Population consequences of movement decisions in a patchy landscape

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Complex, human-dominated landscapes provide unique challenges to animals. In landscapes fragmented by human activity, species whose home ranges ordinarily consist of continuous habitat in pristine environments may be forced to forage among multiple smaller habitat patches embedded in an inhospitable environment. Furthermore, foragers often must decide whether to traverse a heterogeneous suite of landscape elements that differ in risk of predation or energetic costs. We modeled population consequences of foraging decisions for animals occupying patches embedded in a heterogeneous landscape. In our simulations, animals were allowed to use three different rules for moving between patches: a) optimal selection resulting from always choosing the least-cost path; b) random selection of a movement path; and c) probabilistic selection in which path choice was proportional to an animal's probability of survival while traversing the path. The resulting distribution of the population throughout the landscape was dependent on the movement rule used. Least-cost movement rules (a) produced landscapes that contained the highest average density of consumers per patch. However, optimal movement resulted in an all-or-none pattern of occupancy and a coupling of occupied patches into pairs that effectively reduced the population to a set of sub-populations. Random and probabilistic rules, (b and c), in relatively safe landscapes produced similar average densities and 100% occupancy of patches. However, as the level of risk associated with travel between patches increased, random movement resulted in an all-or-none occupancy pattern while occupied patches in probabilistic populations went extinct independently of the other patches. Our results demonstrate strong effects of inter-patch heterogeneity and movement decisions on population dynamics, and suggest that models investigating the persistence of species in complex landscapes should take into account the effects of the intervening landscape on behavioral decisions affecting animal movements between patches.

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Humans have altered landscapes dramatically by developing land for agricultural, residential, and commercial purposes (Andersen et al. 1996, Collinge 1996, Farina 2000). As a result, many landscapes now contain remnant patches of native vegetation surrounded by land converted for human use (Saunders et al. 1991). Animals in these landscapes are exposed to habitat loss and fragmentation as habitat is broken into small patches separated by inhospitable landscape elements (sometimes referred to as "matrix") that have been created or greatly altered by humans (e.g. agricultural crops, residential areas, roads).

Predicting the consequences of habitat loss and fragmentation for animal populations is important for the conservation and management of species (Dooley and Bowers 1998, Nupp and Swihart 2000). The composition of the landscape around fragments can affect species' movement patterns (Sheperd and Swihart 1995, Debinski and Holt 2000), however, large-scale experiments on the effects of landscape composition on the

movement abilities and persistence of animal populations can be difficult to perform. Therefore, as an alternative, modeling can be a useful tool for predicting the effects of fragmentation on a species (Henein et al. 1998).

Results from models that include landscape heterogeneity have been mixed. Gustafson and Gardner (1996) developed an individual-based dispersal model that simulated animals moving in a self-avoiding random walk (SAW) across a landscape composed of habitat islands surrounded by a heterogeneous landscape. Each cover type that composed the landscape was assigned a priori a probability that the SAW would enter that cover type. Movement of SAWs began on a random site at the edge of a deciduous forest patch (preferred habitat for the simulated species), and movement across the grid was simulated as a sequence of steps to adjacent cells. The probability of a SAW entering a particular cell was a function of land cover types in the adjacent cells and the probabilities associated with entering each of the land cover types. An overall dispersal coefficient was calculated based on the proportion of SAW to successfully emigrate from a habitable patch to any other habitable patch in the landscape and the size of the originating patch. Results indicated that the landscape quality had a much smaller effect on variability in landscape-level dispersal success than did the configuration of the suitable habitat. Emigration and immigration rates were not always symmetrical for a particular patch, and changes in landscape heterogeneity could result in a two-fold or more difference in dispersal success indicating a role of landscape heterogeneity in predicting population-level consequences.

Vandermeer and Carvajal (2001) explored the consequences of landscape quality on population persistence, rather than individual dispersal success, by modifying Levins' (1969) metapopulation model to include a migration coefficient representing the effects of landscape quality on migration rate. Their simulations indicated that increasing landscape quality does not guarantee persistence of a population. The increased migration rates associated with higher quality landscapes can result in periodic local (i.e. patch-level) extinctions and possibly simultaneous extinction of all local populations. Further increases in landscape quality can provide "rescue effects" for local populations and result in persistence of the metapopulation by increasing the likelihood that a patch suffering extinction will be recolonized. However, the model of Vandermeer and Carvajal (2001) does not include the effects of heterogeneity on local population dynamics; i.e. the landscape is of uniform quality.

