The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps

William B. Kristan, III

Ecological traps, poor-quality habitat that nonetheless attract individuals, have been observed in both natural and human-altered settings. Until recently, ecological traps were considered a kind of source–sink system, but source–sink theory does not model maladaptive habitat choice, and therefore cannot accurately represent ecological traps or predict their population-level consequences. Although recent models of ecological traps addressed this problem, they used patch-based models containing only two habitats that were very different from one another, but were internally homogeneous. These sorts of patch models may not apply to many real populations, and using them for populations in landscapes with mosaic or gradient habitat structures may be misleading. I developed models that treat source–sink dynamics and ecological traps as special cases of a single process, in which the attractiveness and quality of the habitat are separate variables that can be either positively or negatively related, and in which habitat quality varies continuously throughout the landscape. As expected, sinks are less detrimental to populations than ecological traps, in which preferential use of poor habitat elevates extinction risk. Furthermore, ecological traps may be undetected, and may even appear to be sources, when population sizes are large, but may still prevent recovery in spite of the availability of high-quality habitat when populations drop below threshold levels. Conservation biologists do not routinely consider the possibility that apparent sinks are actually traps, but since traps should be associated with the rapidly changing and novel habitat characteristics primarily produced by human activities, ecological traps should be considered an important and potentially widespread conservation concern.

W. B. Kristan, III, Dept of Biology, California State Univ., San Marcos, CA 92096, USA (wkristan@csusm.edu).

The observation that populations can persist indefinitely in poor habitat when they receive immigrants from good, productive habitat, has inspired important ecological theories, such as source–sink dynamics (Shmida and Ellner 1984, Pulliam 1988, Pulliam and Danielson 1991). Source–sink dynamics has found empirical support (Pulliam 1996), and is considered one of the mechanistic foundations for landscape ecology (Wiens et al. 1993). Although source–sink dynamics were originally described for plants, in which dispersal between source and sink patches was passive (Keddy 1982, Watkinson 1985), source–sink models of animal populations are based on the classic optimal habitat choice models of Fretwell and Lucas (1970) that assume active habitat selection by the organisms for the highest-quality habitat available (Pulliam 1988, Pulliam and Danielson 1991). Following Fretwell and Lucas' example, habitat quality is defined in these models as the expected fitness of organisms occupying the habitat. Important population-level predictions derived from source–sink models, such as that sinks can stabilize source population size fluctuations (Howe et al. 1991), depend on the assumption that individuals accurately judge habitat quality and move from the sink to better habitat in the source as vacancies arise.

Since individual fitness is a consequence of a lifetime of reproductive output, it cannot be observed directly by individuals. It therefore follows that individuals also cannot directly observe habitat quality as defined in source–sink models. Instead, animals respond to environmental cues, which are environmental characteristics that the animals can observe at the time when a habitat choice is made (Williams and Nichols 1984). Equating observation of cues with observation of fitness seems a reasonable simplification, since habitat selection behavior should only evolve when animals respond to environmental cues that predict fitness (Cody 1985, Smith and Sibly 1985, Morrison et al. 1992). However, animals that select breeding territories face a complex forecasting problem, in which they must use the information available in the environment at the time when a choice is made to predict where they are most likely to survive and reproduce at some later time. This fact leaves them vulnerable to spatial or temporal changes in the environment that alter the relationship between the attractiveness of the habitat and its actual quality. Cases of apparently consistent negative relationships between the attractiveness and quality of habitats have been called "ecological traps" (Dwernychuk and Boag 1972, Gates and Gysel 1978, Schlaepfer et al. 2002).

Although ecological traps have been observed in a variety of settings, they have traditionally been explained within a source–sink framework (Pulliam 1996), and they have only recently received the theoretical attention that source–sink dynamics has received (Delibes et al. 2001a, b, Donovan and Thompson 2001). The lack of an appropriate theoretical treatment of ecological traps has prevented accurate predictions of their population-level consequences, and has led to confusion over the relationship between ecological traps and source–sink systems (Remes 2000, Delibes et al. 2001). Theoretical treatments of ecological traps by Delibes et al. (2001) and Donovan and Thompson (2001) established them as a distinct phenomenon, but their models continued the tradition of treating variation in habitat quality as a patch-level effect. This approach implicitly assumes a high degree of spatial structure in the habitat, with areas of good habitat distinct from areas of poor habitat, both of which are internally homogeneous.

In contrast with theoretical representations, habitat structure often varies continuously, either across a mosaic landscape or within relatively distinct patches of habitat "types." Artificially dividing gradients into discrete, homogeneous habitat types can mask important effects. It is important to explore the effects of habitat choice on population dynamics in landscapes with continuous variation in habitat quality to begin to identify potential problems in detecting ecological traps in real landscapes. In this paper I consider the effects of habitat choice on population dynamics and habitat occupancy patterns, and construct models relating habitat attractiveness and habitat quality that produce source–sink dynamics and ecological traps as special cases. With this framework it is possible to identify the conditions under which habitat choice should benefit or harm populations, and the patterns that distinguish sinks from traps, even when variation in habitat quality is continuous. The conservation implications of what may be widespread, pervasive effects of rapid anthropogenic habitat alterations are discussed.

Ideal habitat choice model

In natural settings any given measure of habitat is variable. Organisms can respond to variability in their environment either physiologically or behaviorally, and these responses may in turn affect their fitness. Heterogeneous habitat is thus expected to affect the distribution of organisms in the landscape, to produce habitat-specific population demography, or both. The demographic effect of habitat heterogeneity will be modified by habitat selection behaviors, because the sub-set of habitats that are actually used will determine the population's demographics. Given a heterogeneous landscape, the extent to which habitat choice can modify population demography will therefore increase with increasing mobility and cognitive ability, and mobile vertebrate populations are particularly likely to be strongly affected by their habitat selection behavior. The first models I present assume that organisms have complete knowledge of the cues present in their environment, are able to use the territories with the most attractive cues, but individuals have no direct information about the quality of the habitat. These models are "ideal" in the sense that each individual has complete information about the attractiveness of the territories available, but the usual assumption that individuals have complete information about habitat quality is relaxed (Fretwell and Lucas 1970).

Model structure

The model has three components: the relative frequency distribution f(x) of territories possessing the value x of a habitat variable X, a fitness function g(x) relating the habitat variable to the expected fitness of individuals that occupy the habitat (the quality of the habitat), and a function h(x) describing the degree of preference for particular values of the habitat variable (the habitat's attractiveness). Density effects are solely produced by use of less-attractive habitat as population size increases. Density-dependent declines in the quality of territories can also occur, but this effect would not change the qualitative behavior of these models; thus, I made the simplifying assumption that territory quality is fixed.

