

Habitat matching: alternatives and implications to populations and communities

DOUGLAS W. MORRIS

Centre for Northern Studies, Department of Biology and School of Forestry Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada

Summary

I evaluate habitat matching rules based on ideal distribution models of density-dependent habitat use. Recent approaches and the ideal free continuous input matching rule on which they depend, are restricted to only those habitats that are jointly occupied across the full range of population sizes. These assumptions may often be inappropriate to field applications of habitat matching. I develop alternatives that can be applied to a wide array of ideal forms of habitat selection, including the ideal free, continuous input example. Input matching can be distinguished from assumptions of consumer-resource models and pre-emptive habitat use by regressions of density between paired habitats (isodars). Isodars for continuous input models should be linear on a logarithmic scale, while those for consumer-resource models should be linear on an arithmetic scale. Pre-emptive isodars can be distinguished from the others by dramatic non-linearities at both low and high densities. Field data on white-footed mice support the consumer-resource theory. Implications of the rules for population regulation and community organization are highlighted by new models that specify how the fitness of pre-emptive habitat selectors should decline with increasing density. Strong non-linearities produced by comparisons between variable and homogeneous habitats produce reversing source-sink population regulation and a new form of cyclical community dynamics. Variable habitats act as a source of emigrants at low density and a sink for immigrants at high density. Subordinate species may occupy only the variable habitat at both low and high density.

Keywords: community; habitat; habitat selection; ideal free distribution; isodar; landscape; population regulation

Introduction

Habitat matching rules specify the relationship between population density and resource supply in heterogeneous habitats. When the rules are obeyed they allow us to predict, in advance, how changes in habitat supply might alter spatial patterns in population density. Current rules are limited in application by their restrictive assumptions of an ideal free distribution with continuous resource input.

The habitat matching rules have, nevertheless, accurately predicted spatial patterns in population density in experimental settings where assumptions of continuous input have been strictly controlled (e.g. Parker, 1978; Harper, 1982; Godin and Keenleyside, 1984; Milinski, 1984; Recer *et al.*, 1987). However, many ecologists are likely to remain skeptical of applying habitat matching to field settings because it is difficult to imagine how the models' assumptions apply to the heterogeneity in habitat that typifies many ecological landscapes.

My intent is to explore the rules that may apply to a variety of different forms of density-dependent habitat selection and to develop tests that differentiate among them. I begin by reviewing previous models and their application to ecological landscapes. I demonstrate that these models may frequently misinterpret habitat matching when the assumption of continuous

input is exchanged for equally realistic assumptions related to consumer-resource dynamics and to source-sink regulation. I then develop new alternatives that specify expected patterns in population density between habitats at the landscape scale. Each alternative leaves a unique signature in regressions of population density between habitats. The relationship for pre-emptive habitat selection suggests previously unanticipated reversals in source and sink habitats as well as a new kind of community organization structured on cyclical changes in habitat use. I present a new field test that can distinguish among the three alternatives and conclude with a critique of habitat matching.

Habitat matching rules and the ideal free distribution: a brief review

An ideal free distribution (IFD) (Fretwell and Lucas, 1970) occurs when the density of individuals occupying different habitats is such that the mean reproductive success of individuals in each habitat is equal. Pulliam and Caraco (1984) demonstrated, in a special case of the IFD for a resource-limited population where each individual's fitness is proportional to its fraction of total resources, that

$$K_i/p_i = K_j/p_j \quad (1A)$$

where K is carrying capacity and p is the number of individuals occupying habitat patches i and j . Equation 1A is the habitat matching rule that specifies how individuals should distribute themselves relative to the availability of resources. It follows that the ratio of individuals occupying different patches can be used as a surrogate to estimate relative resource abundance

$$p_i/p_j = K_i/K_j = \text{constant} \quad (1B)$$

from Fagen (1988) (see also Recer *et al.*, (1987).

The model represented by Equation 1B can be generalized by the inclusion of an interference term (Sutherland, 1983; Fagen, 1987) such that

$$p_i = kn_i^{1/m} \quad (2)$$

where p_i is predator density in i , n_i is prey density, m is the degree of interference among predators ($0 < m \leq 1$) and k is a positive constant. This yields the intuitively appealing outcome that the fraction of predators in patch i is proportional to the fraction of prey in that patch,

$$p_i/P_t = (Cn_i/N_t)^{1/m} \quad (3)$$

where P_t is the total population density of predators, N_t represents the total population of prey and C is a scaling constant (Sutherland, 1983; see also Kacelnik *et al.*, 1992a,b; and Oksanen *et al.*, 1992).

Equations 1B and 3 appear to be powerful ways to test the IFD against field data on animal abundance. Equation 3 implies that if prey distribution among patches remains constant, a change in predator population size will have no effect on the proportion of the predator densities in each patch (Messier *et al.*, 1990).

Similarly, if Equation 1B holds, we can use estimates of population density in each habitat to predict changes in population size with changes in habitat supply (Fagen, 1988). In particular, the percent loss in the carrying capacity of the 'landscape' can be estimated by

$$100[1 - (\sum_{i=1}^M n_i Q_i' / \sum_{i=1}^M n_i Q_i)]$$

where M is the number of habitats, Q_i is the proportion of all habitats consisting of habitat i prior to disturbance and Q'_i is the same proportion following disturbance (Fagen, 1988).

Pulliam and Caraco (1984) and Fagen (1987) were careful to note that the matching rule applied only to occupied habitats. The extensions to the rule suggested by Fagen (1988) and Messier *et al.* (1990) implicitly assume that all M habitats are occupied regardless of population size. If Equation 2 is equal to zero for any patch I , the solution given by Equation 3 is also zero.

Habitat matching at the landscape scale: a consumer–resource model

I have shown above how current habitat matching rules assume that animal densities are proportional to per capita resource availability. This assumption is equivalent to that of continuous input models of the ideal free distribution where resources are consumed as soon as they are added to a habitat (e.g. Milinski and Parker, 1991; Kacelnik *et al.*, 1992a). Input matching is most likely on a small spatial scale where individuals compete directly for renewing resources. At larger scales continuous input and instantaneous consumption of resources are probably invalid assumptions and animal density may depend upon other measures of resource availability.

Consider a landscape composed of two habitats within which per capita population growth rate of a particular species is positive at low density. Imagine that resources are renewed in each habitat at different rates and that the spatial distribution of renewal is such that all renewed items cannot be simultaneously consumed by an individual forager. We wish to know how habitat quality is discounted with increased forager density and, in particular, how this discounting varies from the proportional decline that applies to continuous input.

As a simple example, imagine two habitats of equal size with the same random distribution of resources. Imagine further that resource renewal in both habitats exceeds the intake rate of single foragers, but that resources in habitat 1 are renewed more rapidly than in habitat 2. Resource ‘renewal density’, the rate of resource renewal per unit area, will thus be greater in habitat 1 than it is in habitat 2. Assume that each identical forager has a minimum requirement for the resource, as well as a maximum digestive capacity that limits its resource consumption. Assume also that foragers face conflicting demands on their time so that they maximize their evolutionary potential by maximizing the rate of resource acquisition.

The above assumptions suggest that an individual’s expected fitness might be a simple linear function of renewal density,

$$(1/N_i) (dN_i/dt) = g[RD_i - N_i(pE_B/E_i)] \quad (4)$$

where N_i represents the population density in habitat i , RD_i represents renewal density, g is a scaling constant, p is the per capita demand on resource and E_B/E_i is the efficiency of resource extraction, consumption and conversion into descendants in the best habitat (B) relative to habitat i (Morris, 1988). That is,

$$(1/N_i) (dN_i/dt) = a_i - b_i N_i \quad (5)$$

where a_i is the maximum fitness of an individual in habitat i , b_i is the per capita reduction of fitness $\{g[p(E_B/E_i)]\}$ and N_i is population density. If resource renewal density is greater in habitat 1 than it is in habitat 2 and if this rate is an unbiased estimate of an individual’s expected reproductive success, the decline in fitness with increased density in habitat 2 will be parallel to that of habitat 1 (Fig. 1). Furthermore, if an IFD describes their habitat selection, all individuals should occupy only habitat 1 when population size is sufficiently small because the expected reproductive success of each individual is greater there than in habitat 2.

