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*Published in:*  
American Naturalist

2004

[Link to publication](#)

*Citation for published version (APA):*

Jonzén, N., Wilcox, C., & Possingham, H. P. (2004). Habitat selection and population regulation in temporally fluctuating environments. *American Naturalist*, 164(4), E103-E114.  
<http://lup.lub.lu.se/luur?func=downloadFile&fileOld=624541>

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# Habitat Selection and Population Regulation in Temporally Fluctuating Environments

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*Submitted July 7, 2003; Accepted March 29, 2004;*

*Electronically published August 19, 2004*

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**ABSTRACT:** Understanding and predicting the distribution of organisms in heterogeneous environments lies at the heart of ecology, and the theory of density-dependent habitat selection (DDHS) provides ecologists with an inferential framework linking evolution and population dynamics. Current theory does not allow for temporal variation in habitat quality, a serious limitation when confronted with real ecological systems. We develop both a stochastic equivalent of the ideal free distribution to study how spatial patterns of habitat use depend on the magnitude and spatial correlation of environmental stochasticity and also a stochastic habitat selection rule. The emerging patterns are confronted with deterministic predictions based on isodar analysis, an established empirical approach to the analysis of habitat selection patterns. Our simulations highlight some consistent patterns of habitat use, indicating that it is possible to make inferences about the habitat selection process based on observed patterns of habitat use. However, isodar analysis gives results that are contingent on the magnitude and spatial correlation of environmental stochasticity. Hence, DDHS is better revealed by a measure of habitat selectivity than by empirical isodars. The detection of DDHS is but a small component of isodar theory, which remains an important conceptual framework for linking evolutionary strategies in behavior and population dynamics.

*Keywords:* habitat selection, environmental stochasticity, isodar analysis, spatial correlation.

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The fact that different organisms live in different places or habitats was noted by Victorian naturalists (Cody 1985), and the scientific study of habitat use and habitat selection dates back at least to the early 1900s (Grinnell 1917; Mayr 1926; Lack 1933). Since the pioneering papers published more than 50 years ago (Svärdsson 1949; Morisita 1950), competition has played a major role in ecological theories explaining the habitat use of organisms. Starting with the seminal work on the ideal free distribution (IFD) by Fretwell and Lucas (1970) and Fretwell (1972), the ideas about how competition shapes habitat use has been formalized into a theory of density-dependent habitat selection (DDHS; Rosenzweig 1981, 1991). The aim of DDHS theory is to provide a general explanation for how individuals ought to be distributed in a spatially heterogeneous landscape. Today, DDHS theory has extended its explanatory domains and now provides a causal link between individual behavior, population regulation, and community structure (Morris 2003a).

Despite the undeniable success and maturation of DDHS theory (reviewed by Rosenzweig 1991), there is an important element of the natural world that is ignored in classical DDHS theory: temporal variation in habitat quality (but see Morris 2003b). That variation can be a property of the habitat itself or a consequence of the number of individuals using the habitat in concert with the consequences of density dependence. Attempts to include temporal variation in habitat quality assume either a constant rate of movement between habitats, which means that individuals cannot assess or respond to changes in habitat quality from year to year (e.g., Schmidt et al. 2000; Holt and Barfield 2001), or only one of two habitats has fluctuating resources (Recer et al. 1987). In natural systems, resources fluctuate in both time and space, and such environmental stochasticity generates spatiotemporal variation in population density. Hence, if habitat selection theory is going to be useful in practice when decisions about land use, conservation, or exploitation have to be made (Lundberg and Jonzén 1999), the theory should allow for both temporal and spatial fluctuations. On a more fundamental level, including temporal variation in habitat

quality forces us to rethink the whole idea of fitness equalization across space because the fitness concept in temporally fluctuating environments is different from the deterministic case (e.g., Metz et al. 1992; Jansen and Yoshimura 1998). Hence, there are operational as well as fundamental reasons for trying to move beyond the time-homogeneous solutions typical of DDHS theory.

The purpose of this article is to analyze habitat selection in a stochastic setting where habitat quality fluctuates in both time and space. We will use a simple model system to describe the habitat-specific population patterns that result from the interaction between habitat selection, population dynamics, and environmental stochasticity. The key questions are, What are the emerging patterns of habitat use? and Can observations of such patterns be used to infer the underlying processes? Our results will be contrasted with what is predicted by isodar analysis (Morris 1988), an established empirical approach to the analysis of habitat use patterns. We would like to emphasize the distinction between isodars as theory and isodar analysis as a technique. Isodar analysis is often used to detect DDHS, but this is only a small part of isodar theory, which is a conceptual framework for mapping evolutionary strategies in behavior onto their population and community consequences (Morris 2003a).

### Habitat Selection Theory and Isodars

DDHS theory relies on two fundamental assumptions. First, fitness ( $W$ ) is defined as per capita population growth rate and is a function of population density. Let the fitness of individuals in habitat  $i$  be

$$W_i = f(N_i), \quad (1)$$

where  $N_i$  is the population density in habitat  $i$ . Furthermore, unless there is an Allee effect (Greene and Stamps 2001; Morris 2002), one assumes that fitness is a negative function of density over all densities, that is,

$$\frac{df}{dN} < 0. \quad (2)$$

Second, if individuals select habitat according to the IFD (Fretwell and Lucas 1970), the individuals will be distributed such that fitness is equalized across habitats, that is,  $W_i = W_j$  for all  $i$  and  $j$ . For any pair of habitats, one can set  $W_i = W_j$  and solve for density in the habitat with the greatest density,  $N_i$ . If fitness in each habitat declines linearly with density

$$W_i = a_i - b_i N_i \quad (3)$$

and we solve for  $N_i$ , the relationship between  $N_i$  and  $N_j$  will also be linear:

$$N_i = \frac{a_i - a_j}{b_i} + \frac{b_j}{b_i} N_j. \quad (4)$$

This line is called an isodar and specifies the combinations of  $N_i$  and  $N_j$  that give equal fitness in both habitats (Morris 1988). Hence, the isodar specifies the evolutionary attractor and the evolutionarily stable strategy (ESS) for the spatial distribution of individuals. Depending on the relative magnitude of the parameters  $a_i$ ,  $a_j$ ,  $b_i$ , and  $b_j$ , the corresponding isodar will have a unique intercept and slope (see Morris 1988). The relationship between fitness and density can also be nonlinear (e.g., Possingham 1992; Rodriguez 1995). Note that the model above may require a noninteger number of individuals in the two habitats to equalize fitness across habitats. We nevertheless will talk about the distribution of individuals when in fact proportions of individuals are distributed.