Experimental and observational studies support the conclusion that the composition of the landscape can affect patch occupancy (Åberg et al. 1995, Hokit et al. 1999, Pope et al. 2000, but see Moilanen and Hanski 1998). The landscape may negatively affect populations by conferring a high mortality risk (St. Clair et al. 1998, Zollner and Lima 1999, Hanski et al. 2000) or impeding movement (Crist et al. 1992, Schooley et al. 1996). These factors may influence an animal's decision to leave a patch, or decrease the probability of an animal successfully reaching a new patch. Several studies have indicated that the type of landscape surrounding a habitat patch can affect the propensity of an animal to leave a patch (Pither and Taylor 1998, Hokit et al. 1999, Jonsen et al. 2001) or the ability of the animal to travel between patches (Peltonen and Hanski 1991). Species-specific differences in movement ability may be based on physical characteristics such as body size; however, movement propensity differences are more likely to depend on psychological factors such as perceived risk of travel in various landscape types (Haddad 1999, Bhattacharya et al. 2003). Additionally, the direction of travel can be influenced by landscape composition. For, example, Bowne et al. (1999) determined that habitat corridors were the preferred route for cotton rats (*Sigmodon hispidus*) leaving habitat patches, and thus, the composition of the landscape outside of habitat patches appears to influence the direction of animals leaving a patch.

In this paper, we present a spatially explicit model to estimate the persistence of a species in a landscape consisting of habitat patches surrounded by more than one landscape type. Our model explicitly links individual behavior to population-level consequences by incorporating behavioral decision rules to reflect potential choices of animals foraging among patches in a fragmented landscape. The model is based on the notion of a consumer exhibiting a Type II functional response to changes in resource density. The model was used to estimate how equilibrium population size and patterns of patch occupancy were affected by 1) different decision rules for travel through the landscape and 2) multiple landscape elements with different probabilities of survival while traveling between habitat patches.

The model is applicable generally to any mobile organism. To enhance the realism of the model, we have parameterized it for use with small rodents, as explained below.

Model structure

Fryxell and Lundberg (1998) proposed a model of a consumer foraging for a renewable prey resource in a patchy environment. Patches occur at vertices of a lattice, with movements restricted to the four cardinal directions (rook rule). An implicit assumption of the model is that foragers are omniscient; i.e. they know the current rate of energy gain in the occupied patch, the average rate of gain across the landscape, and the travel time between patches.

Consumers exhibit a Type II functional response constrained by handling and searching time. The expected energy gain of a consumer in patch (i,j) is

$$\phi_{i,j} = \frac{eaR_{i,j}}{1 + ahR_{i,j}} \qquad (1)$$

where e is the energy content of each individual prey item or unit of biomass consumed, a is the area searched per time unit, h is the handling time per prey item and $R_{i,j}$ is the abundance of the prey resource (R) in a patch at location (i,j) (Table 1). $R_{i,j}$ changes as

$$\frac{dR_{i,j}}{dt} = rR_{i,j}\left(1 - \frac{R_{i,j}}{K}\right) - \frac{aR_{i,j}N_{i,j}}{1 + ahR_{i,j}},$$

where r is the per capita intrinsic growth rate of the prey resource, K is the patch carrying capacity for the prey resource, and $N_{i,j}$ is the population of consumers in the patch (i,j). $N_{i,j}$ changes as

$$\frac{dN_{i,j}}{dt} = \beta_{i,j}N_{i,j}\left(\frac{ceaR_{i,j}}{1 + ahR_{i,j}} - d\right) - (1 - \beta_{i,j})N_{i,j} + I_{i,j}, \qquad (2)$$

where d is the per capita rate of consumer mortality, and births are represented by converting the expected energy gain in patch (i,j) (Eq. (1)) into the number of offspring produced per energy unit that reach reproductive age. $\beta_{i,j}$ is the probability that an animal will stay in patch (i,j), and $I_{i,j}$ is the number of immigrants entering patch (i,j). $\beta_{i,j}$ was calculated on the basis of a sigmoidal function that weights the rate of energy gain in patch (i, j), $\phi_{i,j}$, against the average rate of energy gain from all patches, $\bar{\phi} = (ea\bar{R}/(1 + ah\bar{R}))$, after discounting for travel time, τ, between patches:

$$\beta_{i,j} = \frac{e^{z\phi_{i,j}}}{e^{z\phi_{i,j}} + e^{z\bar{\phi}/(1 + \tau)}} \qquad (3)$$

Note that the rate at which the curve saturates on either side of the threshold value is determined by the scaling parameter z. As z decreases the function begins to resemble a linear response and represents the foraging decisions of a species whose behavior varies considerably from optimal. Higher z values correspond to a sharper behavioral threshold, reflecting a species whose behavior more closely resembles optimal decisions (Fig. 1). For all values of z, deviations from optimal behavior occur with maximum probability when resource levels in the landscape equal resource levels in the patch. We used z = 4 in our simulations to reflect foragers in a familiar landscape that were able to assess resource levels fairly accurately (Fryxell and Lundberg 1998).