For any given distribution of the habitat variable X, the proportion of the territories occupied between any two values a and b of X is:

$$p = \int_a^b f(x)\,dx \qquad (1)$$

The model assumes that all individuals prefer the same habitat (a particular value of X), that habitat is limited in abundance, and individuals use the most attractive habitat that is unoccupied. The endpoints of the used habitat (a and b) are defined by the attractiveness of the habitat, and habitat is occupied from the most attractive to the least attractive. If the attractiveness function h(x) is unimodal, then the endpoints of the occupied habitat will have equal attractiveness, so that h(a) = h(b). The occupied habitat can be converted to a probability distribution, which by definition is:

$$z(x) = \frac{f(x)}{\displaystyle\int_a^b f(x)\,dx} \qquad (2)$$

and the mean attractiveness for the habitat used is:

$$\bar{h} = \int_a^b h(x)z(x)\,dx \qquad (3)$$

For a given population size, the habitat used will have the highest average attractiveness.

A perfect correlation between attractiveness and quality can be enforced by establishing a linear relationship between quality g(x) and attractiveness h(x):

$$g(x) = v + wh(x) \qquad (4)$$

To simplify examination of the effects of habitat choice on population dynamics I have adopted the convention of interpreting the fitness function as the expected growth rate of a population using habitat X = x, so that g(x) can be considered synonymous with λ, the population growth rate. The sign of w determines whether the model results in a source–sink system (w is positive) or an ecological trap (w is negative), provided that g(x) crosses 1.0 (that is, both source and either sink or trap habitats exist within the population). The coefficient v determines either the maximum or minimum expected fitness.

Model parameterization

Although a variety of functions could be used, I chose to use probability density functions with simple parametric forms for f(x) and h(x). No particular function for the distribution of a habitat variable in the environment is expected to be universal, but asymmetry is an interesting common condition. A particularly simple asymmetrical distribution is the exponential:

$$f(x) = \frac{1}{\theta}e^{\frac{-x}{\theta}} \qquad (5)$$

The parameter θ is the mean of the habitat distribution. I used a fixed habitat distribution for all models, with θ fixed at a value of 5 (Fig. 1A). The proportion of territories occupied between any two values a and b of X is found by integrating the habitat function:

$$p = \int_a^b f(x)\,dx = e^{\frac{-a}{\theta}} - e^{\frac{-b}{\theta}} \qquad (6)$$

Changes in the range of habitats used as population size changes are expressed as changes in the positions of a and b.

The habitat that is actually occupied (i.e. the positions of a and b) is determined by the attractiveness of the habitat, h(x) (Fig. 1B). The values of h(x) were interpreted as the relative attractiveness of territories with habitat X = x, and determined the order in which the territories were used. I used a unimodal form of the gamma probability density function for h(x) with:

$$h(x) = \frac{x}{\phi^2\,e^{\frac{x}{\phi}}} \qquad (7)$$

The parameter ϕ defines the modal value of h(x), which is the position of the most attractive habitat. This function was chosen because it is bounded at 0 and it allowed me to easily change the position of the most attractive habitat by varying the value of ϕ. The habitat used at a given population size was found first by solving Eq. (6) for b, yielding the relationship between the upper and lower endpoints of the habitat used at a given population size, then finding the values of a and b that have equal attractiveness. The endpoints of the occupied habitat at a given population size are related by:

$$b = -\ln\left(e^{\frac{-a}{\phi}} - p\right)\phi \qquad (8)$$

The endpoints used will have equal attractiveness, h(a) = h(b):

$$\frac{a}{\phi^2\,e^{\frac{a}{\phi}}} = \frac{b}{\phi^2\,e^{\frac{b}{\phi}}} \qquad (9)$$
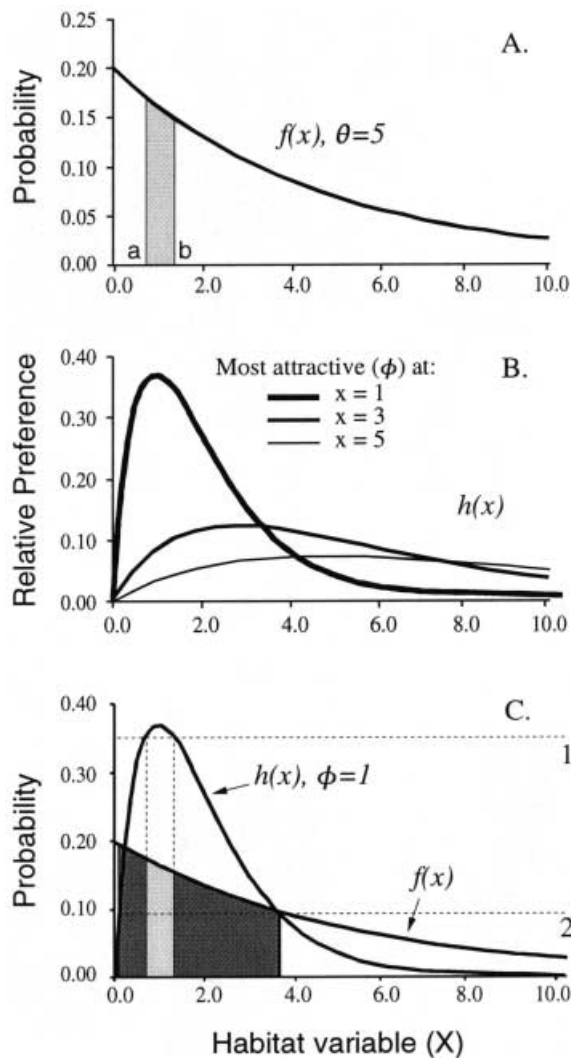
Substituting Eq. (8) for b in Eq. (9) yields:

Fig. 1. Models of ideal selection of the most attractive habitat. (A) The distribution of a habitat variable X in the environment, showing the relative number of territories with a particular value of a habitat variable, f(x). Within this habitat distribution, the habitat that is used at a given population size is represented by the shaded area under f(x) between two endpoints a and b. (B) The relative attractiveness of the habitat to an organism is represented by h(x), the most attractive habitat determined by the position of the mode. (C) The habitat that is actually occupied at a given population size is determined by its attractiveness. Horizontal lines intersect h(x) at points of equal attractiveness, and when these points are projected to the x-axis, they define an area under f(x), representing habitat occupied. Two example lines show how the endpoints of habitat used are found when 10% of the territories are occupied (line 1, lightly shaded area under f(x)), or 50% of territories are occupied (line 2, darkly shaded area under f(x)).

$$\frac{a}{\phi^2 \, e^{\frac{a}{\phi}}} = \frac{-\ln\!\left(e^{\frac{-a}{\theta}} - p\right)\theta}{\phi^2 \, e^{-\ln\!\left(e^{\frac{-a}{\theta}} - p\right)\theta/\phi}} \tag{10}$$

The value of a that satisfies this relationship was found iteratively. This procedure can be viewed graphically (Fig. 1C) by moving a horizontal line up or down along the attractiveness curve h(x) to define an area of a given population size under the habitat curve f(x) constrained to have endpoints of equal attractiveness. Using h(x) in this way imposes a settling order within the habitat as population size increases, and only the most attractive habitats are used at a given population size.