Neither Equation 1B nor the assumption of constant proportions of consumers among habitats

(Equation 3) suitably represent this kind of habitat selection because habitat 2 is unoccupied at low population size. The proportion of individuals occupying the two habitats will not be constant. To see this more clearly, assume an IFD so that the mean fitness is equal in each habitat when both are occupied. Thus,

$$a_1 - b_1N_1 = a_2 - b_2N_2 \quad (6)$$

and rearranging,

$$N_1 = \{(a_1 - a_2)/b_1\} + (b_2/b_1)N_2 \quad (7)$$

specifies a linear isodar (Fig. 1, right; Morris, 1987, 1988, 1989a, 1990), a plot of the joint densities in the two habitats such that the expected reproductive success of an individual is the same in each. The intercept $\{(a_1 - a_2)/b_1\}$ corresponds to the difference in maximum fitness between habitats 1 and 2 corrected by the density-dependent decline in fitness in habitat 1 and the slope (b_2/b_1) is the ratio of the slopes of the fitness-density functions of habitats 1 and 2. Note that, contrary to Equation 1B, the relative proportion of individuals (N_1/N_2) occupying the two habitats varies with total density $(N_1 + N_2)$,

$$N_1/N_2 = \{(a_1 - a_2)/(b_1)(1/N_2)\} + b_2/b_1 \quad (8)$$

$\neq \text{constant}$

Now consider an example where individuals occupy each patch at all predator densities greater

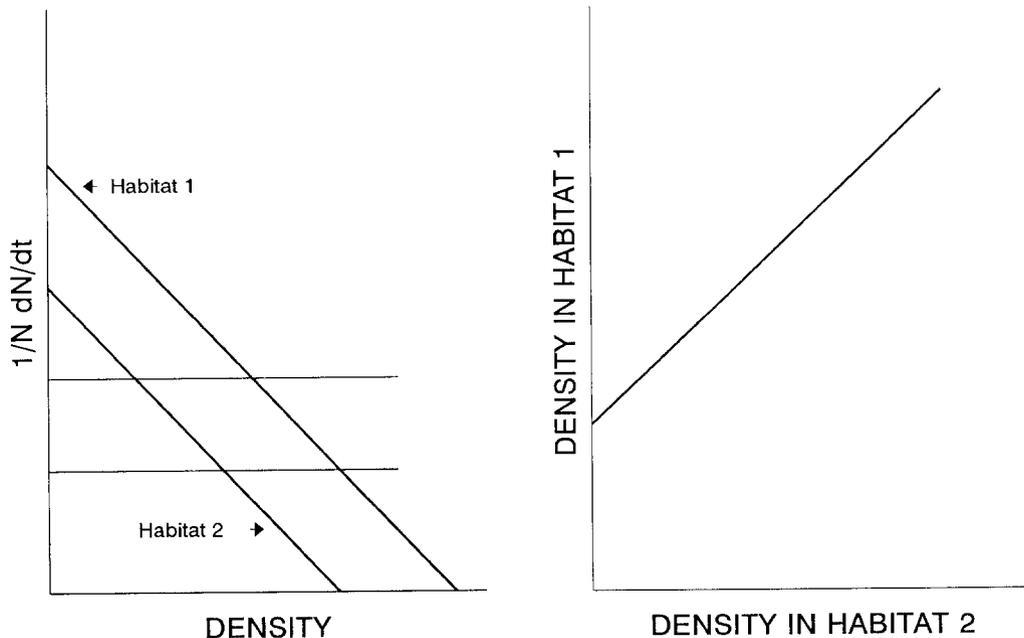


Figure 1. The form of density-dependent habitat selection expected when habitats differ from one another quantitatively (Morris, 1988). Left: per capita population growth rate is greater at all densities in habitat 1 than it is in habitat 2. Each horizontal line connects densities in the two habitats such that the per capita population growth rate is equal in both (an ideal free distribution). Right: the parallel fitness-density curves on the left plotted as isodars. Every point on the isodar specifies the joint density in habitats 1 and 2 such that an individual's expected reproductive success is the same in both.

than zero (Fig. 2). Note that the ratio of densities given by the resulting isodar is constant with total density, (Fig. 2, right). Equations 1B and 3 are, in this case, valid representations of habitat matching.

Differentiating between continuous input and the consumer –resource model

How is one to know, with only field data on density, which form of habitat selection model is closest to reality? The question is solved by isodar analysis. If resource encounter is proportional to the density of consumers in the habitat, then

$$(1/N_i) (dN_i/dt) = R_i/(N_i a_i)^{m_i} \tag{9}$$

where R_i is the availability of resources corrected by renewal rate, a_i is the per capita demand on resources and m_i is an interference coefficient specifying the reduction in a consumer’s intake rate with increased consumer density (Hassell and Varley, 1969; Sutherland, 1983; Milinski and Parker, 1991). For an ideal free distribution

$$R_1/(N_1 a_1)^{m_1} = R_2/(N_2 a_2)^{m_2} \tag{10}$$

This equation yields a linear isodar on a logarithmic scale

$$\log N_1 = \{(\log R_1/m_1) - (\log R_2/m_1) + [(m_2/m_1)\log a_2] - \log a_1\} + [(m_2/m_1)\log N_2] \tag{11}$$

(Morris 1992a). One of the intriguing outcomes of this analysis is that the slope of the regression

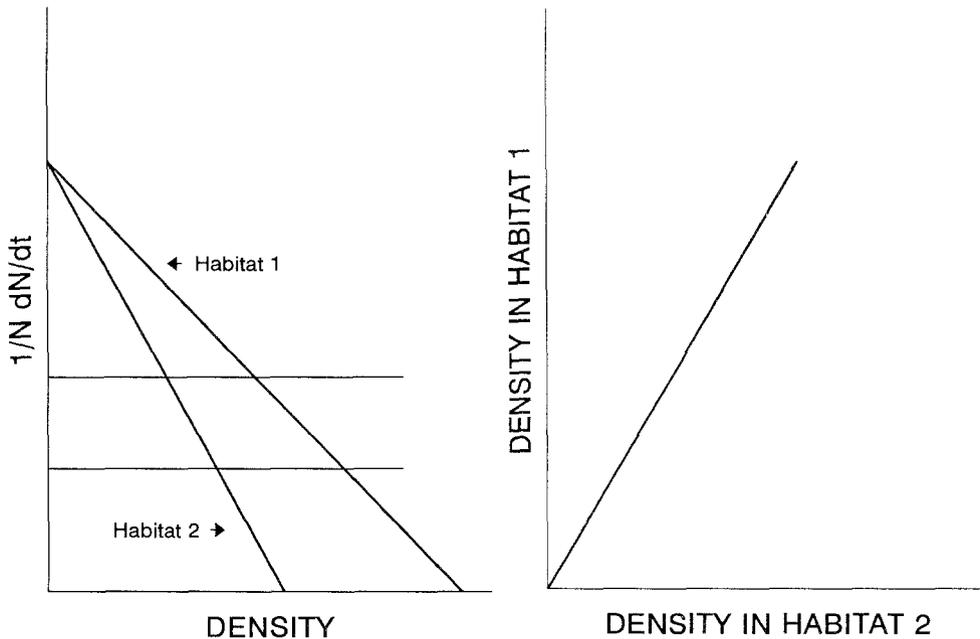


Figure 2. The form of density-dependent habitat selection expected when habitats differ from one another qualitatively (Morris, 1988). Left: per capita population growth rates in the two habitats are equal at some lower population density, but diverge thereafter. Right: the divergent fitness-density curves on the left plotted as isodars. The ratio of densities in the two habitats is identical at all points on the isodar.

is equal to the ratio of interference in the two habitats (the model assumes that the value of m_i is itself independent of consumer density; e.g. Sutherland, 1983). The main point is that the alternatives of consumer – resource versus continuous input may often be differentiated by simply evaluating the fit of a linear isodar on arithmetic (consumer–resource) or logarithmic scales (continuous input).