I_{ij}, the number of immigrants entering patch (i,j), is derived from the following information. Assume that the number of emigrants leaving a patch (i,j) is $E_{i,j} = (1 - \beta_{i,j})N_{i,j}$, and that these emigrants are divided equally between all the paths connecting patch (i,j) to other patches (Fryxell and Lundberg 1998). While traveling for τ time units, emigrants are subject to the same death rate as the patch occupants. Thus, the number of surviving emigrants along each path is $E_{i,j}(1 - d)^{\tau}/n_{i,j}$, where $n_{i,j}$ is the number of paths connecting patch (i,j) to other patches. Therefore, the number of immigrants entering patch (i,j) at time t is calculated by summing the values of emigrants from all the connected patches that survive traveling and reach the patch (i,j) at time t, i.e.

Table 1. List of parameters included in model

| Parameter	Definition
e	energy content of each individual prey item or unit of biomass consumed
a	area searched per time unit
$R_{i,j}$	resource level in patch (i,j)
h	handling time per prey item
r	per capita intrinsic growth rate of the prey resource
K	carrying capacity for the prey resource
h	handling time per prey item
$N_{i,j}$	population of consumers in the patch (i,j)
c	coefficient for converting energy into offspring
$\beta_{i,j}$	probability that an animal will stay in patch (i,j)
$\phi_{i,j}$	rate of energy gain in patch (i,j)
$\bar{\phi}$	average rate of energy gain from all patches
τ	travel time
$I_{i,j}$	immigrants into patch (i,j)
$E_{i,j}$	emigrants from patch (i,j)
d	mortality rate
t	time unit
D	distance along a path
v	velocity
P_p	probability of predation along a path
q_m	probability of death due to predation per time step along path m
P_s	probability of starvation along a path
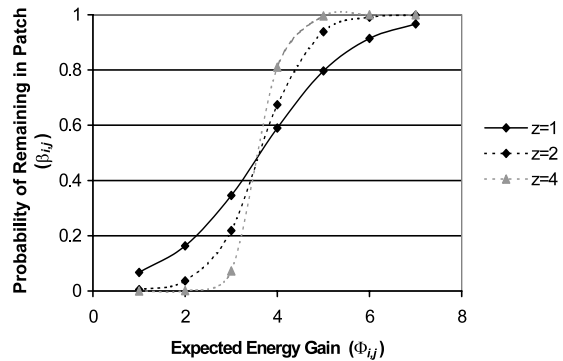
Fig. 1. Probability of a consumer remaining in patch (β_{ij}) with coordinates (i,j). Average energy gain in the landscape was fixed at $\bar{\phi} = 4$. Note that as the scaling parameter z increases, the behavioral threshold becomes more distinct. For any given value of z, indecisiveness is maximal when $\phi_{ij} = \bar{\phi} = 4$.

$$I_{i,j}(t) = \left[\frac{E_{i,j-1}(t-\tau)}{n_{i,j-1}} + \frac{E_{i,j+1}(t-\tau)}{n_{i,j+1}} + \frac{E_{i+1,j}(t-\tau)}{n_{i+1,j}} \right.$$
$$\left. + \frac{E_{i-1,j}(t-\tau)}{n_{i-1,j}} \right] (1-d)^{\tau}$$

Model modifications for foragers in a heterogeneous landscape

We modified several features of the general model to make it more applicable to small mammals foraging in a human-dominated landscape consisting of multiple landscape elements, such as a landscape with pasture, row crops, and residential elements separating woodlot patches for forest-dwelling species. The parameters a, e, h, and c are species- and context-specific and thus should be assigned based on field or laboratory experimentation. Because we were unable to express them as general functional forms for purposes of assigning values for "small mammals", these parameters were set equal to one, effectively dropping them from the equations.

Travel time (τ)

Travel time was calculated as $\tau = D/v$; where $D =$ the distance (km) along a path, and $v =$ the velocity (km hr^{-1}) of the focal animal. Velocity was estimated as the maximum running velocity for small rodents, $v = 20 M^{0.183}$ (Garland 1983). The distance of each path was assigned a unique value by multiplying a uniform random number on the interval [0, 1] by a scaling constant. These scaling constants represented distance factors and were used to model landscapes with varying levels of isolation between patches. We used distance factors of 5, 30, and 60 for our simulations, representing landscapes with increasing distances between patches. Three model landscapes were examined, in which the average distance between patches in a landscape was half the distance factor, or 2.5 km, 15 km, and 30 km.

Probability of remaining in a patch

Rather than relating cost of patch departure directly to travel time, we modified the β function (Eq. (2)) so that the cost of leaving a patch included the time-specific probabilities of being preyed upon (P_p) or starving (P_s) while traveling through a particular landscape type:

$$\beta_{i,j} = \frac{e^{z\phi_{i,j}}}{e^{z\phi_{i,j}} + e^{z\bar{\phi}/(1+P_p+P_s)}}.$$

The probability of death due to predation along the mth path was computed as $P_p = 1 - (1 - q_m)^{\tau}$, where q_m is the probability of death due to predation per time step along path m. q_m is dependent on the landscape element through which the path passes.

