which are closer to the predicted value of 1.0 for parallel regulation. If migration is no longer a successful strategy, fixed costs will also disappear, and manifest their absence through isodar intercepts which should decline in value when directional migration is

toward poorer habitats; intercepts should increase when migration is toward habitats of higher quality.

In the case of apparently divergent curves, which in reality reflect cross overs, the relative densities in the two habitats will reverse themselves. This is because emigration cost originally made the better habitat appear even poorer than the poor habitat from which individuals were emigrating; the density in the poor habitat exceeded that in the rich habitat. Following dispersal, differential population growth between habitats should quickly allow the population density of the better habitat to surpass that in the poorer habitat.

A third alternative to distinguish qualitatively different habitats from those whose densities reflect emigration costs, would be first to evaluate possible slope differences between habitats along a geographical gradient. From this analysis, select pairs of habitats which have similar slopes. Remove animals from the poorer habitat, and monitor density in both habitats through time. If there is a cost to emigration, dispersing individuals should settle in the poorer habitat in such a way as to lead to divergent fitness–density curves (isodar slopes > 1.0). Even if the initial isodar slope is different from 1.0, this experiment can be performed to evaluate significant increases in the isodar slope. A modification of this procedure would replicate the removal of individuals from macrohabitat B across a patchwork landscape in which inter-habitat distances varied. Emigration costs between different patches should be unequal and result in isodars of different slopes between replicate pairs of patches.

A fourth solution would be simultaneously to monitor reproductive success and collect data for the isodar analysis. With emigration cost, fitness should be greater in one habitat than another. These data can often be generated as demographic estimates of survival and recruitment rates from careful censuses of animal abundance. In my work on white-footed mice (Morris, 1987b, in review, a), I interpreted divergent slopes between old-field and forest macrohabitats as evidence in favor of qualitative differences which generated significantly different density-dependent effects on reproductive fitness. That may be the case, but it is intriguing also to note that consistent with emigration cost, demographic estimates of fitness in the low-density old-field exceeded those in the high-density forest and scrub macrohabitats (Morris, 1987b). Other studies, which estimated reproductive success with capture–recapture data of white-footed mice living in nest boxes, have confirmed significant fitness differences between habitats (Morris, in review, b).

Depressed fitness–density curves and unequal fitness between habitats are also expected under ideal-despotic distributions (Fretwell and Lucas, 1970). In this case, the perception of habitat quality is modified by interference from conspecifics which inhibit colonization. Such a process can be viewed as one of the mechanisms which lead to density-dependent emigration cost. The techniques I have outlined should be able to detect this cost, but supplementary research would be required to identify the actual mechanisms influencing the perception of depressed habitat quality.

Tests of the theory will be complicated because emigration is not restricted to dispersal between isolated patches. Emigration includes shifts of foraging epicenters both within and between large-scale patches. Nevertheless, emigration costs between such patches should often exceed those within patches, and inter-habitat comparisons should be an effective means of discovering the existence and nature of emigration cost.

The costs of habitat selection have widely different causes and outcomes on different spatial scales. At the fine-grained microhabitat scale, the cost of habitat selection can be modelled by the time lost moving through sub-optimal microhabitat patches when it could be spent exploiting those or better patches. Microhabitat selection should be abandoned in favor of exploiting

additional patches even though the fitness rewards in the 'preferred' patch exceed those in 'less preferred' patches. At the coarse-grained macrohabitat scale, the cost of habitat selection can be modelled as the time lost from reproduction during emigration. The predictions of habitat selection at this scale are exactly opposite to those at the microhabitat scale. Macrohabitat selection should not be abandoned until the expected fitness rewards in the 'less preferred' patch exceed those in the 'preferred' patch.

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