The mean value of X for the occupied habitat is, by definition:

$$\bar{f} = \int_a^b x \, \frac{\left(\frac{1}{\theta} e^{\frac{-x}{\theta}}\right)}{e^{\frac{-a}{\theta}} - e^{\frac{-b}{\theta}}} \, dx \tag{11}$$

Given the habitat occupied, the mean attractiveness is:

$$\bar{h} = \int_a^b \left(\frac{x}{\phi^2 \, e^{\frac{x}{\phi}}}\right) \left[\frac{\left(\frac{1}{\theta} e^{\frac{-x}{\theta}}\right)}{e^{\frac{-a}{\theta}} - e^{\frac{-b}{\theta}}}\right] \, dx \tag{12}$$

The mean fitness, and thus the growth rate for the population, is:

$$\bar{g} = \lambda = v + w\bar{h} \tag{13}$$

The parameters v and w determine the minimum or maximum mean fitness, and the relationship between attractiveness and fitness (either positive or negative), respectively.

Model variations

The effects of preference for relatively common or relatively rare habitat was modeled by varying the value of ϕ (the position of the most attractive habitat) between 1 and 5. Differences between sinks and traps were modeled by changing the sign of w. Values of v and w were chosen so that the population growth rate at saturation (i.e. the growth rate when all territories were occupied) was the same for sinks and traps for a given value of ϕ. The effects of differences in saturated growth rate upon the growth rate at particular population sizes were explored by setting the saturated population growth rate to 0.95, 1.0, and 1.05.

Model output

These models address the effects of habitat selection behavior on the distribution of organisms, and the effects of habitat choice on their population dynamics. For each variation in the model structure at a given

460

population size, I explored the expected pattern of distribution of the population within the habitat (the upper and lower bounds of occupied habitat, a and b in Eq. (6)), the mean of the occupied habitat (Eq. (11)), the proportion of source habitat that was occupied (i.e. occupied source habitat/total source habitat), and the proportion of the occupied habitat that was source habitat (i.e. habitat occupied that is source habitat/total occupied habitat, see appendix for equations used for the latter two variables), as well as the growth rate for the population as a whole (Eq. (13)).

Probabilistic habitat choice

Model structure

Real animals do not exhibit ideal habitat choice. Among other constraints, individuals do not have complete information about their environment at any given time and do not have equal access to all possible sites (Danielson and Anderson 1999). The probabilistic models are structurally similar to the ideal models, but a distribution of habitat attractivenesses are occupied at any population size. I used the same habitat distribution (f(x)), but used a preference function (h(x)) that related the probability of a territory being occupied at a particular population size to the habitat variable X. Since the probability that territories are occupied is related both to the habitat and to the population size, whereas habitat quality only depended on the value of X, it was not possible to simply treat preference and quality as linear functions of one another, and I used a fixed function of habitat to represent habitat quality (g(x)). This had the disadvantage of breaking the perfect linear correlation between preference and quality, but it was possible to maintain a perfect rank correlation between them.

Model parameterization

I used a logistic equation, commonly used as a resource selection function in field studies, that described the probability that a territory will be used at a given population size (Fig. 2A–C). Thus, any habitat with a non-zero probability of use can be occupied simultaneously, but with differing proportions of the available territories within the habitats used. The equation for the selection function is:

$$h(x) = \frac{1}{1 + e^{\beta_1 + \beta_2 x}} \tag{14}$$

The function used for fitness, g(x), was a linear function of a logistic equation:
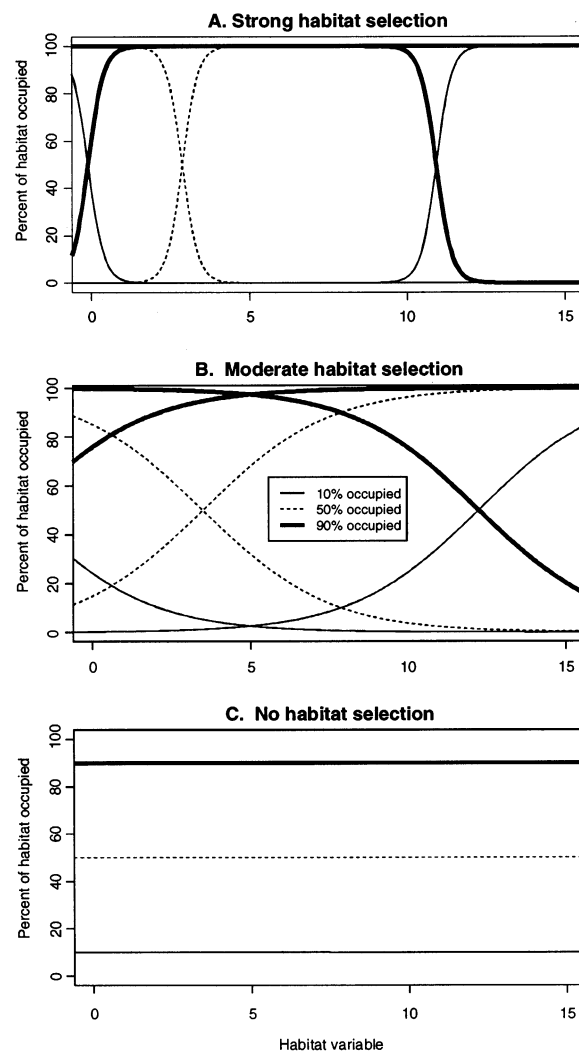

Fig. 2. Models of selection of habitat in proportion to its attractiveness. The percent of territories occupied that had a given value of a habitat variable are represented with logistic curves. For a given model, organisms exhibit either strong, moderate, or no preference for habitat, and the habitat they preferred could either be common or uncommon (habitat is represented by an exponential, and habitat values of 0 are most common). As a greater proportion of territories are occupied, progressively more of the less attractive habitat is used (from A to C).

$$g(x) = v + w \left(\frac{1}{1 + e^{\beta_1 + \beta_2 x}} \right) \tag{15}$$

evaluated for two sets of parameters: one in which fitness increased with increasing values of the habitat variable x, and one in which fitness decreased with increasing values of the habitat variable. The parameters of g(x) were selected so that the population growth rate was 1.0 when all territories were occupied for both sets of parameters.