The probability of starvation while traveling between patches varies depending on the rate of energy expenditure and the amount of stored energy available for use by the traveling animal. For simplicity, we assumed that no energy is gained while traveling between patches. We used empirical relationships for terrestrial mammals to determine the probability of death due to starvation for a given body mass (M, in kg). The number of days (represented by time units, τ, in our model) a mammal can survive without feeding, T_s, is determined allometrically (Lindstet and Boyce 1985) as $T_s = (2948M^{0.75}/E_{survive})$, where the energy needed to survive during transit ($E_{survive}$) is given by Calder (1984) as the energy needed for running between patches; i.e. $E_{survive} = 6.03M^{-0.0303} + 38.5M^{-0.316} v$. We modeled starvation as a binary process; i.e. $P_s = 1$ if $T_s < \tau$ and $P_s = 0$ if $T_s \geq \tau$.

Rules governing movement between patches

We explored three rules governing animal movements between patches, varying in the efficiency with which animals could assess costs of movement: (1) random, (2) least-cost, and (3) probabilistic movement rules. Randomly moving foragers selected each of the four paths emanating from a patch with an equal probability. We chose the random rule as a null model, consistent with Fryxell and Lundberg's (1998) model in which emigrants were divided evenly among the total number of pathways connected to a patch.

Probabilistic and least-cost rules assume that foragers are, to a certain extent, cognizant of the risk associated with traveling through different types of habitat. Several observational studies have concluded that small rodents adjust their foraging behavior by modifying their velocity, path tortuousity, or pausing frequency or duration in response to changes in their perceived vulnerability to predators (Longland and Price 1991, Lagos et al. 1995, Vasquez et al. 2002). Least-cost and probabilistic rules incorporate the effects of these behavioral decisions on foraging movements. According to the least-cost path rule, foragers always choose to travel the path that provides them with the greatest probability of surviving the entire journey. This rule assumes complete knowledge on the part of the forager, no mistakes in perception, and optimal decision-making. In contrast to the least-cost path, the probabilistic rule assigns choice of a path in proportion to the probability of survival associated with traveling along it. Accordingly, animals do not always behave optimally when adhering to this rule (Bitterman and Mack-

intosh 1969, Kirk and Bitterman 1965). Non-optimal path choice can be the result of imperfect information regarding the environment (Schooley et al. 1996) or exploratory behavior (Aars et al. 1999, Ims and Andreassen 2000).

Methods

Structure of simulated landscape

The landscape was composed of 49 patches arranged in a 7×7 lattice to maintain consistency with Fryxell and Lundberg (1998). The landscape between patches was composed of the paths that connected the patches. Paths passed through four different landscape elements in our simulations. Each landscape element had associated with it a different predation risk per unit time. Landscape elements were assigned randomly to paths between patches until there was an equal number of each element in the landscape.

Simulations

Consumer populations in each patch began with an initial population of $K/4$, whereas resource levels started at K. To approximate a continuous process, each time unit during a simulation run was divided into 100 time steps, therefore the entire equation for change of state variable parameters in each time-dependent equation was multiplied by 0.01. Simulations were conducted until the average consumer density per patch changed less than 5% between time steps. Hypothetical species with body mass values of 0.01, 0.1, 1.0, 2.0, and 5.0 kg were compared for each movement rule and landscape.

Analysis

A quantitative estimate of the strength of the relationship between matrix composition and population density and distribution can provide useful information for landscape planners and conservation biologists. We devised a quantitative estimate of matrix "hostility", or average risk experienced by a consumer leaving a patch, by determining the overall patch-specific risk of death due to predation and starvation. For randomly foraging consumers hostility was calculated by summing the risk of death $(P_p + P_s)$ for each path that connected the focal patch to another patch and dividing by the number of paths. For consumers in simulations utilizing the least-cost rule, hostility was tallied from the path exhibiting the minimum risk of departure from the focal patch. Hostility for consumers in simulations utilizing the probabilistic rule was determined by using the

weighted average of the risk associated with each path. Weights were assigned by determining the probability that an animal would leave along a particular path (i.e. $\beta_{i,j}$).

Logistic regression was conducted to determine whether patch occupancy could be predicted accurately by the index of hostility and the movement rules utilized by individuals within a population. Non-linear regression was performed to determine whether hostility of the landscape around a patch and rules governing movements were good predictors of variation in the equilibrium consumer densities of patches. Best-fit models were chosen using Akaike's Information Criterion (AIC).