Interference may also modify habitat choice in the linear consumer–resource model. Territorial individuals, for example, reduce the apparent quality of the better habitat (the ideal despotic distribution; Fretwell and Lucas, 1970; Fretwell 1972). Isodars, in this instance, plot densities in the two habitats such that an individual's perceived fitness is identical in each even though the mean fitness is unequal. One way to model the interference is to assume that territorial individuals reduce the efficiency of resource use of subordinates equally in the two habitats. The cumulative effect increases with density because there are more dominant individuals in the population. This produces perceived fitness-density curves (*sensu* Fretwell and Lucas, 1970) with lower slopes that yield a lower isodar intercept (higher relative density in the poorer habitat) than would occur with ideal free habitat selection (Fig. 3). Asymmetries in the aggression of dominants in the two habitats could produce either diverging (more aggression in the best habitat) or converging (more aggression in the poor habitat) fitness-density curves that would also modify the isodar slope relative to the ideal free alternative.

Interference could, of course, be multiplicative rather than additive as suggested here. In the multiplicative case, a logarithmic model is likely to give a better fit to the isodar. This creates a problem with field data because the logarithmic solution would appear similar to that for continuous input. The two models can be differentiated as follows: the consumer-resource model will apply (1) when the investigator knows *a priori* that the continuous input assumption is violated (e.g. when the scale of habitat is too large for instantaneous consumption), (2) when behavioural studies have documented the absence or nature of interference or (3) when the researcher knows that mean fitness is different between the habitats (not an ideal free

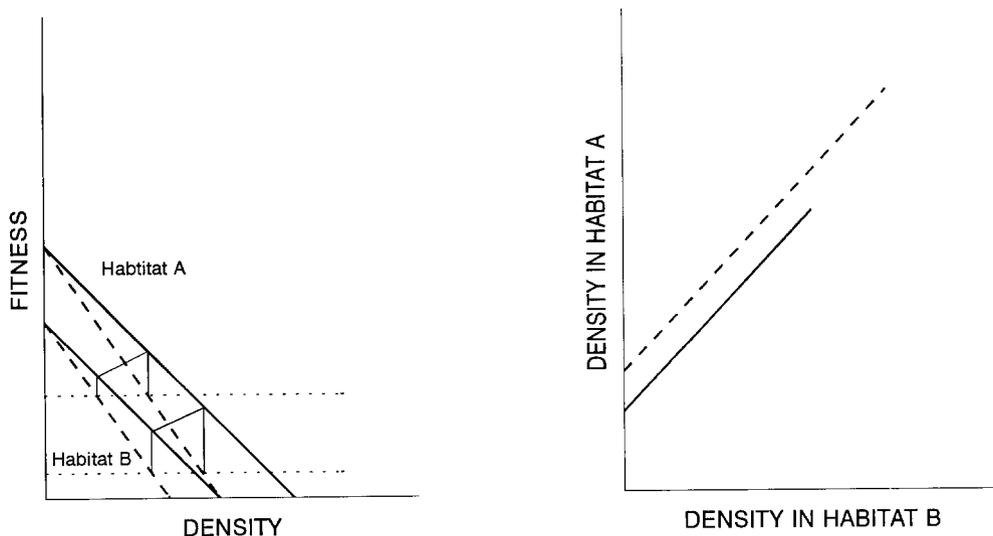


Figure 3. The effect of an ideal despotic distribution on the resulting isodar. Left: if dominant individuals reduce the efficiency of resource use by subordinates, the fitness-density curves perceived by individuals are rotated clockwise (dashed lines). Mean fitness will be greater in the best habitat. Right: the isodar-intercept is reduced relative to the ideal free alternative.

distribution). In the latter case, a comparison of the linear versus logarithmic solutions will document whether interference is additive (the linear model gives the best fit to the data) or multiplicative (the logarithmically transformed data give the best fit).

A pre-emptive habitat selection model

Pulliam (1988) and Pulliam and Danielson (1991) introduced a pre-emptive model where individuals select habitats on the basis of the quality of individual breeding sites. Their model assumes that individuals can achieve exclusive access to breeding sites and that each individual selects the best site known to be available. The quality of the poorest occupied site will be the same in each habitat. Population density in different habitats will mirror the distribution of breeding-site quality. What will the resulting isodar look like?

Imagine two habitats within which the distribution of breeding-site quality is normally distributed (any reasonable distribution can be substituted without changing the qualitative predictions I make here). Further imagine that the mean quality of habitat *A* exceeds that in habitat *B* (Fig. 4). The ideal pre-emptive solution can be attained graphically by drawing vertical lines that represent breeding sites of equivalent quality in the two habitats. At any given density all better sites will be occupied. Only the best sites in habitat *A* are occupied when population density is low. Only the poorest sites in habitat *B* are unoccupied when population density is high.

The density of individuals in a habitat will depend upon the number of breeding sites and the distribution of their quality. Assume, for convenience, that the two habitats contain equal numbers of breeding sites and that the variances of breeding site quality are the same (e.g. Fig. 4). Now plot the quality of the poorest occupied breeding site against population density to

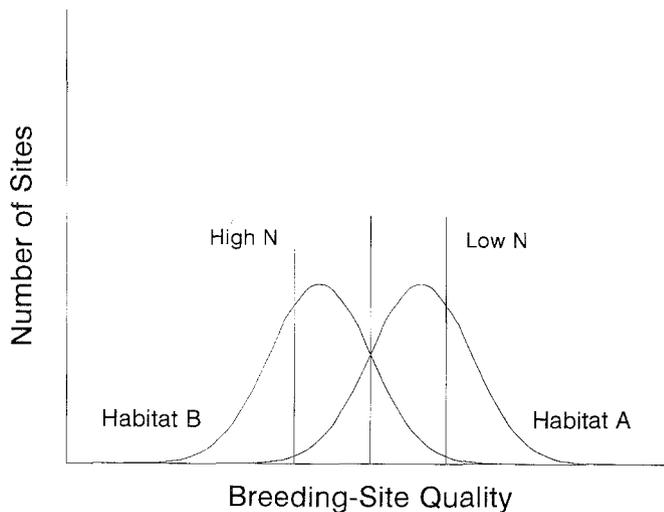


Figure 4. One illustration of the ideal pre-emptive distribution for two habitats within which the quality of breeding sites are normally distributed. Habitat *A* has proportionally more high quality sites than does habitat *B*. The vertical lines represent the poorest occupied breeding site at high, moderate and low population sizes. At low population size, only the best sites in habitat *A* are occupied (those to the right of the low *N* line), whereas at high population size only poor sites in habitat *B* remain unoccupied (those to the left of the high *N* line).

illustrate how fitness declines with increasing density (Fig. 5: the shapes of these curves are easily created for any probability density function by calculating the function's cumulative frequency distribution and then rotating it counterclockwise 90°).

Pre-emptive isodars depend upon the availability of sites and the shapes and locations of the distributions of breeding-site quality. The isodars will often be more complex than those we have examined previously (Fig. 6). Differences in the density of sites available for occupancy (Fig. 7), differences in the mean quality of breeding sites (Fig. 8) and differences in their variance (Fig. 9) create isodars ranging from logarithmic through rectangular to logistic curves. The predominant signature of a pre-emptive distribution is strong non-linearity in the isodar.