To determine the relative number of territories occupied at a given habitat value x, I multiplied the logistic selection function h(x) by the distribution function f(x) for the habitat variable ($\theta = 5$). This distribution of occupied territories was converted to a probability distribution, and mean growth rate was calculated:

$$\bar{g} = \lambda = \int_0^\infty g(x) \left(\frac{h(x)f(x)}{\int_0^\infty h(x)f(x)dx} \right) dx \qquad (16)$$

This equation was solved numerically.

Model variations

Effects of variation in the strength of preference for habitat were modeled by changing the magnitude of β_2 (i.e. the steepness of the slope at the inflection point) and the effects of preference for common or rare habitat was examined by changing the end of the habitat distribution that was preferred (determined by the sign of β_2). The effects of changes in population size were modeled by changing the position of the inflection point (determined by β_1) to change the amount of the habitat that was occupied for a given strength of preference. I modeled five variations in model conditions (Fig. 2): strong preference for uncommon habitat, moderate preference for uncommon habitat, no habitat preference ($\beta_2 = 0$), moderate preference for common habitat, and strong preference for common habitat. Each of these variations was modeled for populations that occupied 10%, 30%, 50%, 70% and 90% (10%, 50%, and 90% shown in Fig. 2) of the available territories.

Model output

For each variation in model conditions and population sizes I measured the growth rate for the population as a whole (Eq. (16)), the proportion of source habitat occupied, and the proportion of occupied habitat that is source (see Appendix for equations for the latter two variables).

Results

Ideal habitat choice

Consistent with classical ideal despotic models (Fretwell and Lucas 1970) less-attractive habitats were used with increasing population size (Fig. 3). If the preferred habitat is not at the mean of the habitat distribution ($\phi \neq \theta$), the mean of the habitat used is only near the
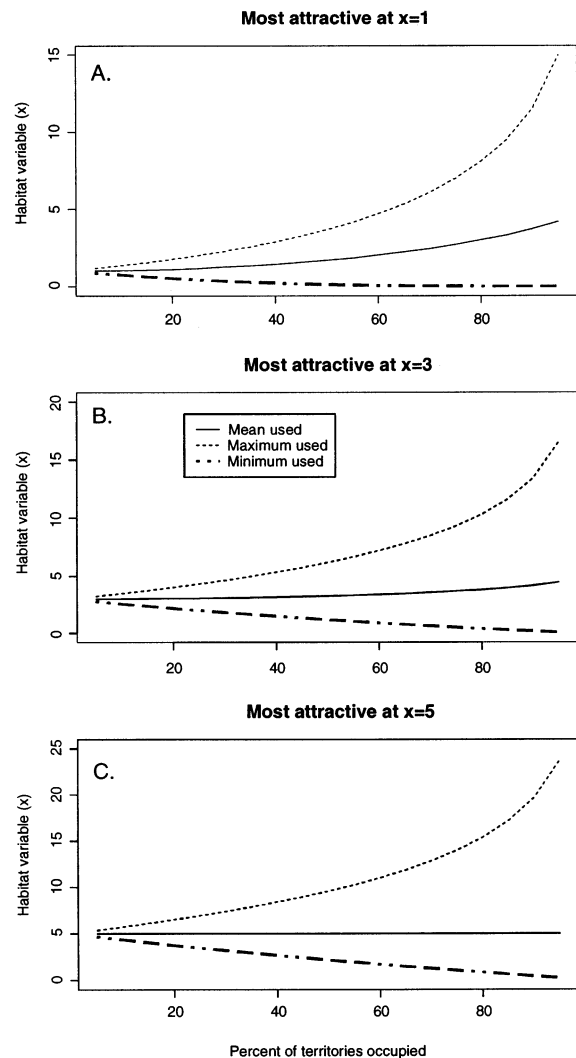

Fig. 3. The range of habitats occupied (i.e. values of X) increases as population size increases. The mean of the habitat that is actually used moves away from the habitat preferred to the mean of the habitat distribution ($\theta = 5$) as population size increases (A and B), unless the mean of the habitat distribution is the most attractive (C).

preferred habitat (ϕ) at small population sizes, but moves towards the mean of the habitat distribution ($\theta = 5$ for these models) as population size increases (Fig. 3).

Habitat choice behavior is beneficial in source–sink systems, but detrimental in ecological traps. Mean population growth rates are highest at small population sizes for source–sink systems, but lowest at small population sizes for ecological traps (Fig. 4). Different saturated population growth rates produced parallel results, as can be seen in Fig. 4A–C. For each saturated growth rate, a horizontal line is placed at $\lambda = 1.0$. With a saturated growth rate of 1.0, ecological trap populations could not increase, even though some of the habitat occupied was source habitat (Fig. 4A).
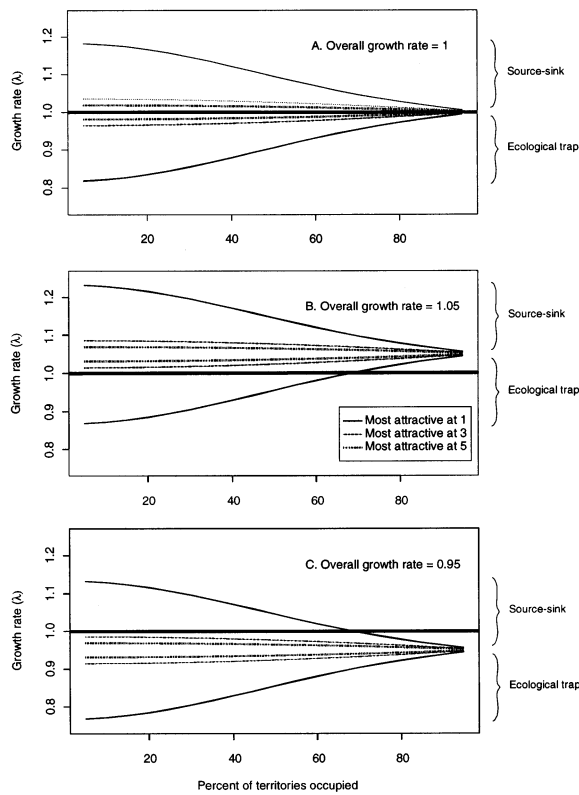
Fig. 4. Habitat choice reduces population growth rate when ecological traps are present, but increases growth rates in source–sink systems. Growth rate curves for source–sinks and ecological traps converge on the same overall growth rate when all territories are filled, and curves above the point of convergence represent source–sink systems whereas curves below the point of convergence represent ecological traps. Each curve represents preference for a different habitat value from 1 to 5. Examples of overall growth rates of 1.00 (A), 1.05 (B), and 0.95 (C) are shown. Horizontal lines are drawn at growth rate = 1.0, and when the source–sink curves cross below this line the population as a whole becomes a pseudo-sink (C, most attractive at 1), whereas when the ecological trap curves cross above this line the population becomes a pseudo-source (B, most attractive at 1).