The idea behind isodar analysis is that the isodars can be estimated from census data on population density. Hence, a plot of population density in one habitat against population density in another habitat should tell us something about the relationship between fitness and density in each habitat, given that individuals are distributed according to the IFD. More specifically, one treats the population density in the habitat having the lowest density as the independent variable ( $N_j$  in eq. [4]) and population density in the high-density habitat as the dependent variable ( $N_i$  in eq. [4]) and fits a linear regression model to the data. The point estimates of the intercept and slope are assumed to be informative with respect to the habitat-specific relationship between fitness and density (i.e., the parameters  $a$  and  $b$  for each habitat). For a detailed treatment of isodar analysis, see Morris (1988).

To find an isodar using empirical data, densities in each habitat must vary from year to year (otherwise we can define only a single point in  $N_i/N_j$  space). But if there are population fluctuations, then the measure of fitness may no longer be valid. We will return to this interesting discrepancy in the "Discussion." However, note that habitats are sometimes defined by their vegetation (e.g., habitat 1 = forest, habitat 2 = meadow), and isodars are estimated from such discrete classes of paired habitats that can be replicated in space. In this article, we let a habitat be equal to a patch that is repeatedly sampled, and isodar analysis based on spatial replicates of types of vegetation is not treated here. Let us now present our theoretical study system where we will generate temporal variation in population density by including environmental stochasticity in habitat quality.

## Methods

DDHS theory applies to all species independent of their life-history characteristics or the number of habitats available in the landscape. We have chosen to analyze a very simple system to study habitat selection in spatiotemporally fluctuating environments. Consider a two-habitat system inhabited by a semelparous species with nonoverlapping generations and an age of maturity equal to 1 year. We will assume that the fitness of individuals in each habitat is a linear function of population density in that habitat and has a stochastic element that may or may not be correlated with the other habitat. At the start of each year, the adults will select habitat according to the expected fitness rewards in each habitat. After the habitat selection process, the adults in each habitat give rise to  $W_i N_i$  descendants. Following reproduction, the adults die, and the offspring gather in a common pool. At the next time step, the offspring produced last year are now adults and distribute themselves between the two habitats according to the fitness rewards in each habitat. In our model, individuals will choose their habitat in one of two ways. In the first way, we assume individuals distribute themselves so that no individual could do any better by changing habitat. In the second way, they choose habitats randomly, favoring the best habitat given the current population densities in each habitat.

### Stochastic Fitness Functions

We assume that the adults have full knowledge about the fitness rewards in each habitat and that they are free to move without any cost. At each time step  $t$ , we let the fitness functions for each habitat be a density-dependent random variable

$$\begin{aligned} W_{i(t)} &= \log_e \left( \frac{N_{i(t)}}{N_{i(t-1)}} \right) \\ &= a_i - b_i N_{i(t-1)} + E_{i(t)} - 0.5\sigma_i^2, \end{aligned} \quad (5)$$

where  $a_i$  and  $b_i$  are the habitat-specific constants, often referred to as the growth parameter and statistical density dependence, respectively. Environmental variation is modeled by inserting the random variable  $E_{i(t)}$ . We assume that  $E_{i(t)}$  is drawn from a bivariate normal distribution with zero mean and a variance-covariance matrix  $\Sigma$ . The SD of the environmental stochasticity in habitat  $i$  is denoted  $\sigma_i$ , and we further assume that the SD of the environmental stochasticity is equal across habitats. The  $0.5\sigma^2$  term is an adjustment to ensure that the expected rate of change in

each habitat  $i$  at each time step  $t$ ,  $N_{i(t)}/N_{i(t-1)}$ , equals  $\exp(a_i - b_i N_i)$  (Hilborn and Mangel 1997).

### A Deterministic Habitat Selection Process

At each time step  $t$ , we assume that all  $N_{i(t)}$  individuals will know the value of  $W_{i(t)}$  in both habitats and distribute themselves such that  $W_{1(t)} = W_{2(t)}$ ; that is, the ideal free distribution is achieved at each time step. One reason why it makes sense to let the habitat selection process be deterministic is that we get a simple stochastic equivalent to the DDHS theory. However, in real ecological systems, individuals may not be ideal and free. One could think about the habitat selection process as individuals estimating (with an error) the fitness consequences of settling in a given habitat. We will therefore add this extra level of complexity and also study stochastic fitness-driven habitat selection in stochastic environments.

### A Stochastic Habitat Selection Process

In practice, individuals are not ideal and free. However, it is indeed reasonable to assume that individuals assess the fitness consequences of selecting a given habitat. To model the kind of patterns generated by fitness-driven habitat selection under uncertainty, we assume that once in their life, individuals select habitats with a probability affected by the expected fitness reward in each habitat at the time they make the choice. Hence, there is a sequence of choices in which each individual's choice is based on the current number of individuals per habitat as they fill up. To achieve this mathematically, we let each individual select habitat 1 in turn with probability  $P_{1(t)}$  equal to the relative fitness of habitat 1 at the time they are selecting it:

$$P_{1(t)} = \frac{W_{1(t)}}{W_{1(t)} + W_{2(t)}}, \quad (6)$$

where  $P_{1(t)}$  is updated for each individual as the habitats fill up. The expected number of individuals in each habitat will obey the IFD, but because of stochasticity, the actual number of individuals in each habitat will not follow the IFD exactly, especially when the total number of individuals is very small.

### Population Simulations and Statistics

After selecting habitats, the individuals in each habitat give rise to offspring, and the sum across the two habitats will give the population size next year:

$$N_{(t+1)} = \text{round} \left[ \sum_i N_{i(t)} e^{(a_i - b_i N_{i(t)} + E_{i(t)} - 0.5\sigma_i^2)} \right]. \quad (7)$$

We round off the population size to produce an integer-valued number of offspring in each habitat (Henson et al. 2001). By implementing a probabilistic but fitness-driven habitat selection process and rounding the number of produced offspring, we avoid having to distribute proportions of individuals (as we do with the deterministic habitat selection rule above).