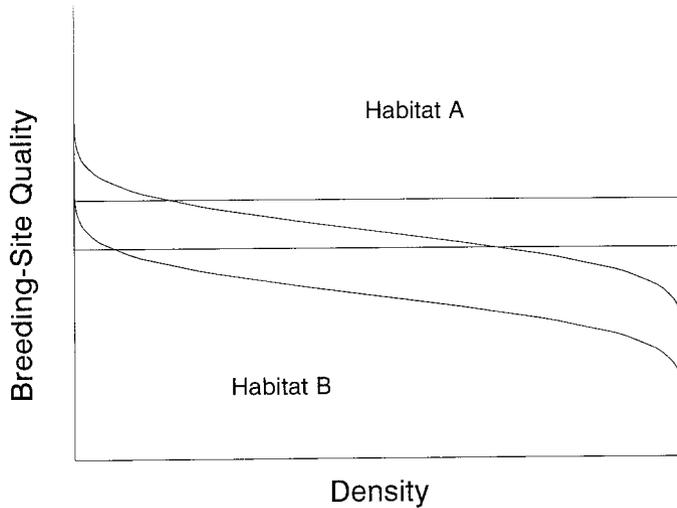


Figure 5. Fitness-density curves for the two distributions of breeding-site quality illustrated in Fig. 4. The density in each habitat corresponding to an ideal pre-emptive distribution for sites of a given quality (i) is the sum of all sites of equivalent or greater quality in that habitat (i.e. the integral of the curve 'above' i). Note that at high population size, the density in habitat A has stabilized near its maximum value (all sites occupied) whereas the density in habitat B is still increasing (many sites of lower quality remain to be occupied).

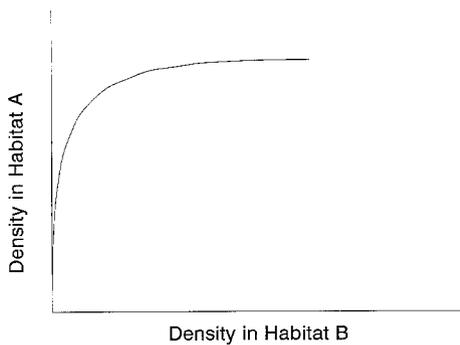


Figure 6. The rectangular isodar corresponding to the ideal pre-emptive fitness-density functions displayed in Fig. 5.

Pre-emptive isodars can often be estimated by non-linear regression. Sigmoidal shapes, for example, can be estimated from the logistic equation

$$N_A = K_A / (1 - e^{\alpha + \beta N_B}) \tag{12}$$

where K_A is the density in habitat A when all of its breeding sites are occupied and α and $\beta < 0$. Comparison of the fit among alternative non-linear solutions to field data may allow us to differentiate among processes that influence relative population densities. Sigmoidal isodars reflect high variance in the habitat with the lowest mean quality and are produced by fitness-density functions that cross one another. The cross-over produces a reversal in the ‘preferred’ habitat. The point where such cross-overs occur, if at all, will be difficult to predict because the poorest occupied breeding site depends upon the density where the overall population growth rate in all habitats sums to zero (Pulliam, 1988; Pulliam and Danielson, 1991).

Implications of the pre-emptive model to ecological communities

Crossing pre-emptive fitness-density curves are likely to be of particular interest to community ecologists because they herald unexpected niche shifts in response to increased density. To the

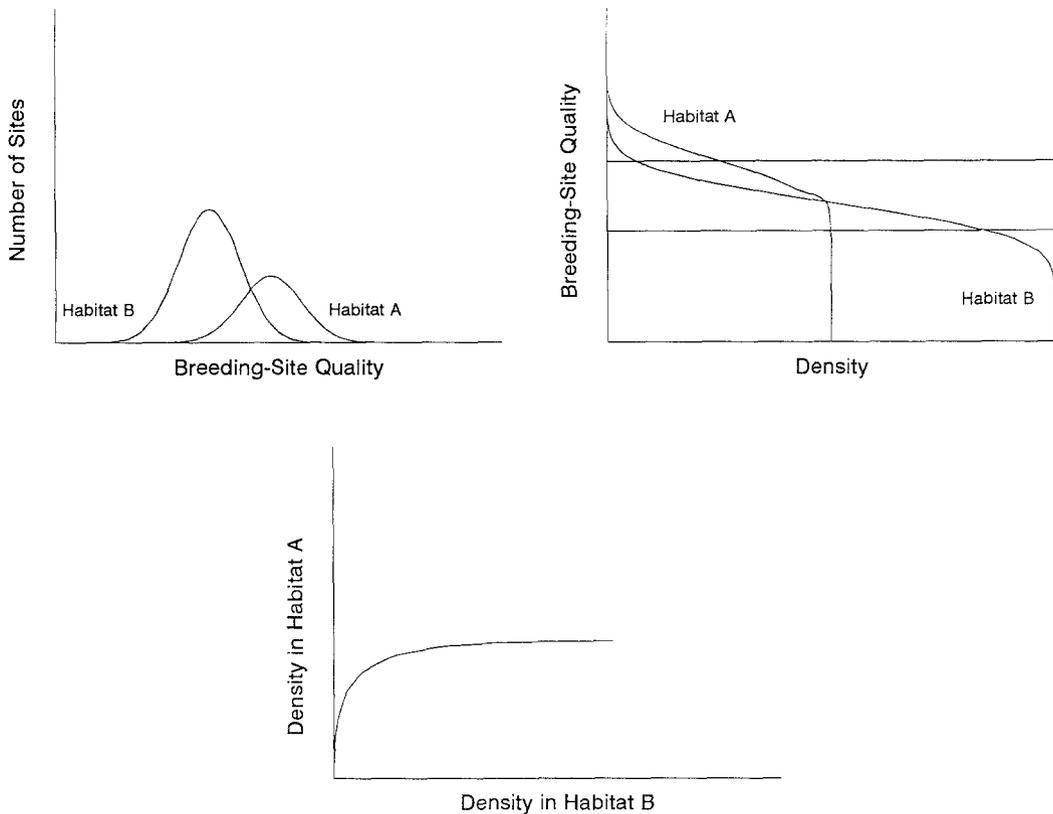


Figure 7. The relationship between habitat quality, fitness-density curves and resulting isodars for the ideal pre-emptive distribution when the best habitat has fewer sites available than does the poorer one. The fitness-density curves cross one another but the habitat with high mean quality contains the best breeding sites.

left of the cross-over, the habitat with the lowest mean quality has the highest density, at the cross-over the densities are equal and to the right the habitat with the highest mean quality supports the greatest density of consumers. The rate of change in niche width for a pre-emptive habitat selector, when measured by the proportional occupation of the two habitats, will cycle with increases in population density. It accelerates from preferential occupation of the variable habitat toward the point where the fitness-density curves cross, then declines at an increasing rate until all suitable sites are occupied.

Current models of habitat-dependent competitive interactions demonstrate that competing species should share preferences for the quantitatively superior habitat (Pimm and Rosenzweig, 1981; Rosenzweig, 1981, 1985, 1991; Pimm *et al.*, 1985). Shared preference competition is resolved by interference and is asymmetrically biased in favour of the dominant species. An alternative, called centrifugal organization (Rosenzweig and Abramsky, 1986) occurs when species share a preference for the same core habitat, but have distinct preferences for alternatives. These models have implicitly treated habitats as homogeneous units. The variance exploited by pre-emptive habitat selectors raises the intriguing possibility of reversing source-sink population regulation coupled with a new (but perhaps very common) kind of hybrid cyclical community structure that contains elements of both shared preferences and centrifugal organization.