A sensitivity analysis was performed on body mass and risk per unit time to determine the extent to which small changes in these parameters produced changes in patch occupancy and average consumer density. Each body mass and risk value used in the initial simulations was adjusted by 10%, and the simulation was rerun with all other parameters the same. Sensitivity was then quantified as

$$S.I. = \frac{\dfrac{N_0 - N_1}{N_0}}{\dfrac{P_0 - P_1}{P_0}},$$

where N_0 = original consumer density, N_1 = consumer density when the parameter of interest (P = risk or body mass) is changed by 10%. We investigated the effects of the reproductive coefficient c and the carrying capacity K on model results by simulating populations with combinations of c and K values that were lower or higher than the values used to run all other simulations ($c = 1$, $K = 8$).

Distribution of landscape elements

We investigated the effects of varying the distribution of landscape elements on population dynamics in a smaller 4×4 landscape. Three types of landscapes were examined, varying according to the distribution of landscape elements separating habitat patches: homogeneous, clumped, and barrier. Homogeneous landscapes contained a single landscape element between patches; i.e. pathways all had equivalent risks of mortality per unit time step, q_m. Clumped landscapes exhibited a gradient of riskiness in which 1/3 of the patches were embedded in a high-risk element, a middle 1/3 were in an element of intermediate risk, and the remaining 1/3 were in a low-risk element. Landscapes with barriers contained an element of high risk separating two areas of low-risk elements. Parameters were equivalent to the original model parameters and the mean distance between patches was 10 km (distance factor = 20).

Results

Local population density

The average density per patch was greater for populations that moved along least-cost paths than for populations that followed random or probabilistic movement rules (Fig. 2). Variation in consumer densities per patch was greatest for populations whose members exhibited optimal (least-cost) movements, due to the large numbers of unoccupied patches that resulted from the "paired" pattern of occupancy exhibited by these populations (Fig. 3). The only occupied patches in the landscapes occupied by optimal foragers were patches whose least-cost path was also the least-cost path of a neighboring patch, creating sub-populations of dyads that exchanged emigrants in equal numbers.

For most parameter values, there were no significant differences between local densities for randomly moving consumers and consumers following probabilistic rules. However, at an average inter-patch distance of 30 km and a body mass of 0.01 kg, patch occupancy for randomly moving populations was zero, whereas patch occupancy of populations of individuals following probabilistic rules was 94%. In addition, when average landscape risk and the variation between the highest and lowest risk per time was increased threefold, the average equilibrium density per patch was twice as high for animal populations using probabilistic movement rules as those using random rules (Fig. 4).

An exponential curve was fitted to the equilibrium population density for each patch, to determine whether patch density could be predicted by the movement rule employed by consumers in a population and by an index of hostility of the landscape around each patch. When results from all three movement rules were included in the model, only 27% of the variation was explained by differences in hostility (Table 2). Omitting optimal (least-cost) foragers from the model dramatically improved the fit; hostility of the surrounding
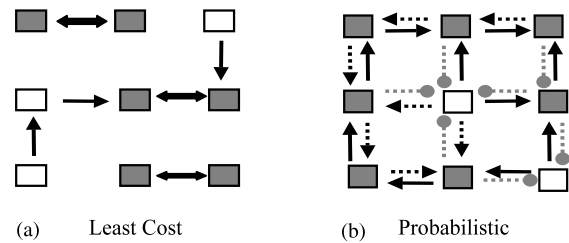

Fig. 3. Diagrammatic representation of occupancy patterns for (a) least-cost foragers and (b) probabilistic foragers. Solid black lines represent least-cost paths, dotted black lines represent paths of intermediate risk, and dotted gray lines with circles on the end represent high-risk paths.
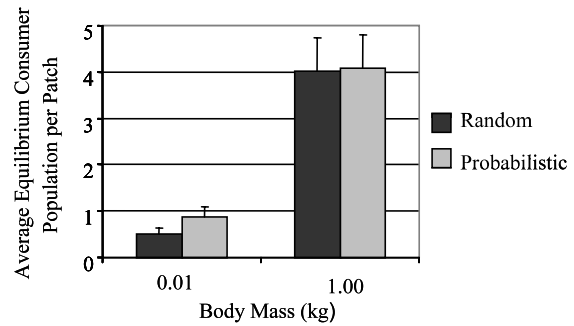

Fig. 4. Average consumer abundance per patch (± 1 S.E.) when average risk per path and the variation in average risk per path for the entire landscape was increased three-fold for 0.01 kg and 1 kg mammals at a distance factor of 30.

landscape explained 68% of the variation in local population density for consumer populations adopting behavioral and random movement rules (Table 2).