In this article, we are most interested in the stochastic properties of habitat selection, and therefore, we restrict the values of the deterministic parameters and present only three scenarios: both habitats are the same ( $a_1 = a_2 = 1$  and  $b_1 = b_2 = 0.02$ ), habitats show density-dependent parallel regulation ( $a_1 = 1.5$ ,  $a_2 = 1$ , and  $b_1 = b_2 = 0.02$ ), and habitats show density-dependent divergent regulation ( $a_1 = a_2 = 1$ ,  $b_1 = 0.02$ , and  $b_2 = 0.04$ ). Each of these parameter combinations gives rise to asymptotically stable population dynamics and hence, a single equilibrium point in the absence of stochasticity. For more details on the differences between these three forms of regulation (as well as other types of regulation), see Morris (1988).

For each of the three cases, we let the standard deviation of the environmental stochasticity ( $\sigma$ ) vary between 0.1 and 0.5 ( $\sigma$  is always identical in the two habitats). We will also study the effect of spatially correlated environments by adjusting the variance-covariance matrix,  $\Sigma$ , such that the correlation between the environmental stochasticity in the two habitats is equal to 0 (no correlation, local noise), 0.25, 0.5, 0.75, or 1 (perfect correlation, global noise). For each regulation scenario, standard deviation, and environmental correlation, we simulate the population for 80 generations, discarding the first 30 generations. This is repeated 100 times for each parameter combination, which gives us a 100-time series of length 50 years. These Monte Carlo data are used to calculate the isodar by regressing  $N_1$  on  $N_2$  and estimating the slope and the intercept for the 50 points generated by each parameter combination. Regression slopes and intercepts are compared with the predictions based on the deterministic skeleton of the model. Putting fitness in the two habitats equal to each other and solving for  $N_1$  gives us the linear equation

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

The intercept is a function of the growth parameters and the strength of density dependence in habitat 1, whereas the slope is given by the relative strength of density dependence in the two habitats.

Finally, we calculate the proportion of the population

that is found in habitat 1 and whether this proportion changes with total density in habitats 1 and 2. We call this statistic “density-dependent (DD) selectivity,” which refers to the sign of the relationship between the proportion found in habitat 1 and the total density. Hence, if the proportion found in habitat 1 declines with total density, the DD selectivity is negative. The expectation based on deterministic theory is that the proportion found in the best habitat should decline with total population density (DD selectivity is negative) if the regulation is parallel and stay the same (DD selectivity is 0) if there is divergent regulation (Morris 1987).

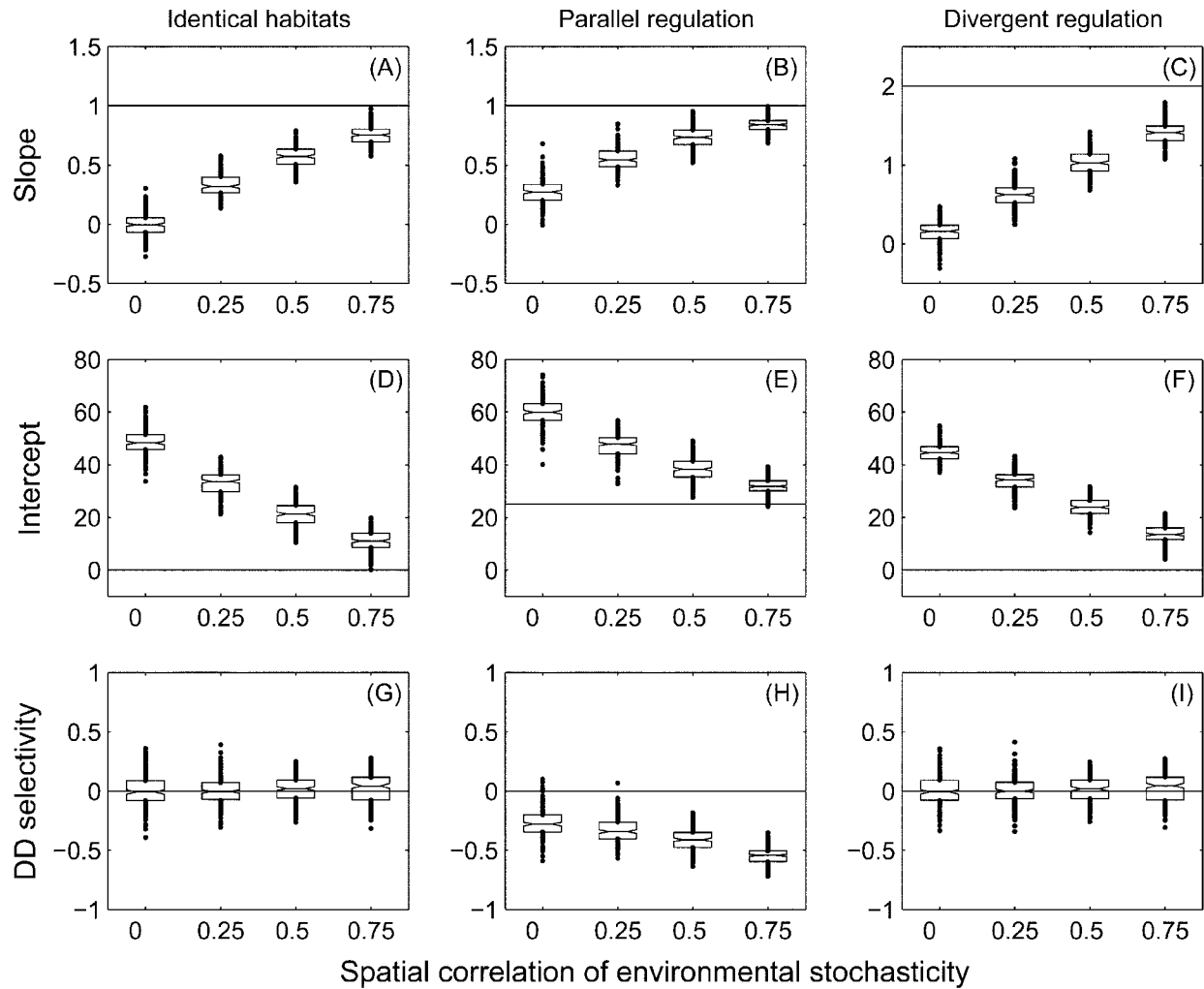
## Results

Starting with the deterministic habitat selection process, where individuals will be perfectly distributed according to the isodars, it is clear that if we add stochasticity that is perfectly correlated between habitats,  $\text{corr}\{E_{1(t)}, E_{2(t)}\} = 1$ , and set the stochastic fitness functions (eq. [5]) equal to each other, the stochastic terms cancels out:

$$\begin{aligned} N_{1(t)} &= \frac{a_1 - a_2 + E_{1(t)} - E_{2(t)}}{b_1} + \frac{b_2}{b_1} N_{2(t)} \\ &= \frac{a_1 - a_2}{b_1} + \frac{b_2}{b_1} N_{2(t)}. \end{aligned} \quad (9)$$

Hence, we will always get the deterministically predicted isodar slope and intercept as given by equation (8). If the environmental correlation between habitats deviates from 1, we will get biased estimates of the isodar slope and intercept (fig. 1). Using the simulated data, we can see that the slope is always underestimated and the intercept is consistently overestimated (fig. 1A–1F). The plots of how the DD selectivity varies with the spatial correlation of environmental stochasticity show a coherent picture in accordance with the deterministic predictions (figure 1G–1I). If the two habitats are identical or if there is divergent regulation, there is no relationship between the proportion of the population found in habitat 1 and total density. This is true for all values of spatial correlation. For parallel regulation, the DD selectivity is negative (the proportion found in habitat 1 decreases with total density), and the negative relationship gets stronger as the spatial correlation of environmental stochasticity approaches 1.

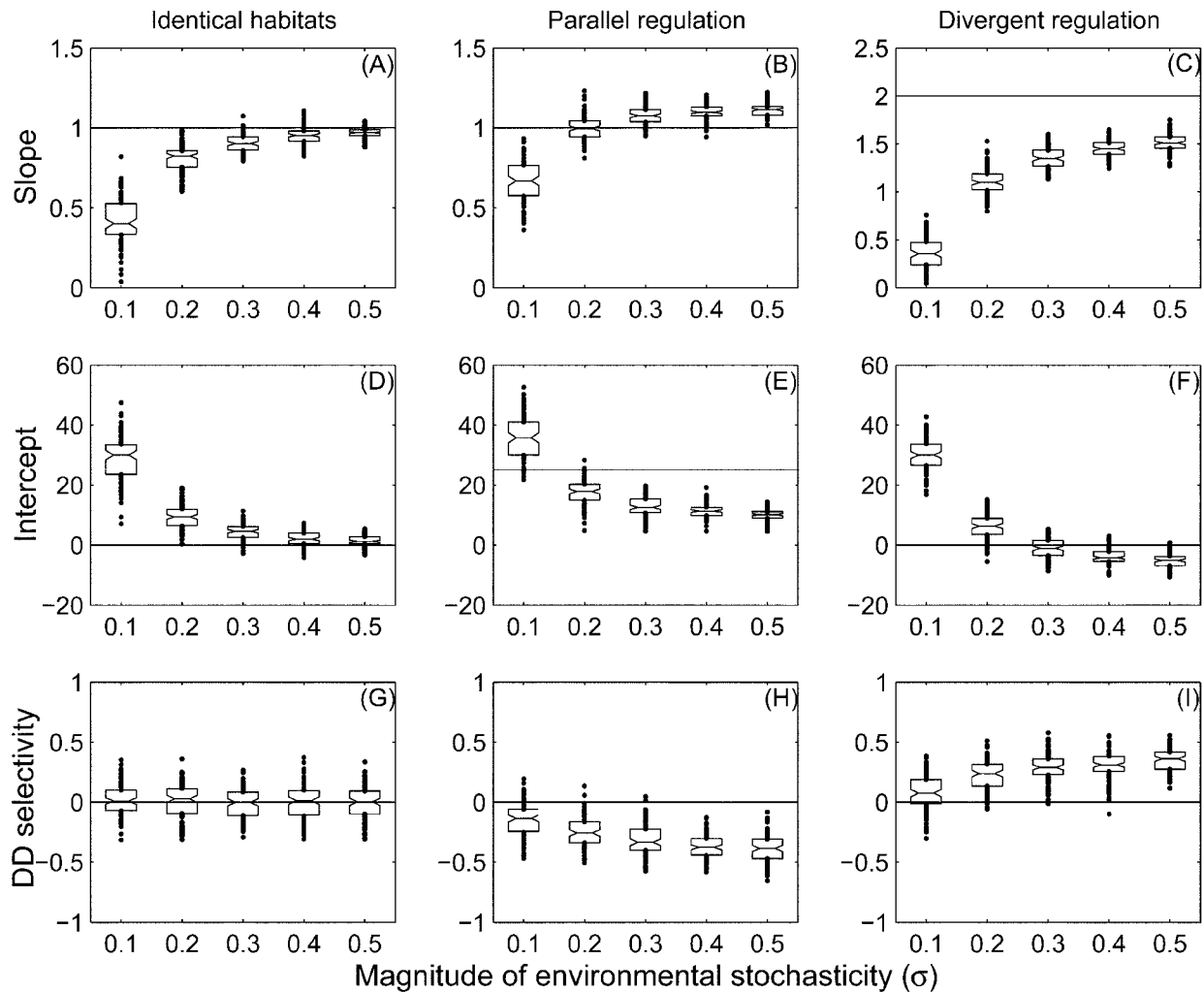
For a given environmental correlation, there is no effect of changing the magnitude of environmental stochasticity (not shown). This result is changed when the habitat selection process is stochastic (eq. [6]). In figure 2 we present how environmental stochasticity affects the spatial distribution of individuals, assuming stochastic habitat selection