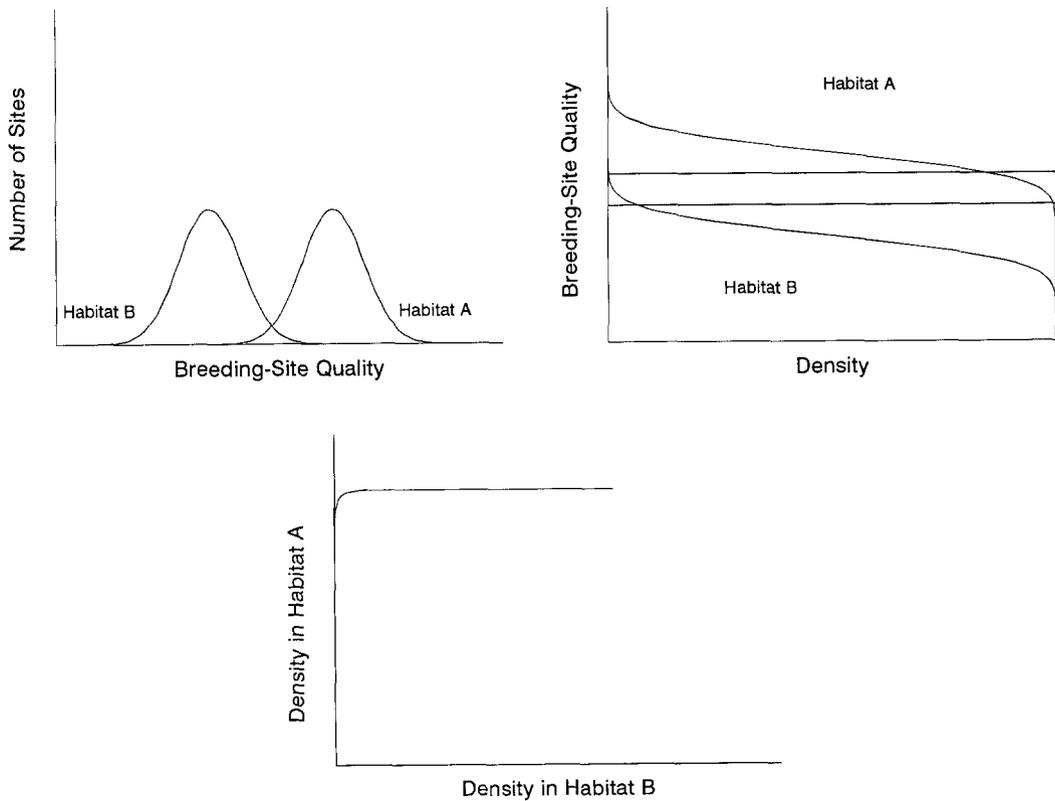


Figure 8. The relationship between habitat quality, fitness-density curves and resulting isodars for the ideal pre-emptive distribution when the mean quality of breeding sites is much greater in habitat A than it is in habitat B. The intercept of the isodar is directly proportional to the differences in mean quality (e.g. compare with Figs 4–6 where the variances in breeding-site quality are identical to those displayed here).

If the variance is greatest in the habitat with the lowest mean quality (e.g. Fig. 9), the best breeding sites will be located within it, not in the more homogeneous 'high quality' one. At low density, these sites will be preferentially occupied and the variable habitat will act as a source of emigrants to the habitat with higher mean quality. At higher density, when only poor sites remain to be occupied, the more variable habitat will serve as a sink for immigrants. Similarly, as density increases, a dominant species will first be most abundant in the variable habitat, but will later become most abundant in the less variable one.

A subordinate species responding to these density shifts by the behaviourally dominant one will exhibit complementary habitat shifts in density (Fig. 10). The dominant will continue to occupy high quality breeding sites in both habitats, whereas the subordinate species may occupy only the variable habitat at low density, use both at a somewhat higher density and be completely excluded from the homogeneous habitat at high density. If the high quality habitat also supports a relatively low density of breeding sites, the fitness-density curves may cross twice (e.g. a combination of Figs 7 and 9). Cyclical organization is maintained, but the point where the subordinate species occupies only the very poorest sites in the variable habitat of low quality occurs at a lower density of the dominant species.

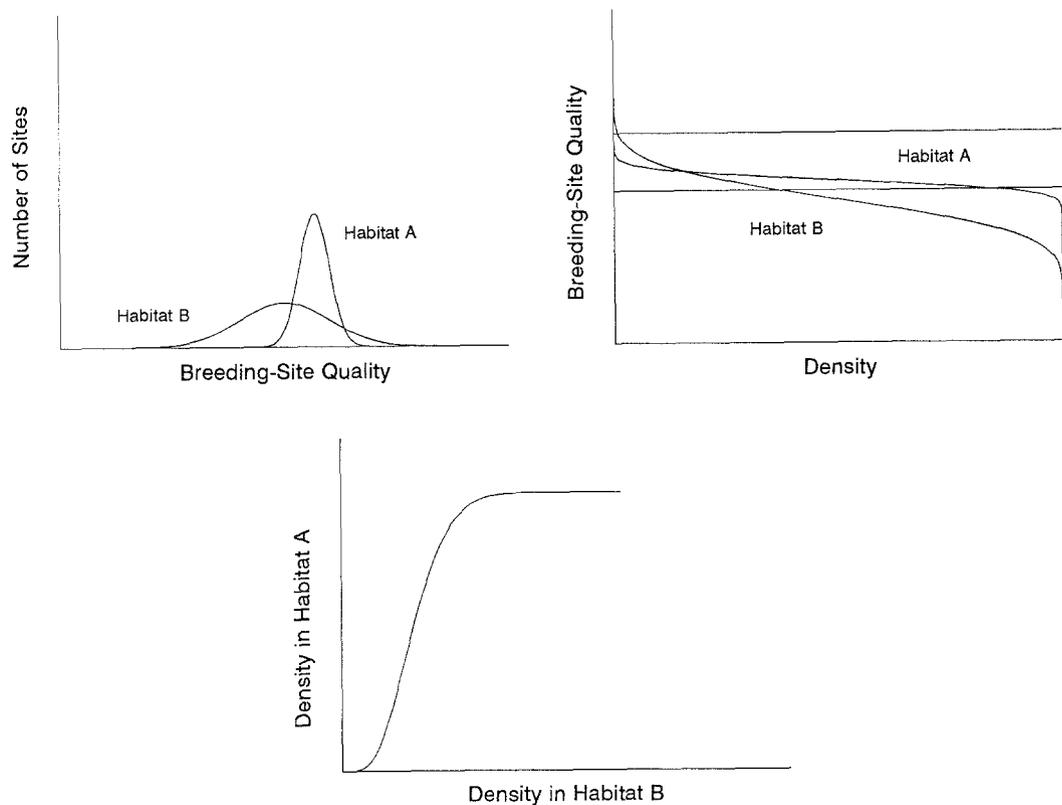


Figure 9. The relationship between habitat quality, fitness-density curves and resulting isodars for the ideal pre-emptive distribution when the variance of breeding-site quality is less in the high quality habitat than it is in the low quality habitat. The fitness-density curves cross one another, but in contrast to Fig. 7, the variable habitat of low mean quality contains the best breeding sites. The isodar shifts from a logarithmic or rectangular shape to sigmoidal.

A modified protocol for habitat matching and a field test

In all of the models presented here, the potential applicability of habitat matching is enhanced by isodar analysis. Previous matching rules apply only when the habitats are occupied at all population sizes. This corresponds to a zero intercept of a linear regression of the population density in one habitat against that in another (isodar analysis: Fig. 2). At a minimum, this suggests that an isodar analysis should be the first phase of any field study using habitat matching rules to assess habitat selection. Indeed, recent applications of isodar theory demonstrate that isodars can even be used to specify the patch size of different forms of habitat selection (Morris, 1992a). If the intercept is not significantly different from zero, the original habitat matching analysis can proceed. If the intercept is significantly different from zero (Fig. 1), habitat matching rules should not be applied.

Messier *et al.*'s (1990) protocol is easily adjusted to accommodate forms of habitat selection other than continuous input. Their test of ideal density-dependent habitat selection using census data can be based simply on the plot of the resultant isodar (Morris, 1988). The empirical regression equation from that plot can then be used to provide supplementary information on differences between habitats and on the form of population regulation.