Patch occupancy

Patch occupancy was 100% for all simulations exhibiting random movement, except for the extinction of 0.01

Fig. 2. Average equilibrium consumer abundance (± 1 S.E.) per patch for hypothetical small-mammal consumers of five different body masses at three different distance factors and for random, probabilistic, and least-cost movement rules. Parameter values are $c = d = e = h = a = 1$, $r = 1/365$, $K = 8$.
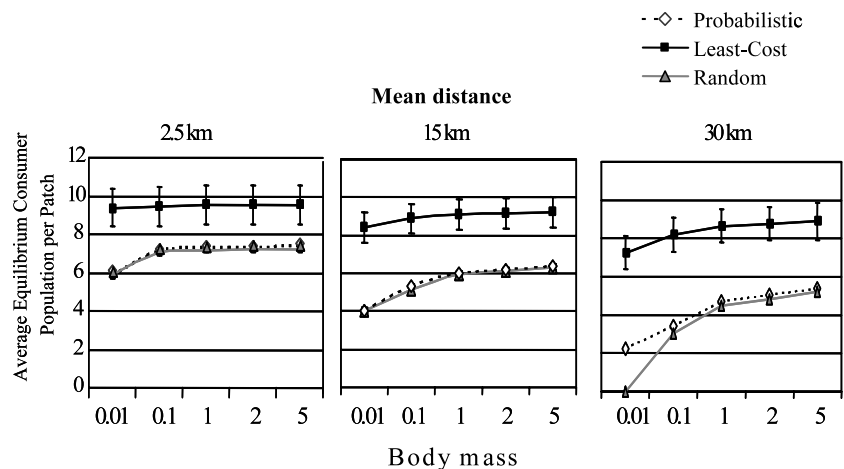
Table 2. Results of non-linear regression models for predicting the equilibrium density of consumers in patches, when patches vary in levels of hostility of the surrounding landscape and consumer populations differ in the movement rules adopted by individuals. Hostility refers to the average risk experienced by a consumer leaving a patch.

Non-linear (exponential regression)	Constant		Slope		R-square
	B	S.E.	B	S.E.	
All models	1.14	0.03	53.30	4.60	0.28
Probabilistic and random	0.88	0.01	38.80	1.87	0.68
Least-cost	1.46	0.08	57.00	10.83	0.16

kg animals at an average inter-patch distance of 30 km. Foragers exhibiting probabilistic behavior occupied 100% of the patches for all simulations except 0.01 (94% occupancy) and 0.1 (96% occupancy) kg animals at an average inter-patch distance of 30 km. Patches in probabilistic models were not paired, and individual patches became unoccupied without notably affecting surrounding patches. Populations whose members obeyed the least-cost rule occupied patches that were paired in sub-populations (Fig. 3). Therefore, both patches become unoccupied once one of the two in the pair went extinct as matrix hostility increases and migrants between the two patches perish. The percentage of patches occupied by consumer populations exhibiting least-cost movements was 65%, except for 0.01 kg animals at a mean path length of 30 km when patch occupancy was 61%.

The best-fit model for predicting patch occupancy using logistic regression based on results from all simulations included (1) the index of hostility of landscape elements surrounding a focal patch and (2) the type of movement rule employed by individuals. Both parameters were significant predictors of patch occupancy (Nagelkerke's $R^2 = 0.404$), and the model correctly classified 86% of patches (Table 3). When the model included only the results from simulations of populations using probabilistic and random movement rules, the fit improved ($R^2 = 0.44$, 95% of patches correctly classified), whereas the model including only occupancy data from least-cost populations provided a poor fit (Nagelkerke's $R^2 = 0.11$, 67% of patches correctly classified).

Distribution of riskiness

Landscapes with a single homogeneous landscape element around patches resulted in different distributions of forager density than landscapes in which risk was distributed non-randomly across the landscape. For populations using probabilistic movement rules, the average population per patch was lower in landscapes with a high-risk barrier separating less risky halves of the landscape than in landscapes of identical overall risk but with clumped or homogeneous distributions of landscape elements (Fig. 5a). In landscapes where risk was clumped into one area of high-risk paths and one of low-risk paths, average populations per patch were identical to populations in landscapes with homogeneous risk. However, the distribution of density across patches differed. Densities in the low-risk areas of the clumped-risk landscape were higher, and densities in high-risk areas were lower, than for corresponding local populations in a homogeneous landscape (Fig. 5b).

Model sensitivity

The sensitivity of average consumer density per patch to a 10% increase in body mass was lowest for least-cost foragers and highest for probabilistic foragers (Fig. 6). A 10% increase in average landscape risk always resulted in a negative change in average density of consumers per patch. As with changes in body mass, smaller mammal species seemed to be more sensitive to the changes. Overall, animals following probabilistic rules were the most sensitive to any changes.

Table 3. Logistic regression models for predicting patch occupancy of consumers. Hostility refers to the average risk experienced by a consumer leaving a patch.