**Figure 1:** Box plot of the estimated slopes and intercepts of the isodar analysis (A–F) and “density-dependent selectivity” (G–I), the sign of the relationship between the proportion found in habitat 1 and the total density in habitats 1 and 2 when habitat selection is deterministic. Data reflect 100 replications of each simulated scenario. The boxes have lines at the lower, median, and upper quartile values. Values outside the box are marked by rectangles. In all panels, the spatial correlation of the environmental noise varies between 0 (local) and 0.75, but the SD of the normal random deviate  $E_{i(t)}$  is always equal to 0.2. The other parameter values for the different types of regulation are as follows: identical habitats,  $a_1 = a_2 = 1$  and  $b_1 = b_2 = 0.02$ ; parallel regulation,  $a_1 = 1.5$ ,  $a_2 = 1$ , and  $b_1 = b_2 = 0.02$ ; divergent regulation,  $a_1 = a_2 = 1$ ,  $b_1 = 0.02$ , and  $b_2 = 0.04$ . The horizontal lines in the upper and middle row panels are the deterministic predictions according to isodar theory (Morris 1988). Bottom row panels the horizontal lines indicate no relationship between the proportion in habitat 1 and the total population density.

and complete spatial correlation of the environment (global noise). Starting with identical habitats, we note that the estimates of the slope and intercept are far from the deterministic predictions unless the magnitude of the environmental stochasticity is very high (fig. 2A, 2D). When there are parallel regulations such that  $a_1 > a_2$  and  $b_1 = b_2$ , we get the best match between the estimates and the deterministic skeleton for intermediate levels ( $\sigma = 0.2$ ) of stochasticity (fig. 2B, 2E). An underestimation of the slope means that we underestimate the ratio of the

density dependence,  $b_2/b_1$ . A close inspection of figure 2B shows that we may conclude that  $b_1 = b_2$ ,  $b_1 > b_2$ , or  $b_1 < b_2$  depending on the magnitude of the environmental stochasticity. Note, however, that we always get a positive estimate of the intercept, which is what the deterministic model predicts. However, the point estimates are often far from the deterministic predictions. Furthermore, the estimates are uncertain as indicated by the distance between the quartiles. In the scenario that assumes divergent regulation ( $b_1 < b_2$ ), the estimated slope is consistently well



**Figure 2:** Box plot of the estimated slopes and intercepts of the isodar analysis (A–F) and the “density-dependence selectivity,” the sign of the relationship between the proportion found in habitat 1 and the total density in habitats 1 and 2 (G–I) when habitat selection is stochastic. Data reflect 100 replications of each simulated scenario. The boxes have lines at the lower, median, and upper quartile values. Values outside the box are marked by rectangles. In all panels, the environmental stochasticity is global; that is, the same noise term is added to both habitats. The magnitude of the environmental stochasticity refers to the SD of the normal random deviate  $E_{i\sigma}$ . The other parameter values for the different types of regulation are as follows: identical habitats,  $a_1 = a_2 = 1$  and  $b_1 = b_2 = 0.02$ ; parallel regulation,  $a_1 = 1.5$ ,  $a_2 = 1$ , and  $b_1 = b_2 = 0.02$ ; divergent regulation,  $a_1 = a_2 = 1$ ,  $b_1 = 0.02$ , and  $b_2 = 0.04$ . A–F, Horizontal lines are the deterministic predictions according to isodar theory (Morris 1988); G–I, horizontal lines indicate no relationship between the proportion in habitat 1 and the total density.

below the deterministic predictions (fig. 2C), but the intercept is estimated as approximately 0 (= the deterministic prediction) when the magnitude of stochasticity  $\sigma = 0.3$ .

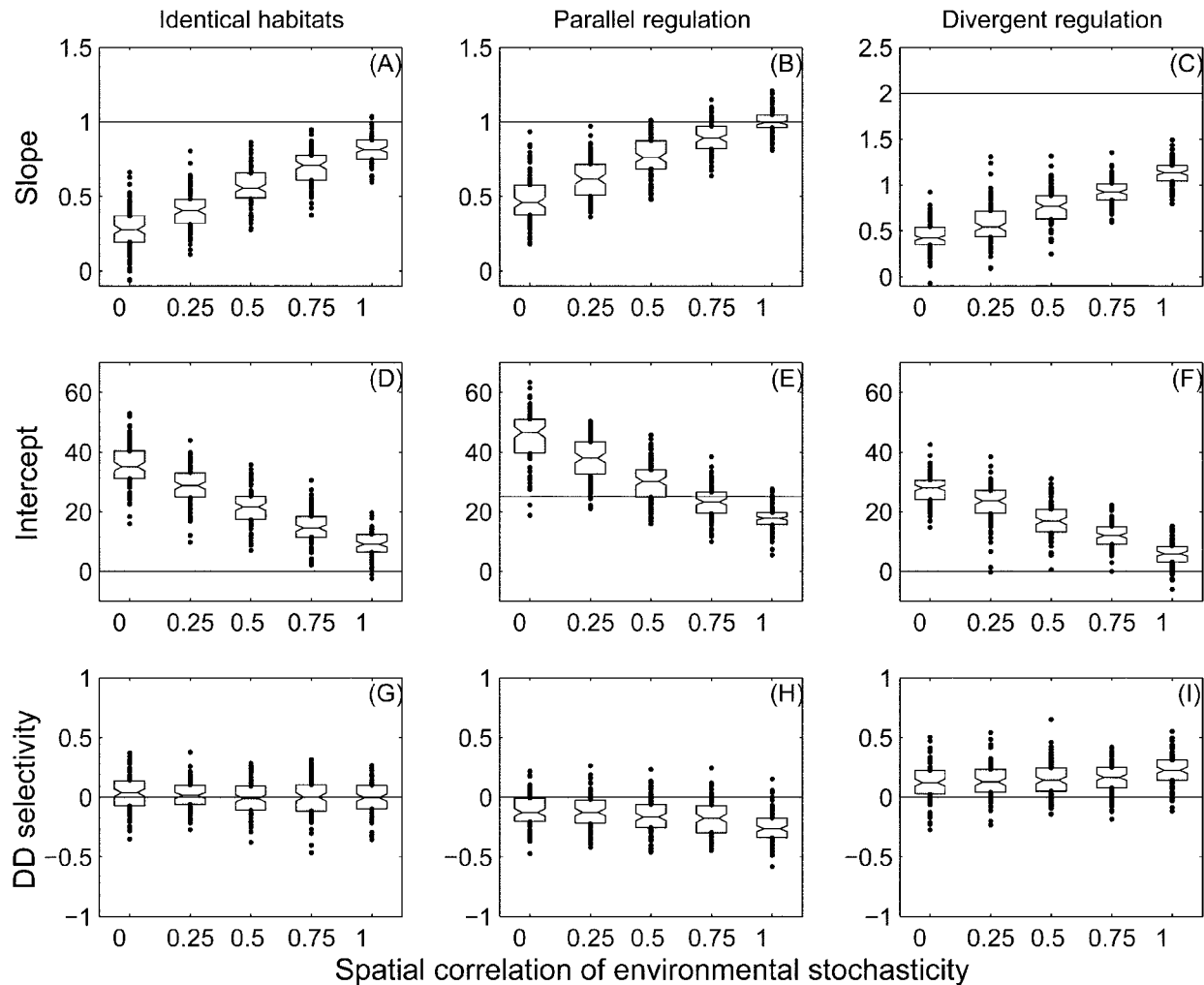
The plots of how the DD selectivity varies with the magnitude of environmental stochasticity when the habitat selection process is stochastic show a coherent picture (fig. 2G–2I). First, DD selectivity is 0 (as predicted by deterministic theory; Morris 1987) when the habitats are identical, and this does not change with the magnitude of