Fagen's (1988) method can also profit from an isodar analysis. Once the functional forms of the pairwise isodars are known, it is a simple matter to calculate the effects of changes in habitat supply. If an IFD describes habitat selection by a particular species, the relative population size in

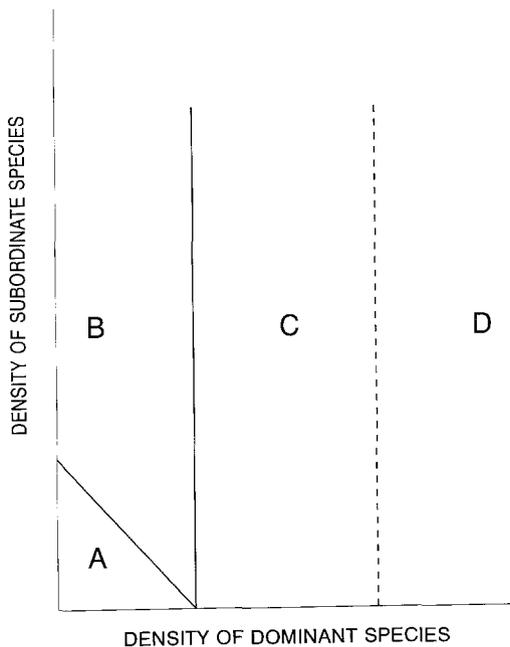


Figure 10. An isoleg diagram for cyclical community organization generated by reversing source-sink population regulation. Solid lines represent the isolegs (lines separating regions of different habitat choice; Pimm and Rosenzweig, 1981; Rosenzweig, 1981, 1985) of the subordinate species, the dashed line is the dominant's isoleg. In region *A* both species occupy only the variable habitat of low mean quality (habitat *B*). In region *B* the subordinate species is excluded from the best sites in habitat *B* by the dominant which occupies only habitat *B*, the subordinate occupies lower quality sites in both habitats. In region *C*, both species occupy both habitats. In region *D* the dominant occupies all sites in habitat *A* and all sites of equivalent and greater quality in habitat *B*. The subordinate, if it can exist in lower quality sites, is again restricted to habitat *B*.

a habitat varying in abundance between A_i and A_i' can be estimated from the isodar. To calculate the population size in habitat 1 relative to that in habitat 2, weight the isodar by the ratio of the abundances of the two habitats. For linear isodars,

$$N^*_1 = (a' + b'N_2)/q \quad (13)$$

where N^*_1 is the population size in habitat 1 relative to habitat 2, the isodar intercept, $a' = (a_1 - a_2)/b_1$, its slope, $b' = (b_2/b_1)$ and $q = A_1/A_2$. Repeat for $q' = A_1'/A_2'$. The percent change in relative population size in habitat 1 is proportional to the change in habitat supply

$$100[1 - \frac{(a' + b'N_2)/q}{(a' + b'N_2)/q'}] = 100(1 - q'/q) \quad (14)$$

This protocol could be repeated for all habitat pairs. The overall change in relative population size in the landscape is then estimated from the summed solutions of the isodar equations. A similar protocol could be applied to logarithmic or logistic isodars.

Despite its simplicity, Equation 14 may dampen the spirits of those who would like to predict the effect of changes in landscape composition on population size. The message of isodar analysis is that the density of individuals in habitat *A* can be estimated from the density in habitat *B*, regardless of whether or not the population is at equilibrium. Whereas Equation 14 can be used to estimate overall maximum population size based on the largest observed values of population density, to do so would ignore the dynamics included in isodar analysis.

I demonstrate the feasibility of isodar approaches to habitat matching with data collected on the life history and spring and autumn population density of white-footed mice (*Peromyscus leucopus*) occupying nest boxes in forest, edge and fencerow habitats in southern Ontario since 1981 (Morris, 1986, 1989b, 1991, 1992b, c). Animals move among the three habitats (Morris, 1989b). More animals move between the adjacent forest and edge than between either of these and the linear fencerows. Opportunities for successful dispersal into and out of fencerow habitats are reduced because (1) these linear habitats have a narrow boundary with the forest and (2) because the mean distance from any one point in the fencerows to the forest or edge is substantially greater than the mean between the forest and edge. Reproductive success is greater in forest habitat than in either edge or fencerow habitats (Morris, 1989b, 1991). Estimates of reproductive success across individual breeding sites are inconsistent with pre-emptive habitat selection and suggest, instead, that this territorial species obeys the predictions of despotic habitat selection (Morris, 1991).

The density of adult animals occupying nest boxes in forest habitat is highly correlated with the number of different adults captured in independent live-trap studies ($r = 0.95$, $N = 13$; Morris, unpublished). I can thus use my estimates of population density from animals living in nest boxes to construct isodars that test for linear (consumer–resource), curvilinear (input matching or multiplicative interference) and non-linear (pre-emptive habitat selection) effects. I plot the nest box estimates of adult population density for each pair of habitats on both arithmetic and logarithmic scales to differentiate between linear and curvilinear effects. The pattern of the data will reveal whether I should attempt non-linear solutions predicted by pre-emptive habitat selection. The detailed analysis and interpretation of the resulting isodars will be presented elsewhere (Morris, unpublished).

All correlations among the three habitats were highly significant even though covariation in density was less in the contrasts with fencerows than it was between the forest and edge habitats (Figs 11 and 12). The relatively large scatter of density in the fencerow correlations reflects a reduced capacity of habitat selection to modify population densities when opportunities of movement between habitats are reduced (Morris, 1992a). Comparisons between edge and

fencerow and between forest and edge habitats gave a better fit to linear models than to curvilinear ones (arithmetic scale: $r = 0.81$, $N = 22$, $p < 0.001$ and $r = 0.93$, $N = 22$, $p < 0.001$; logarithmic scale: $r = 0.74$, $N = 21$, $p < 0.001$ and $r = 0.91$, $N = 21$, $p < 0.001$, respectively; Fig. 11). Comparisons between forest and fencerow appeared to give a better fit to the logarithmic solution ($r = 0.82$, $N = 22$, $p < 0.001$) than to the arithmetic one ($r = 0.78$, $p < 0.001$), but the logarithmic model is heavily influenced by one point of low density in both habitats (Fig. 12). When this problematic point is removed, the fit of the arithmetic model is better than that of the logarithmic one ($r = 0.76$, $N = 21$, $p < 0.001$ and $r = 0.68$, $p = 0.001$, respectively).

The differences between arithmetic and logarithmic solutions were, nevertheless, less than spectacular. There was no hint of the dramatic non-linear signature of the pre-emptive model. I interpret these combined results as tentative support for an interference consumer–resource model of habitat selection by territorial white-footed mice. Similar degrees of covariation between the linear and logarithmic solutions suggest that the effect of per capita interference may increase with increasing density. Yet it is clear that linear solutions give a reasonable fit to the data. Furthermore, all isodars pass through the origin (Morris, unpublished). Equation 14 could thereby be used to predict changes in relative population size with changes in habitat supply in