When the total amount of source habitat is reduced, thereby reducing saturated population growth rate to 0.95 (Fig. 4C), source–sink systems have higher growth rates than ecological trap systems, but choice of the best habitat does not always produce mean population growth over 1.0 for source–sink systems (i.e. those with the most attractive habitat at X = 3). When the total amount of source habitat is increased, thereby increasing saturated population growth rate to 1.05 (Fig. 4B), all of the trap populations could grow, but models with the most attractive habitat at X < 3 only had λ > 1.0 at large population sizes. Under these conditions ecological traps would be prone to unstable equilibria because decreases in population

size would result in growth rates less than 1.0, and the populations would be unable to recover.

The proportion of source habitat occupied increased with increasing population size with both source–sink systems and traps, but started high and increased to saturation in source–sink systems, and started at 0 and only increased after populations were large enough to fill all of the habitat with growth rates less than 1.0 in traps (Fig. 5A). Expressed alternatively, at small population sizes all of the occupied habitat was source in source–sink systems but none of the occupied habitat was source in ecological traps (Fig. 5B).
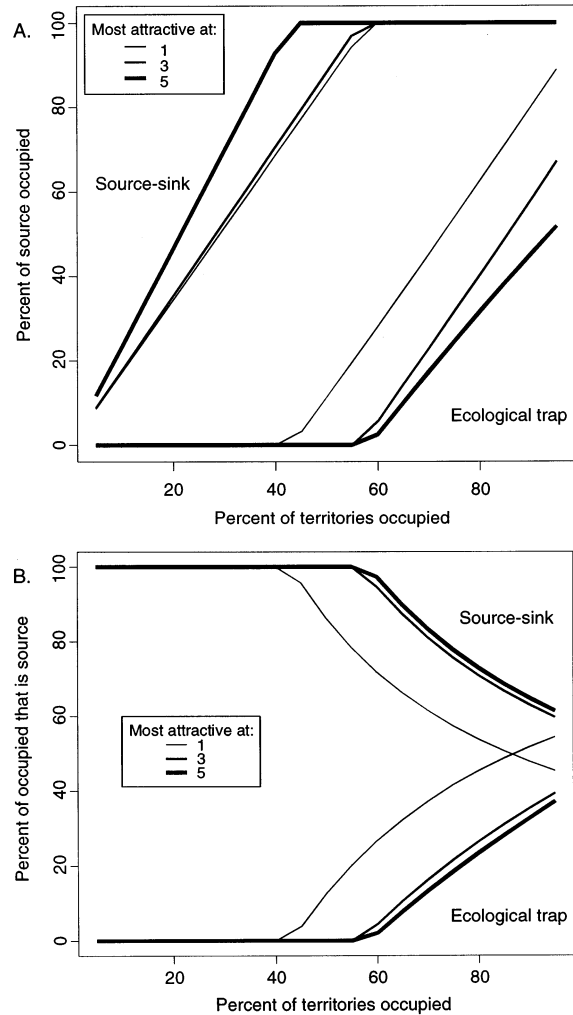

Fig. 5. (A) The percent of source habitat occupied increases with increasing population size when populations are small in source–sink systems, but only increase in ecological trap systems when populations are large. (B) All occupied habitat is source habitat at small population sizes in source–sink systems but none of the habitat occupied is source at small population sizes in ecological traps.

Probabilistic habitat choice

With ideal assumptions relaxed, the probabilistic model yielded qualitatively similar results to the ideal habitat choice model. In source–sink systems habitat choice increased mean population growth rate, whereas in ecological traps habitat choice decreased mean population growth rate (Fig. 6). Strong habitat preference increased the proportion of source habitat occupied at small population sizes in source–sink habitats, but not in ecological traps (Fig. 7A). The proportion of occupied habitat that is source approaches 1.0 at small population sizes in source–sink systems, but approaches zero in ecological traps (Fig. 7B). As with the ideal models, increased population size decreased mean growth rate in the source–sink systems as habitat of decreasing quality was used, but increased mean growth rate in ecological traps as higher quality habitat was used.

Discussion

Occupancy patterns

At small population sizes, the range of habitat used was small and close to the preferred value, but the range of habitats used increased as population size increased (Fig. 3). This pattern has often been observed in bird populations, has been termed the "buffer effect" (Brown 1969, Krebs 1971), and is a common feature of habitat selection models (Fretwell and Lucas 1970, Rosenzweig 1981). When a habitat variable is asymmetrical about its mean, a practical consequence of density-
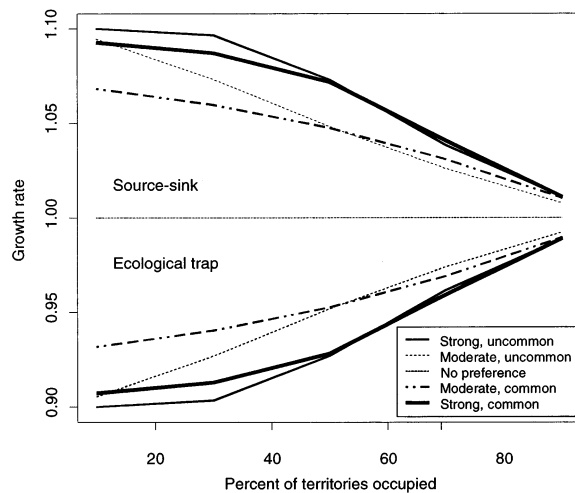
Fig. 6. When habitat choice is probabilistic, habitat choice still enhances population growth rates in source–sink systems and decreases growth rates in ecological traps relative to random habitat use. The effect is greatest at small population sizes when habitat is rare and habitat selection is strong.
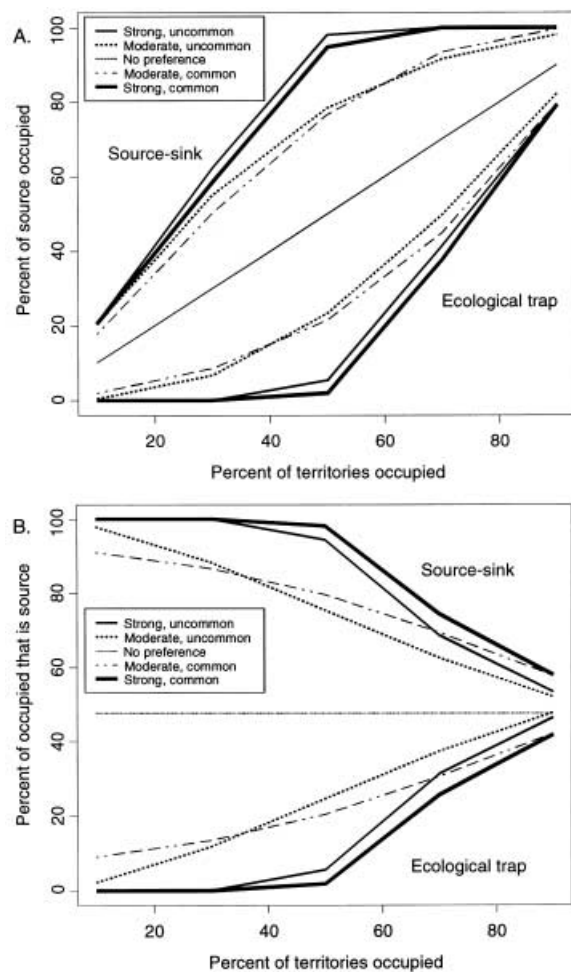
Fig. 7. (A) When habitat choice is probabilistic, the percent of source habitat occupied increases rapidly at low population sizes in source–sink systems compared with random habitat use. In ecological traps source habitat use is low at low population sizes, particularly when preference is strong. (B) When habitat choice is probabilistic, a greater proportion of occupied habitat is source habitat at small population sizes in source–sink systems than in ecological traps or with random habitat use.