environmental stochasticity (fig. 2G). Second, DD selectivity is always negative (i.e., the proportion found in habitat 1 decreases with total density) when there is parallel regulation (fig. 2H) and always positive when there is divergent regulation (fig. 2I). The negative DD selectivity for parallel regulation is in accordance with deterministic predictions, but we would expect DD selectivity to be 0 when regulation is divergent (Morris 1987). Third, the magnitude of the negative (positive) relationship for parallel (divergent) regulation increases with  $\sigma$  (fig. 2H, 2I).

Next we look at varying the correlation in environmental stochasticity between habitats, and we continue to assume that the habitat selection process is stochastic. Let  $\sigma = 0.2$ , and instead we now vary the correlation of the environmental stochasticity in the two habitats between 0 (local noise) and 1 (global noise as in fig. 2). The general pattern is that the estimated slope and intercept are closer to the deterministic predictions as the environmental correlation between habitats approaches 1 (fig. 3A–3F), similar to the case with deterministic habitat selection (fig.

1). The only exception is the estimate of the intercept when there is parallel regulation (fig. 3E).

The effect of increased environmental correlation on the DD selectivity is similar to the effect of increased magnitude of the environmental stochasticity (fig. 3G–3I). Again, DD selectivity is consistent with deterministic theory, and the magnitude of the negative (positive) relationship for parallel (divergent) regulation increases with environmental correlation. Different values of  $\sigma$  ranging from 0.1 to 0.5 did not change any of the patterns pre-



**Figure 3:** Box plot of the estimated slopes and intercepts of the isodar analysis (A–F) and the “density-dependent selectivity,” the sign of the relationship between the proportion found in habitat 1 and the total density in habitats 1 and 2 (G–I) when habitat selection is stochastic. Data reflect 100 replications of each simulated scenario. The boxes have lines at the lower, median, and upper quartile values. Values outside the box are marked by rectangles. In all panels, the spatial correlation of the environmental stochasticity varies between 0 (local) and 1 (global), but the SD of the normal random deviate  $E_{i(t)}$  is always equal to 0.2. The other parameter values for the different types of regulation are as follows: identical habitats,  $a_1 = a_2 = 1$  and  $b_1 = b_2 = 0.02$ ; parallel regulation,  $a_1 = 1.5$ ,  $a_2 = 1$ , and  $b_1 = b_2 = 0.02$ ; divergent regulation,  $a_1 = a_2 = 1$ ,  $b_1 = 0.02$ , and  $b_2 = 0.04$ . A–F, Horizontal lines are the deterministic predictions according to isodar theory (Morris 1988); G–I, horizontal lines indicate no relationship between the proportion in habitat 1 and the total density.



sented in figure 3G–3I. Compared with the deterministic expectations, we always find undermatching; that is, for a given density, the proportion of the population found in the suboptimal habitat is too large.

Finally, we reduced the environmental stochasticity to 0 and let the only source of randomness be the probabilistic habitat selection process (eq. [6]), which generates isodars with a slope of approximately  $-1$  (identical habitats) or  $-0.9$  (parallel and divergent regulation). The intercepts estimated using isodar analysis are far above the deterministic expectations (due to the negative slope), and the DD selectivity is equal to 0.

### Discussion

Classical models of density-dependent habitat selection are deterministic, and habitat quality is assumed to be time invariant. In deriving a stochastic equivalent of the ideal free distribution, we have studied the effect of temporally fluctuating habitat quality across two habitats. The immediate effect of including environmental stochasticity is that the deterministic fitness measure may no longer be valid (Metz et al. 1992). Hence, it is not clear how individuals should select a habitat to maximize fitness.