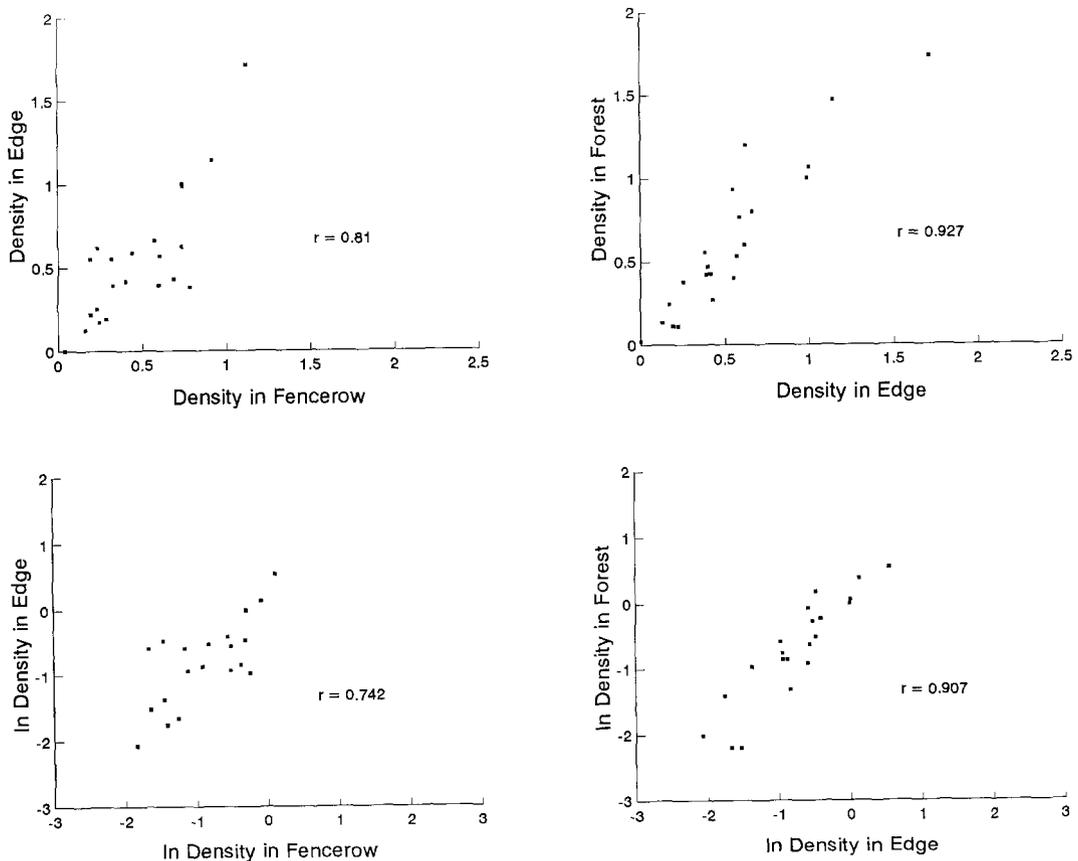


Figure 11. Consumer–resource models (top) represent a better fit to empirical data on the population density of white-footed mice between edge and fence, and forest and edge habitats than do either input matching (curvilinear) or pre-emptive (non-linear) models.

other forest/fencerow landscapes. Regardless, in this population of white-footed mice at least, the consumer–resource model appears to be a better predictor of habitat use than either input matching or pre-emptive habitat selection.

Discussion

Applications of matching rules

Input matching and isodar matching (Equation 14) represent effective and potentially powerful predictors of population density with changing habitat composition. The matching models that I have addressed here include only rules of habitat selection; they assume no interaction with landscape structure (*sensu* Danielson, 1992; Dunning *et al.*, 1992). Predictions about changes in relative population size should, nevertheless, be made cautiously and tested prior to application.

A change in the proportions of available habitats may violate the independence from landscape assumption. Changes in habitat proportions may often interact with a variety of other landscape

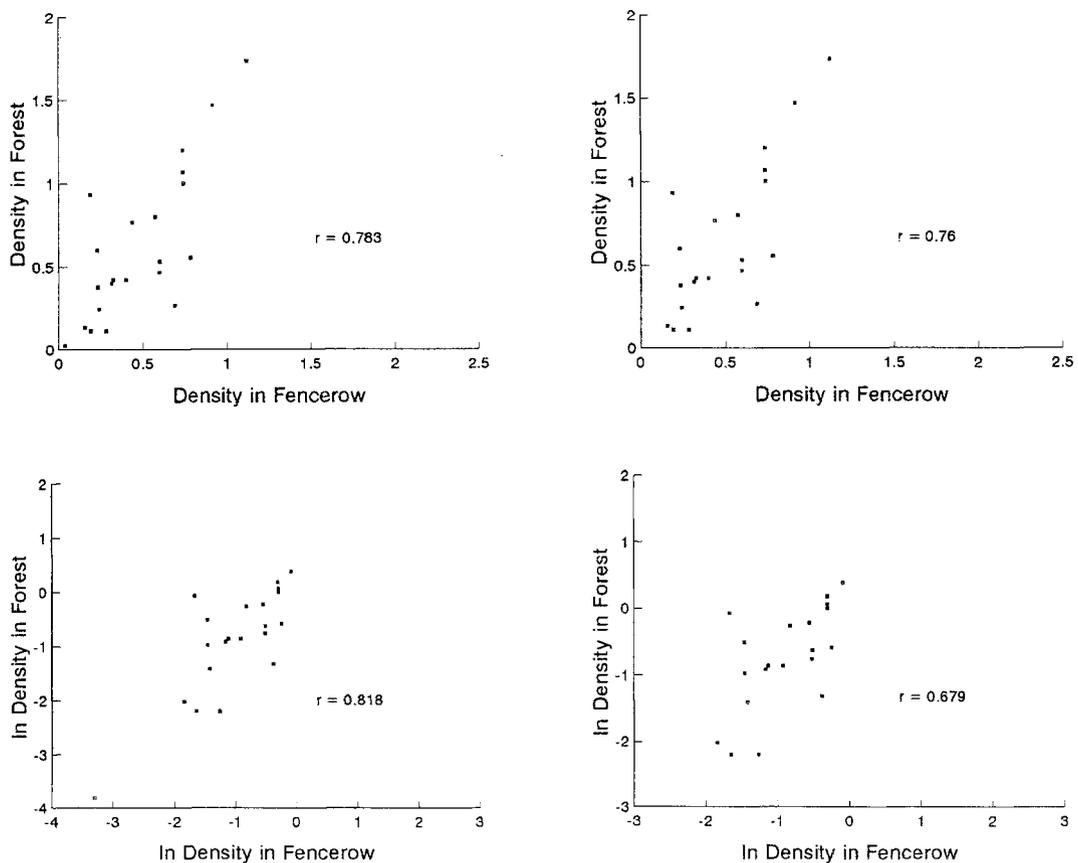


Figure 12. The apparent support for input matching by white-footed mice occupying forest and fencerow habitats (bottom left) is eliminated following removal of a single point of low density that has a disproportionate effect on the fit of the data to the logarithmic input matching model (right).

features that modify density-dependent habitat selection and the associated isodars. Predictions about changes in population density would then depend not only on the weighted means of habitat supply, but also on their non-additive interactions with the changed landscape. In this case, predictions of isodar theory represent null models for population distribution.

Reaction–diffusion models also predict persistent spatial variation in population density and represent another form of ‘null model for spatially distributed population dynamics’ (Kareiva, 1990). Unlike habitat selection, the spatial patterns in reaction–diffusion models are created independently of habitat heterogeneity (persistent spatial patterns depend upon the scale of habitat patches; Kareiva, 1990). The spatial patterns predicted by reaction–diffusion equations thus represent, at the appropriate scale, null hypotheses for theories of habitat selection. The overlay of habitat selection completes a two-step hierarchy of null models for spatial patterns. Landscape influences need only be invoked when both sets of null models are incapable of predicting the spatial pattern in population density.

The different forms of isodars enable us to do much more. Qualitative and quantitative differences in habitat modify the slopes and intercepts of linear isodars. Differences in logarithmic isodars capture the effects on density caused by differences in interference between habitats. Effects caused by changes in the variance and mean quality of breeding sites can similarly be detected by differences in pre-emptive isodars. Changes in the isodars among landscapes can thus be used to infer what otherwise might have been undetected differences in habitat or in the ways that individuals respond to habitat in different landscapes.

Detection of the mechanisms generating landscape differences will be complicated by interactions among habitat and landscape processes. Different mechanisms can produce similar isodars (Fig. 7), so one cannot argue that similar isodars are caused by identical processes. Some processes may, however, leave unique signals. Unequal variances tend to destroy the symmetry assumed by the logistic isodar (e.g. Fig. 7), a pattern that should be detected by the scatter of points about the non-linear idealized solution.

Isodars and habitat matching

Morris (1988) demonstrated that the differences between the forms of habitat selection represented by Figs 1 and 2 may correspond, respectively, to quantitative and qualitative differences in habitat. Quantitative and qualitative differences determine the form of spatial population regulation of any species capable of density-dependent habitat selection. The isodar specifies the magnitude of each effect and, by inference, the form of population regulation.