dependent habitat use is that at large population sizes the mean of used habitat does not correspond to the preferred habitat. When the preferred habitat does not equal the mean of the available habitat, the mean of used habitat draws away from the preferred value and moves towards the mean of the habitat distribution as population size increases (Fig. 3). This is expected to be a very general result because only a limited number of combinations of habitat distributions and preference functions would position the mean of used habitats at the preferred habitat value for all population sizes. Habitat selection analysis approaches that compare the mean of used habitat to the mean of available habitat will be quite misleading in these circumstances.

Animals select habitat based on environmental cues

It is standard practice in habitat selection models to assume that animals can observe habitat quality directly. However, if habitat quality is defined as the expected fitness of individuals occupying the habitat, habitat quality cannot be observed by individuals. Individuals can observe physical characteristics of their environment, and selectivity for habitat is expected to evolve when observable cues correlate with expected fitness (Schlaepfer et al. 2002). In other words, the environmental cues to which an animal responds should be those that carry information about habitat quality.

The distinction between the attractiveness of habitat and its quality becomes increasingly important as the relationship between a habitat choice and the fitness consequences becomes increasingly indirect. For example, the distributions of foraging oystercatchers among mussel beds can be predicted quite precisely, given information about the amount of food available (Stillman et al. 2000). The cues, such as the size distribution of mussels in exposed beds, are closely related to food availability, which is closely related to survival. In addition to the environmental information available, oystercatchers can assess their own state, and leave a mussel bed that is not sufficiently productive to maintain positive energy balance. A system such as this is information rich, and good matches between the attractiveness and quality of habitats are expected. In contrast, breeding habitat selection necessarily involves longer intervals between the choice and its consequence. Environmental cues that are either unchanging (e.g. elevation, aspect, etc.), or that change deterministically (e.g. seasonal leaf emergence, etc.), during a breeding attempt can carry information about habitat quality. However, habitat characteristics that change stochastically carry less information about fitness, and thus even if they have a large impact on fitness they may be less useful to an animal selecting habitat (e.g. distributions of predators, variation in food availability). In this sense, to understand how variation in habitat affects population dynamics it is necessary to treat the attractiveness of the habitat and the quality of the habitat as separate properties, which respectively influence the habitat choice and the consequence of the choice (Misenhelter and Rotenberry 2000).

Effects of habitat selection on population growth in continuously varying habitat

Selectivity for habitat increases population growth if animals are able to choose habitat accurately, particularly when the best habitat is rare (Fig. 4 and 6). Whereas habitat choice is expected to ameliorate the effects of habitat heterogeneity on population growth if habitat quality can be judged accurately, habitat choice should amplify the detrimental effects of low-quality habitat if habitat quality is judged inaccurately. These effects are most strongly expressed when the relationship between the attractiveness and quality of the habitat is strongest (Fig. 6).

I modeled population dynamics using continuous variation in habitat rather than the discrete patch structure frequently used in source–sink models (Pulliam 1988), and in other ecological trap models (Donovan and Thompson 2001). Patch models are based on the assumption that sources and sinks are discrete places that are very different from each other, but are internally homogeneous. This model structure is difficult to apply to real landscapes that are dominated by heterogeneous habitats. My models show that the variation in habitat quality found in a habitat gradient can produce effects similar to classical source–sink dynamics and to recent ecological trap models, but imposing a patch structure on a gradient in the landscape would mask these effects. A form of this problem has been modeled for source–sink systems, in which density-dependent effects within a source can create a pseudo-sink (Watkinson and Sutherland 1995). Pseudo-sinks are patches in which density-dependence reduces the population growth rate to less than 1.0 at large population sizes, but at smaller population sizes the growth rate increases sufficiently that the population is actually self-sustaining. Although Watkinson and Sutherland (1995) did not explicitly tie density-dependence to habitat selection for within-patch variation in habitat quality, any form of within-patch density dependence could produce a pseudo-sink. For example, in my models pseudo-sinks resulted when the best habitat within an area has an expected growth rate greater than 1.0, but the population exhibits a mean growth rate less than 1.0 because of density-dependent use of poor habitat. An extension of this concept is that populations can produce "pseudo-sources" in the presence of ecological traps. Pseudo-sources exhibit a mean growth rate greater than 1.0 when population sizes are large, but at smaller population sizes the growth rate declines below 1.0 (Fig. 4). Whereas any form of density-dependence could produce a pseudo-sink, only density-dependent habitat use could produce a pseudo-source.

Pseudo-sources in heterogeneous habitats may represent latent threats to populations that would go undetected with conventional population analysis methods. Although my models do not include effects of stochastic perturbations, it is clear that if pseudo-source populations are reduced to the point that population growth is less than 1.0 then the trap habitat should push the population to extinction. In comparison, stochastic population decreases in source–sink systems would be less likely to cause an extinction, because the remaining individuals would occupy the best habitat available, which would speed recovery (Howe et al. 1991). There-

fore, whereas source–sink systems would promote stable equilibria, ecological traps would promote unstable equilibria and population extinction.