Logistic regression	Probabilistic model		Least-cost model		Hostility		% Correct	Nagelkerke R-square	AIC
	B	S.E.	B	S.E.	B	S.E.			
All models	2.16	0.62	−1.84	0.26	−10.30	1.50	86	0.4	591
Probabilistic and random					−11.88	1.49	95	0.44	238
Least-cost					−76.50	19.90	67	0.11	362

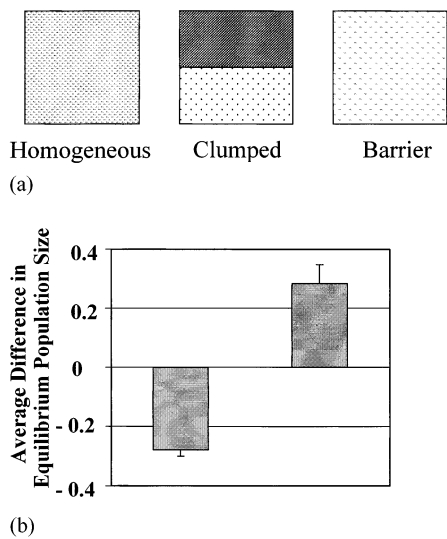Homogeneous   Clumped   Barrier

(a)

(b)

Fig. 5. Effects of varying the distribution of landscape elements, and thus risk of travel, on consumer populations. Simulated populations were of hypothetical small-mammal consumers adopting a probabilistic movement rule. (a) Diagrammatic representation of consumer density throughout the landscape. Dots represent relative numbers of consumers. Distributions of density were uniform for homogeneous and barrier landscapes but dichotomous for the clumped landscape. Overall density was highest in the uniform landscape. (b) Average differences (± 1 S.E.) in equilibrium consumer abundance between landscapes characterized by a clumped distribution of risk (low and high) and landscapes with a homogeneous distribution of risk.

Four different combinations of reproductive coefficients, c, and carrying capacities, K, were tested to reflect combinations of high and low carrying capacity and high and low growth rates. For all combinations, trends were identical to those observed with the original parameters. Least-cost foraging movements produced greater average consumer abundances per patch and

lower patch occupancies than any other movement rule. As expected, favorable conditions (high K and high c) produced the highest average consumer abundance per patch.

Discussion

In our simulated landscapes, the decision rules used by members of a population when traveling between patches affected both the abundance and distribution of the population. The conclusion that populations of least-cost (optimally) foraging consumers do the best is not surprising. However, the lower rate of patch occupancy and the ultimate establishment of paired populations that resulted from adoption of a least-cost strategy have interesting ecological implications. If animals perceive differences among pathways, selective choice among pathways may potentially create clumps of isolated patches in response to a landscape's structure rather than because of its structure. In other words, if a pathway between two habitable patches exists from a structural standpoint, but is not utilized for behavioral reasons, the pathway is in effect non-existent (Brooker et al. 1999, Haddad 1999).

If the majority of a population travels along one route emanating from a patch, (such as a corridor), the formation of an isolated sub-population is a likely outcome, potentially leading to increased rates of inbreeding and decreased resource quality. Bélisle and St. Clair (2001) observed that translocated birds were more likely to move parallel to barriers such as roads. They concluded that such directed movements could result in patches with exploitable resources remaining unoccupied. Moreover, environmental stochasticity may actually result in a lower persistence of metapopulations of optimal foragers if their least-cost movements between
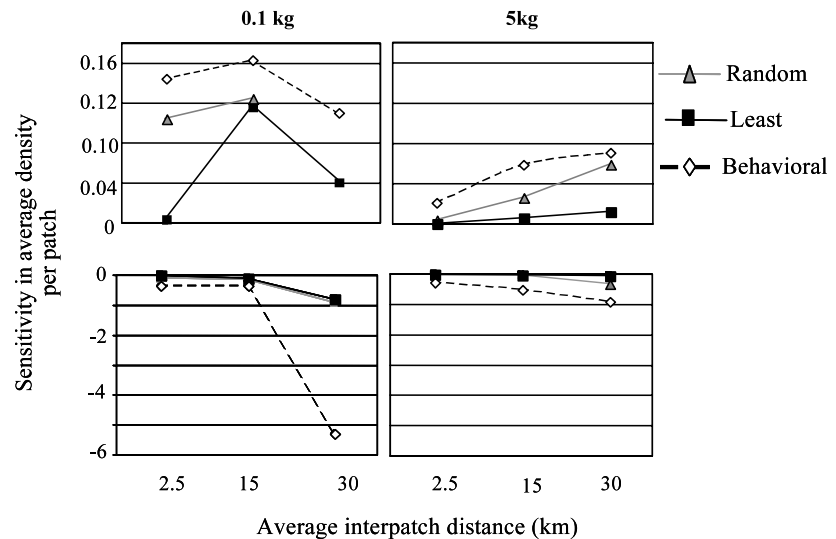

Fig. 6. Sensitivity of average consumer density per patch to a 10% change in a) body mass and b) average isolation of patches, for three levels of isolation and two body mass classes.

patches result in fewer occupied patches and hence a greater risk of simultaneous extinction of local populations. Whether the effect of lower occupancy is compensated for by increased population density would be an interesting topic for future research.