If isodar models are correct in their assumptions, tests based on habitat matching rules apply only to habitats that are qualitatively different. It is probable that the habitats used by Messier *et al.* (1990) to reject an IFD for muskrats in central Saskatchewan were qualitatively different from one another because habitats were classified on the basis of differences in the dominant emergent plant species (Messier *et al.*, 1990). These differences would, presumably, also be reflected in the foraging and/or diets of the muskrats. But there is also a strong possibility that the habitats were quantitatively different as well. The dependence of different kinds of emergent vegetation on water depth, the correlation between winter food availability and water depth and the manipulation of water depth during the census (Messier *et al.*, 1990) are all suggestive of quantitative habitat differences. It seems, therefore, premature to reject the IFD as an explanation of muskrat habitat use.

I agree with Messier *et al.* (1990) that distribution data alone are insufficient to differentiate among alternative models of density-dependent habitat selection. Indeed, their data on habitat-dependent differences in overwinter survival represent a convincing case against an ideal free distribution and their overall conclusions regarding habitat occupancy by muskrats are probably

correct. My point is, that proportional occupancy represents, at best, an inefficient protocol for tests of density-dependent habitat selection.

Population projections based on Equation 1B face similar restrictions. Imagine two habitats that differ quantitatively, as in Fig. 1 and assume that they are not saturated with individuals. The ratio of densities in the two habitats will tend to give a biased estimate of the ratio of their respective carrying capacities (Equation 8). The bias depends upon population size. It becomes progressively reduced with increased density (i.e. as N_2 increases). The result is that input matching, which assumes that ratios of population density are unbiased estimates of differences in carrying capacity, may frequently produce distorted estimates of changes in population size with changes in habitat supply.

Regardless, empirical studies demonstrate an unambiguous fit to habitat matching under conditions of continuous resource input where individuals cannot monopolize foraging space (e.g. mallards being fed bread at artificial patches, Harper, 1982; Recer *et al.*, 1987). The mean gain rate per individual in a given patch corresponds to per capita resource renewal. Mallards are clearly capable of assessing the profitability of different patches and of adjusting their densities toward an ideal free distribution.

Foraging experiments, such as those on mallards that assess habitat matching, typically create patches by providing a pulse of high resource renewal capable of supporting a large number of opportunistic consumers. Consumer–resource models address a fundamentally different kind of patch where individuals are incapable of consuming resources as quickly as they are renewed. I suspect, that for many species, including the white-footed mice studied here, it is the more realistic representation of habitat occupation. To my knowledge, habitat matching experiments have not been performed on spatial scales corresponding to assumptions of the resource consumption models. Yet there are numerous cases where researchers have added nutrients or food to large habitat patches. It may be possible to mine these studies for tentative tests of both habitat matching and isodar models of ideal habitat selection. If not, it would at least be interesting to see what insights may be recovered from their tailings.

Limitations

All methods based on ideal habitat selection, including isodar analysis, are limited in application. The most severe constraints to using the theory would appear to fall into four categories: (1) intrinsic factors that alter the relationship between population density and resource availability, (2) extrinsic factors that destroy equal opportunities to move among patches, (3) non-logistic population growth and (4) sampling biases that may fail to reveal the complete shape of curvilinear or non-linear isodars.

Intrinsic factors would include social interactions whereby ‘dominant’ individuals occupying high ‘quality’ source habitats inhibit colonization or reproduction by conspecifics. The resulting migration of ‘subordinates’ to reproductive sinks (Lidicker, 1962; Van Horne, 1983; Łomnicki, 1988; Pulliam, 1988) creates inequalities in reproductive success between source and sink habitat(s). Interference maintains reproductive success at a higher mean value in source habitats than in the sink(s). Given a constant landscape, the isodar equation should still provide a true representation of relative habitat occupancy with changes in population size. A serious problem occurs, however, in attempting to project the effects of an altered landscape on relative or total densities. The population density in the sink is not simply a function of the density in the source, but also of the relative abundances and spatial distribution of the two kinds of habitat in the landscape (Pulliam, 1988; Pulliam and Danielson, 1991).

State-dependent ideal free distributions (McNamara and Houston, 1990) create additional complications. Increased density should reduce the mean foraging rates in exploited patches.

Animals with low energy reserves may occupy variable and risky habitats in order to avoid starvation. Current models are most likely to apply to foraging scales of habitat selection (e.g. Morris, 1992a) but related state-dependent models considering, for example, animals at different stages in their life history, could apply to larger scales of density-dependent habitat selection. Isodar analyses are still appropriate protocols, but they may, in this instance, be unable to differentiate among underlying mechanisms of habitat choice.

Yet another complication may arise when differences in resource quantity and resource quality between habitats complement one another. Under these conditions, a 'rich' habitat with relatively low quality but abundant resources may be selected at low population density, whereas a 'poorer' habitat with high quality resources in low abundance may be preferred at high density (Hobbs and Hanley, 1990). Hobbs and Hanley (1990) argued that habitat matching rules are insensitive to such cross-overs in habitat preference with population density. Isodar theory has explicitly addressed switched preferences involving identical cross-overs (Morris, 1988).

Other extrinsic factors may be more problematical. Temporal changes in habitat 'quality' will, at the very least, confound predictions about patterns of habitat occupancy (Van Horne, 1983; Fagen, 1988; Morris, 1990). Fagen's (1988) projection of the carrying capacity of coastal forests for deer, for example, was complicated by temporal changes in the costs of foraging in alternative habitats. In years when snow accumulation is relatively low, deer can attain a higher foraging profit at a given resource level from young clearcuts than they can in years with deep snow when their mobility is compromised. Temporal changes in snow depth not only modifies carrying capacities within each habitat, but may also alter the relative carrying capacities among habitats if the effects of changes in snow depth are unequal in different habitats. Thus, temporal differences in resource levels or in the costs of foraging may confuse projections of future predator density.

The role of temporal differences may seem to depend upon the 'response time' of habitat selection. Yet, if changes in habitat 'quality' occur at a slower rate than the ability of animals to assess differences and to adjust their density, estimates of density at different times should adequately reveal the relative differences among habitats. Similarly, if habitat quality changes much more rapidly than the habitat selection response, individuals are likely to select a habitat based on its average value (Recer *et al.*, 1987). Patterns of population density should still be reliable indicators of average differences between habitats. Difficulties in interpretation are more likely to arise from attempts to predict changes in abundance when it is known that both the habitats and the selection response by the occupants have changed. Other difficulties will emerge whenever the frequency of habitat sampling fails to match any underlying population responses via habitat selection.

Response time will also be a function of the spatial configuration of habitat. Local population density in a patchy environment may be more closely related to the rate of dispersal, dispersal distance and colonization ability than it is to either resource abundance or resource quality (Fahrig and Paloheimo, 1988). The pattern of white-footed mouse density between nearby (forest and edge) versus more 'distant' habitats (fencerows) is consistent with this expectation. Within limits, opportunities for ideal habitat selection are thereby compromised by increased habitat fragmentation and changes in habitat orientation, compounding the methodological difficulties encountered by the field biologist (non-ideal habitat selectors may frequently select habitats close to the expectations of ideal individuals; Pulliam and Danielson, 1991). Isodar analyses of census data collected at appropriate temporal and spatial scales should, nevertheless, be able to successfully assess density-dependent habitat selection. The results of those analyses can be used to predict the theory's consequences.

Curvilinear and non-linear isodars complicate the utility of using patterns of population density to infer processes of spatial population regulation, habitat matching, and community organiz-

ation. Curvilinear functions can be generated by many forms of non-logistic population growth (Holt, 1984, 1985), as well as by state-dependent ideal free distributions (McNamara and Houston, 1990). It is currently unknown how serious a problem this may pose for isodar matching. We can be certain, however, that an analysis failing to include the entire range of population densities may misinterpret curved functions as linear trends. It is especially crucial to obtain samples at very low population density in order to capture the non-linearities expected with differences in the variance of breeding site quality between habitats (Fig. 9). The rewards, in terms of our potential to first reveal differences and then predict the effects of changes in landscape composition, the effects of differences between habitats, the mechanisms of habitat selection, the form of population regulation and resulting community organization, would seem to justify the effort.

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