Uncoupling attractiveness and quality

Ecological traps are clearly bad for individual fitness, and it is counter-intuitive that animals should judge habitat quality so poorly that they would choose to occupy a trap. Although in general ecological traps have been observed when the usual relationship between cues and habitat quality become uncoupled, this uncoupling could occur in several different ways. The first description of an ecological trap reported that ducks that usually nested in association with terns, which provided some protection from predators, sometimes nested in association with gulls, a nest predator (Dwernychuk and Boag 1972). The authors postulated that the ducks nested near gulls in spite of the risk because they failed to distinguish between gulls and terns. Even apparently obvious, persistent features of habitats, such as proximity to nests of predators, either may not be perceived as threats or may be poor predictors of quality over evolutionary time scales compared to other cues in the environment (Møller 1988), leading to mistakes in individual animal habitat choices. Traps in unperturbed, natural systems would only occur in the presence of spatial variation in the relationship between cues and habitat quality, combined with immigration from more productive areas where response to the cue is adaptive into less productive areas where response to the cue is maladaptive. This would be true when the underlying mechanism is a lack of local adaptation due to gene flow, or immigration of naive individuals that lack the appropriate learned responses to local conditions.

Although natural ecological traps may be rare, they may be common where human activities have rapidly changed the relationship between the attractiveness and quality of habitat (Pulliam 1996, Remes 2000, Delibes et al. 2001a, b). Activities such as agriculture (Best 1986) or refuse dumping (Pierotti and Annett 1990) can attract individuals, but then lead to reproductive failures (Delibes et al. 2001a, b). Additionally, changes that affect the distribution of predator communities independent of the habitat may uncouple the traditional relationship between habitat and risk of predation, thereby producing a trap (Misenhelter and Rotenberry 2000). Cases in which changes in vegetation concentrates both predators and prey, to the detriment of the prey, have also been observed (Gates and Gysel 1978, Purcell and Verner 1998). Thus, traps can form by any combination of changes in cues (thereby providing a super-normal stimulus that strongly attracts individuals to habitat in spite of its poor quality) or

changes in habitat quality (thereby rendering the usual response to natural variation in cues maladaptive).

Identifying pathological habitat choice

It is important to evaluate choices made by individuals in terms of the alternatives that are available, and conclusions about ecological traps should be drawn cautiously, particularly in natural systems. For example, Wheelwright et al. (1997) found that savannah sparrows that nested near relatively ineffective predators (gulls) were protected from effective predators (crows), although sparrows nesting away from both predators were the most successful. In this natural population, apparent cases of maladaptive habitat choice (nesting near gulls) may actually prove to be choice of the best habitat available from a set of poor choices.

Typically, attempts to classify sources and sinks have been based solely on the performance of individuals or populations within habitat patches, but the nature of the response of the animals to variation in habitat quality and the effects of within-patch variation in quality are seldom addressed (Knight et al. 1988, Beshkarev et al. 1994, Donovan et al. 1995, Paradis 1995, Skupski 1995, Hatchwell et al. 1996, Ellison and Van Riper 1998). Sinks and ecological traps have very different population-level consequences, yet they differ only in the ability of individuals to accurately judge habitat quality. Sources have been distinguished from sinks based on whether populations are net exporters or importers of recruits (Brawn and Robinson 1996, Pulliam 1996, Trine 1998), and this distinction would also differentiate sources from ecological traps. Distinguishing sinks from ecological traps additionally requires knowledge of the relationship between preference and quality.

Continuous variation in a habitat variable can occur with a variety of spatial arrangements of habitat, ranging from highly structured habitat gradients (such as elevation gradients on a mountain slope) to habitat mosaics in a landscape. If there is substantial variation in habitat quality, but with little structure in the spatial distribution of habitat qualities, the usual methods of delineating different sub-populations for which demographic rates are estimated may yield misleading assessments of population health. For example, Misenhelter and Rotenberry (2000) found a negative correlation between the reproductive success of pairs of sage sparrows and the vegetation gradient that predicted habitat selection, but vegetation characteristics were finely interspersed on their study area, and territories could not easily be assigned to good and poor sub-populations. This type of ecological trap may be the most problematic for conservation biologists even once its presence

has been established, since it cannot be fixed by removing or rehabilitating a patch of trap habitat.

Although the distinctions between sources, sinks, and ecological traps emerge from the relationship between individual behavior and individual performance, it is not possible to conserve populations at the scale of individual territories. However, because boundaries imposed on gradient habitats can be misleading, an alternative approach to identifying sources is needed. It is possible to evaluate the expected growth rate of a population within small areas, preferably the least indivisible unit such as the breeding territory (Franklin et al. 2000). The "source–sink threshold" approach (Brawn and Robinson 1996, Trine 1998) could be adapted to the level of individual territories, and each territory could be scored by whether it exceeds values of fecundity or survivorship required to produce a net surplus of recruits. At this scale, population growth rate and individual fitness nearly converge (McGraw and Caswell 1996). It would then be possible to evaluate whether source territories form spatial clusters, and aggregate them into larger units, which would then form the source patches. Such a bottom-up approach would avoid many of the current problems of classifying sources and sinks.

References

Beshkarev, A. B., Swenson, J. E., Angelstam, P. et al. 1994. Long-term dynamics of hazel grouse populations in source- and sink-dominated pristine taiga landscapes. – Oikos 71: 375–380.

Best, L. B. 1986. Conservation tillage: ecological traps for nesting birds? – Wildl. Soc. Bull. 14: 308–317.

Brawn, J. D. and Robinson, S. K. 1996. Source–sink population dynamics may complicate the interpretation of long-term census data. – Ecology 77: 3–12.

Brown, J. L. 1969. The buffer effect and productivity in tit populations. – Am. Nat. 103: 347–354.

Cody, M. L. 1985. An introduction to habitat selection in birds. – In: Cody, M. L. (ed.), Habitat selection in birds. Academic Press, pp. 4–56.

Danielson, B. J. and Anderson, G. S. 1999. Habitat selection in geographically complex landscapes. – In: Barrett, G. W. and Peles, J. D. (eds), Landscape ecology of small mammals. Springer Press, pp. 89–103.

Delibes, M., Ferreras, P. and Gaona, P. 2001a. Attractive sinks, or how individual behavioural decisions determine source–sink dynamics. – Ecol. Lett. 4: 401–403.

Delibes, M., Gaona, P. and Ferreras, P. 2001b. Effects of an attractive sink leading into maladaptive habitat selection. – Am. Nat. 158: 277–285.

Donovan, T. M. and Thompson III, F. R. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. – Ecol. Appl. 11: 871–882.

Donovan, T. M., Thompson III, F. R., Faaborg, J. et al. 1995. Reproductive success of migratory birds in habitat sources and sinks. – Conserv. Biol. 9: 1380–1395.

Dwernychuk, L. W. and Boag, D. A. 1972. Ducks nesting in association with gulls – an ecological trap? – Can. J. Zool. 50: 559–563.

Ellison, L. E. and Van Riper, C. 1998. A comparison of small-mammal communities in a desert riparian floodplain. – J. Mammal. 79: 972–985.