We have chosen to study a theoretical organism that has either full knowledge about the fitness consequences of choosing one habitat or the other and at each time step either selects the best habitat (deterministic habitat selection) or, in face of uncertainty, selects a habitat with a probability equal to the relative fitness in that habitat (stochastic habitat selection). Finding the “correct” optimal evolutionary strategy in a density-dependent and stochastic environment is indeed difficult, and the current trend is to use invasibility arguments to identify the evolutionarily unbeatable strategy (Benton and Grant 2000). We make no claims about having used such a strategy here. It is clear that the deterministic habitat selection process should be an ESS when the individuals have perfect information. However, when the individuals do not have perfect information, it is not clear to what extent the stochastic habitat selection rule implemented here would also be ESS. The motivation for the implemented rule is simply that individuals are not ideal and free, but it is reasonable to assume that individuals somehow assess the fitness consequences of selecting a given habitat. Letting the probability of selecting a given habitat at a given time be equal to the relative fitness of that habitat at each time step is a simple way of weighing the fitness functions. It would of course be interesting, given a certain amount of knowledge, to evaluate different habitat selection strategies from the perspective of game theory and search for ESS solutions. However, a full-blown ESS analysis is out of scope here; such an analysis may be the next step to study habitat

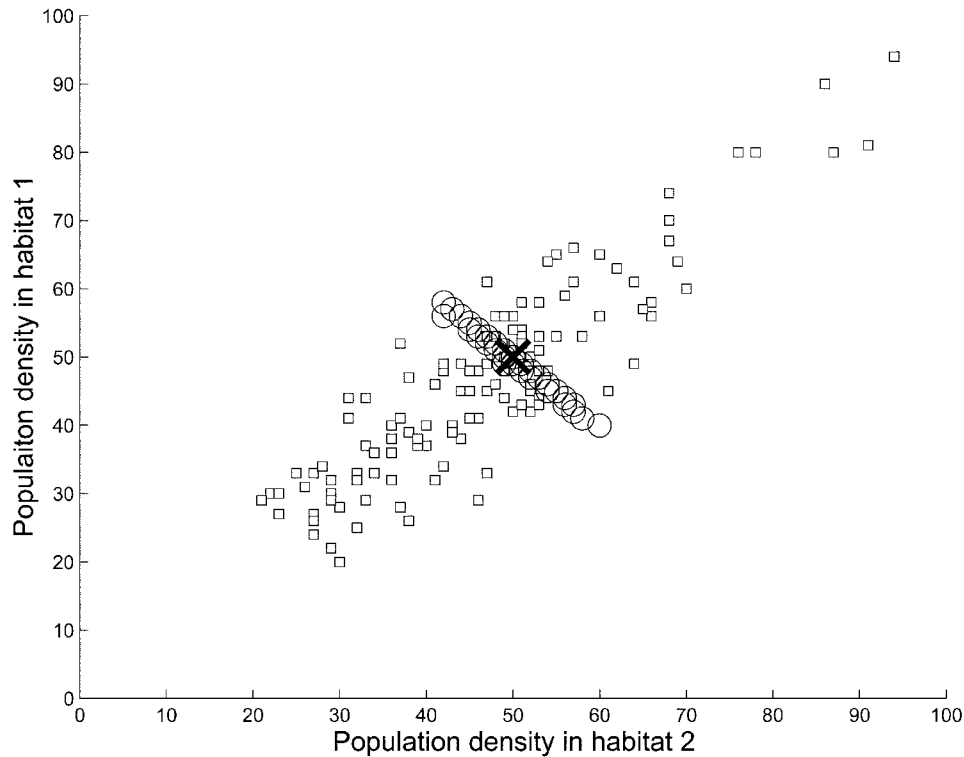
selection in a stochastic environment in the face of uncertainty. Schmidt et al. (2000) suggest ways for finding ESS behaviors for similar sorts of dilemmas, and their article provides a starting point.

In conclusion, we think the two approaches described here are reasonable null models for ideal and free habitat selection, with and without perfect knowledge, respectively. Furthermore, the logic of our analysis makes it easy to compare the results with predictions from classical DDHS theory. The results are patterns of habitat use that are very different from what is predicted by the deterministic DDHS theory.

### *DDHS Is Better Revealed by Density-Dependent Selectivity than by Isodars*

So what kinds of patterns emerge from the underlying processes modeled here? For example, can we determine from census data whether regulation is equivalent (identical habitats), parallel, or divergent? If we regress population density in the high-density habitat on population density in the low-density habitat, we get an estimated isodar slope and intercept. If habitat selection is deterministic and perfect, the isodar slope and intercept are always underestimated and overestimated, respectively, unless environmental stochasticity between habitats is perfectly correlated. Assuming stochastic habitat selection, the general pattern is that the slope and the intercept increases or decreases, respectively, with the magnitude and spatial correlation of the environmental stochasticity. This means that there are several combinations of spatial correlation, magnitude of environmental stochasticity ( $\sigma$ ), and types of regulation that generate similar or identical patterns. Unless we have prior knowledge about the magnitude and spatial correlation of the environmental stochasticity, there is no way the isodar analysis can separate the different scenarios with any reasonable degree of certainty (cf. panels A–C as well as D–F in figs. 2, 3). This is similar to the problem of estimating density dependence in serially correlated environment and a special case of making inference about processes by analyzing patterns (Jonzén et al. 2002; Wiegand et al. 2003). Sometimes, however, the isodar analysis finds the correct relationships, as in the case of parallel regulation (figs. 2E, 3E). Here the isodar analysis correctly identifies the intercept as positive throughout the range of magnitudes of the environmental stochasticity ( $\sigma$ ) and spatial correlation of environmental stochasticity, even though the point estimates are biased compared to the deterministic predictions.

DD selectivity seems to be the most instructive measure of density-dependent habitat selection when the habitat selection process is stochastic. When the habitats are identical, the DD selectivity is always 0 (on average, 50% of



**Figure 4:** Effect of the stochastic habitat selection process and environmental stochasticity on the relationship between population densities in habitats 1 ( $N_1$ ) and 2 ( $N_2$ ). In the absence of randomness (or complex intrinsic dynamics), the populations would settle at an equilibrium point (marked by the cross). Implementing a stochastic but fitness-driven habitat selection rule generates a negative relationship between  $N_1$  and  $N_2$  (circles). By introducing environmental stochasticity, especially if spatially correlated and of high magnitude, the population densities become positively correlated (squares).

the population is found in each habitat independent of total population density), but it gets negative (positive) when regulation is parallel (divergent). These patterns are robust to variation in the magnitude and spatial correlation of environmental stochasticity. The deterministic prediction is that when regulation is divergent, the proportion found in each habitat should be independent of population density (Morris 1987). This is the case when the habitat selection process is deterministic (fig. 1I). When habitat selection is probabilistic, in the divergent case, we find a positive relationship between the proportion in habitat 1 and the total density. This is because the expected fitness in the two habitats is very similar at low density, which means that the sampling errors in the habitat selection will be more important at low density than at high density. At low density, variability in the proportion found in each habitat increases. This variability is also biased toward lower values. Hence, deviations are simply more likely in this direction because the probability of being in habitat 1,  $P_1$ , is naturally bounded between 0 and 1, and the expectation  $E(P_1)$  is above 0.5; that is, habitat 1 has the

highest equilibrium density. Another general finding is that the proportion found in the best habitat is less than expected based on the deterministic theory. Such “undermatching” is also a very general empirical finding when analyzing the distribution of foraging animals (Kennedy and Gray 1994; but see Earn and Johnstone 1997 for a systematic error in many empirical studies).