Franklin, A. B., Anderson, D. R., Gutiérrez, R. J. et al. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. – Ecol. Monogr. 70: 539–590.

Fretwell, S. D. and Lucas, H. L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 14: 16–36.

Gates, J. E. and Gysel, L. W. 1978. Avian nest dispersion and fledging success in field–forest ecotones. – Ecology 59: 871–883.

Hatchwell, B. J., Chamberlain, D. E. and Perrins, C. M. 1996. The demography of blackbirds *Turdus merula* in rural habitats: Is farmland a sub-optimal habitat? – J. Appl. Ecol. 33: 1114–1124.

Howe, R. W., Davis, G. J. and Mosca, V. 1991. The demographic significance of 'sink' populations. – Biol. Conserv. 57: 239–255.

Keddy, P. A. 1982. Population ecology on an environmental gradient: *Cakile edentula* on a sand dune. – Oecologia 52: 348–355.

Knight, R. R., Blanchard, B. M. and Eberhardt, L. L. 1988. Mortality patterns and population sinks for Yellowstone grizzly bears, 1973–1985. – Wildl. Soc. Bull. 16: 121–125.

Krebs, J. R. 1971. Territory and breeding density in the male great tit, *Parus major* L. – Ecology 52: 2–22.

McGraw, J. B. and Caswell, H. 1996. Estimation of individual fitness from life-history data. – Am. Nat. 147: 47–64.

Misenhelter, M. E. and Rotenberry, J. T. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. – Ecology 81: 2892–2901.

Møller, A. 1988. Nest predation and nest site choice in passerine birds in habitat patches of different size: a study of magpies and blackbirds. – Oikos 53: 215–221.

Morrison, M. L., Marcot, B. G. and Mannan, R. W. 1992. Wildlife-habitat relationships: concepts and applications. – Univ. of Wisconsin Press.

Paradis, E. 1995. Survival, immigration and habitat quality in the Mediterranean pine vole. – J. Anim. Ecol. 64: 579–591.

Pierotti, R. and Annett, C. A. 1990. Diet and reproductive output in seabirds. – BioScience 40: 568–574.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.

Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. – In: Rhodes Jr., O. E., Chesser, R. K. and Smith, M. H. (eds), Population dynamics in ecological space and time. Univ. of Chicago Press, pp. 45–69.

Pulliam, H. R. and Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. – Am. Nat. 137: s50–s66.

Purcell, K. L. and Verner, J. 1998. Density and reproductive success of California towhees. – Conserv. Biol. 12: 442–450.

Remes, V. 2000. How can maladaptive habitat choice produce source–sink population dynamics? – Oikos 91: 579–582.

Rosenzweig, M. L. 1981. A theory of habitat selection. – Ecology 62: 327–335.

Schlaepfer, M. A., Runge, M. C. and Sherman, P. W. 2002. Ecological and evolutionary traps. – Trends Ecol. Evol. 17: 474–480.

Shmida, A and Ellner, S. 1984. Coexistence of plant species with similar niches. – Vegetatio 58: 29–55.

Skupski, M. P. 1995. Population ecology of the western harvest mouse, *Reithrodontomys megalotis*: a long-term perspective. – J. Mammal. 76: 358–367.

Smith, R. H. and Sibly, R. M. 1985. Behavioral ecology and population dynamics towards a synthesis. – In: Sibly, R. M. and Smith, R. H. (eds), Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Publications, pp. 577–592.

Stillman, R. A., Goss-Custard, J. D., West, A. D. et al. 2000. Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. – J. Appl. Ecol. 37: 564–588.

Trine, C. L. 1998. Wood thrush population sinks and implications for the scale of regional conservation strategies. – Conserv. Biol. 12: 576–585.

Watkinson, A. R. 1985. On the abundance of plants along an environmental gradient. – J. Ecol. 73: 569–578.

Watkinson, A. R. and Sutherland, W. J. 1995. Sources, sinks, and pseudo-sinks. – J. Anim. Ecol. 64: 126–130.

Wheelwright, N. T., Lawler, J. J. and Weinstein, J. H. 1997. Nest-site selection in savannah sparrows: using gulls as scarecrows? – Anim. Behav. 53: 197–208.

Wiens, J., Stanseth, N., Van Horne, B. et al. 1993. Ecological mechanisms and landscape ecology. – Oikos 66: 369–380.

Williams, B. K. and Nichols, J. D. 1984. Optimal timing in biological processes. – Am. Nat. 123: 1–19.

Appendix

To find the proportion of source habitat occupied and the proportion of occupied habitat that is source, I first identified which habitat was source habitat. Source habitat is found by solving for the points on the fitness function that equal 1.0. The proportion of the habitat that is a source is the area under the habitat distribution $f(x)$ in which fitness $g(x)$ is greater than 1.0. For a source–sink system, the proportion of source habitat that is occupied is the proportion of the source habitat that falls between a and b:

$$p_{so} = \frac{p}{e^{\frac{-1}{\theta}} - e^{\frac{-u}{\theta}}} \qquad p_{so} \le 1$$

with l and u representing the lower and upper values of the habitat variable that are source habitat. For an ecological trap system, the equation is:

$$p_{so} = \frac{\left(e^{\frac{-a}{\theta}} - e^{\frac{-1}{\theta}}\right) + \left(e^{\frac{-u}{\theta}} - e^{\frac{-b}{\theta}}\right)}{e^{0} - e^{\frac{-1}{\theta}} + e^{\frac{-u}{\theta}}} \qquad p_{so} \le 1$$

Similarly, the proportion of occupied habitat that is source habitat can be computed. This value is the area under the habitat distribution that is occupied (falls between a and b), and has expected fitness $g(x)$ greater than 1.0. For source–sink systems, the equation is:

$$p_{os} = \frac{e^{\frac{-1}{\theta}} - e^{\frac{-u}{\theta}}}{p} \qquad p_{os} \le 1$$

For ecological traps the equation is:

$$p_{os} = \frac{\left(e^{\frac{-a}{\theta}} - e^{\frac{-1}{\theta}}\right) + \left(e^{\frac{-u}{\theta}} - e^{\frac{-b}{\theta}}\right)}{p} \qquad p_{os} \le 1$$

Similar calculations were used to find the proportion of source habitat occupied and proportion of occupied habitat that was source for models with a distribution of attractiveness. The proportion of source habitat occupied was:

$$p_{so} = \int h(x)f(x)\,dx$$

integrated either from 0 to u (when $g(x)$ was a declining function of x) or from l to infinity (when $g(x)$ was an increasing function of x). The proportion of occupied habitat that is source was:

$$p_{os} = \frac{p_{so}}{\int_{0}^{\infty} h(x)f(x)\,dx}$$

These quantities were calculated numerically.