#### *The Role of Stochastic Habitat Selection*

The reason why the isodar slope and intercept change the way they do in relation to the magnitude and spatial correlation of the environmental stochasticity when habitat selection is probabilistic can be understood by reducing the environmental stochasticity to 0. Now the only variation in population density is due to the stochastic fitness-driven habitat selection rule that gives an isodar with a negative slope (fig. 4, open circles), which is completely inconsistent with deterministic theory. Remember that without stochastic variation in habitat selection, we would get only a single point in  $N_1/N_2$  space (fig. 4, X). The small

deviations from the negative slope are due to the rounding of the continuous-state model (eq. [7]), and this is the only effect of the rounding. If we now increase the magnitude of the environmental stochasticity, the relative importance of this source of variation increases, and by increasing the spatial correlation of the environmental stochasticity, the two populations get more similar (fig. 4, *open squares*). Hence, we get a positive slope and a lower intercept. This is an interesting difference between the deterministic DDHS theory and the stochastic habitat selection model presented here. The DDHS prediction is that two identical habitats should generate an isodar having a slope of 1 and a 0 intercept (Morris 1988). If we reduce the environmental stochasticity to 0 in our model, the corresponding isodar slope is  $-1$ . The reason for that is that we are letting the fitness-driven habitat selection be a stochastic process. Hence, the randomness in the habitat selection process adds a form of demographic stochasticity in behavior, and it would be difficult to argue that individuals would be able to do better than the fitness-driven habitat selection rule implemented here. Having said that, we would like to emphasize that the effect of the stochastic habitat selection rule is minor when reasonable levels of stochasticity are introduced (cf. figs. 1, 3).

#### *The Problem of Estimating Empirical Isodars*

There are basically two approaches for observational data to test for density-dependent habitat selection: isodar analysis (Morris 1988) and a test based on a change in habitat selectivity with population density (Rosenzweig and Abramsky 1985). Whereas the Rosenzweig/Abramsky test is reasonably robust at detecting habitat selection, it does not quantify differences in habitat quality. Isodar analysis, in contrast, may give us some idea about the underlying fitness functions, but if environmental stochasticity is present, we may get misleading results. As we have shown here, isodar analysis is often a rather blunt tool for making an inference about habitat selection from time series data. However, one should remember that most isodar analyses have been built with discrete classes of paired habitats that can be replicated in space, where a habitat is often defined as a type of vegetation. That is a situation not dealt with in this article, where replication of measurements is in time only.

Furthermore, the method cannot identify density-dependent habitat selection from a situation where two regulated populations, one in each habitat without dispersal, have temporally correlated dynamics. Morris (1988, p. 265) approached this shortcoming in two ways, either by suggesting that "If our interest is focused on relative abundance and distribution, we have no need to differentiate between the two alternatives because each gives us

the same answer" or by suggesting alternative methods. If we are interested only in estimating the underlying fitness functions given by the local population parameters ( $a_i$  and  $b_i$  in this study), we recommend formulating a model that is explicit about spatial covariance in environmental stochasticity.

In general, plots of densities in two different habitats over time may be hard to interpret without an underlying process model that is fitted using maximum likelihood estimation, and failing to account for spatial patterns can lead to biased parameter estimates and erroneous conclusions (this study). A maximum likelihood framework for analyzing space–time series data on local population abundance estimates, where local populations share the environment but are not connected by dispersal, is described by Dennis et al. (1998).

#### *Isodars as Theory*

Though isodar analyses may be misleading (depends on scale and intent), individuals still select habitats, and this will necessarily result in a relationship between habitats connected by dispersal. A different question is to what extent the observed patterns correspond to the predicted isodar in a given model formulation. Therefore, we have to separate the issues of using isodars as analytical tools in theoretical analysis (isodars being the evolutionary attractors for fitness optimizing individuals) and the empirical problem of trying to reconstruct them from data analysis. Those are different things, and our concern in this article is mainly the latter. Isodars must exist; the questions are what they look like, to what extent they are manifested, and what it takes to estimate them from data. One must also remember that the detection of density-dependent habitat selection is but a small component of isodar theory. Hence, the isodar theory and habitat selection theory in general remain an important conceptual framework for linking evolutionary strategies in behavior onto their population and community consequences (Morris 2003a).

#### *The Role of Isodars in Empirical Studies*

We do not suggest that throwing out isodar analysis will solve the problems raised here. In fact, we would certainly recommend that anyone interested in understanding why individuals are distributed the way they are should plot pairwise densities. For some situations, the assumptions behind the isodar analysis may be more likely to be fulfilled, for example, if we have experimental data where we can reduce environmental stochasticity. Either way, we would recommend that isodar analysis be used as an exploratory rather than a confirmatory tool. As such, it could

help to generate hypotheses about the underlying processes, similar to the role of descriptive time series analysis in population dynamics (Berryman and Turchin 2001). The most appropriate use of empirical isodars may be to identify relevant scales of habitat selection. Isodar analysis may sometimes be a clever approach for doing that (see Morris 1992), but the question remains of how we should formulate our models to make robust inference when spatiotemporal patterns of stochasticity make the isodar analysis inappropriate.

#### Acknowledgments

N.J. is grateful to the Swedish Foundation for International Cooperation in Research and Higher Education for financially supporting his postdoctoral visit to the Ecology Centre, University of Queensland. We are very grateful to D. Morris and K. A. Schmidt for a detailed and helpful review of this article. We also would like to thank D. Morris and P. Lundberg for discussions and comments at various stages of this work.

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Associate Editor: Joel S. Brown