Patch occupancy for randomly moving populations reflected the dependence of a local population on all other patches in the landscape. If one patch was unoccupied due to high hostility levels in the area surrounding the patch, then all other patches in the landscape eventually became unoccupied as well. In contrast, foragers that followed behavioral rules created a more complex occupancy pattern, as patches dropped out seemingly independently and the remaining patches continued exchanging migrants between all other patches.

Presumably, animals do not always pick the least-cost path and occasionally may mistakenly or purposely choose a riskier path, depending on their level of information about the environment and their motivational state. Probabilistic movement rules attempt to take into account the possibility of an animal choosing a non-optimal path. Although the resulting populations were smaller on average when animals used probabilistic movement rules rather than optimal rules, patch occupancy was higher and all occupied patches were potentially connected to all other occupied patches. The detrimental effects of moving ignorantly (i.e. randomly) through the landscape were barely perceptible in our baseline simulations, except at the greatest mean inter-patch distance. Of course, the level of hostility of landscape elements plays a dominant role in determining densities and patch occupancy at equilibrium (Table 2 and 3). Our simulations were conducted using landscape elements through which movement was relatively safe, which minimized costs associated with choosing paths at random. However, populations of individuals adhering to the random rule were outperformed by those using the probabilistic rule as the overall riskiness of travel and the variation in interpatch quality were increased (Fig. 1). When the landscape-level risk and the variation between the least risky and the most risky interpatch types was increased threefold, the difference in the average population per patch using probabilistic and random movement rules becomes more dramatic for small animals (Fig. 4).

We assumed that animals travel at the maximum velocity while moving between patches, but this likely is not true for some species. The time taken to travel between two points is a function of the velocity of the organism, the tortuousity of the path taken, and the number of pauses during travel. Few studies, however, have addressed the movement speed of animals in a natural environment. Field observations of golden-mantled ground squirrels (*Spermophilus saturatus*) have suggested that these squirrels run at their maximum aerobic speeds to reduce exposure to predation while moving around their home range (Kenagy and Hoyt 1989). Maximum speeds were associated with straight-line movement between two points, intra-specific social interactions, and escape from predators.

Pausing during locomotion is often exhibited by small mammals. Lagos et al. (1995) determined that degus (*Octodon degus*) pathways between shrub habitats were straighter in the presence of predators than in the absence of predators. The velocity of movement and the pause duration of degus while traveling along bare ground runways were observed by Vasquez et al. (2002). Travel speed was faster, and pause durations were longer in open habitats, possibly due to the increased visibility of mobile degus to predators. Kramer and McLaughlin (2001) discussed the ways that animals adjust their speed, pausing frequency, and duration of travel in response to changing environmental conditions. These factors could easily be incorporated into our rules for inter-patch movement, given enough information.

Substantial increases in travel time between patches could increase the probability of starvation and alter the time of arrival at the new patch. Increases in starvation probability would obviously reduce the predicted density of consumers in a patch, however, in our model we focused on foraging behavior and P_s achieved a value of one only for animals less than 1 kg in landscapes with the farthest distances between patches. Extending the model to incorporate dispersal behavior would lead to increasing probabilities of starvation.

Lima and Dill (1990) identified predation risk as an important factor in determining small mammal behavior. We believe that including behavioral responses to changes in levels of risk should increase the predictive value of models incorporating animal movements. Rodríguez et al. (2001) determined that predation risk by pygmy owls (*Glaucidium passerinum*) was the primary deterrent to gap crossing frequency for four species of birds. Bright (1998) observed a similar gap avoidance in dormice (*Muscardinus avellanarius*) and attributed this aversion to the increased risk of predation associated with habitat gaps. To determine the responses of animals to large-scale variability in predation risk, the cues animals use when choosing among pathways should be investigated. For example, Joly et al. (2001) determined that in contrast to small mammals, salamanders appeared to lack the cognitive ability to travel around potentially hostile habitats such as cultivated fields, but instead traveled in a straight line between aquatic and terrestrial sites. For species that do exhibit preferences, their perspectives of hostile versus non-hostile pathways will vary depending on how the species perceives the landscape. In human landscapes consisting of a patchwork of habitat remnants of varying suitability surrounded by a complex of agricultural and residential elements of varying risk, not all paths will be equally appealing to all species. Understanding how animals

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make decisions regarding movement and incorporating behavioral decisions into population models is an important step for predicting the consequences of fragmentation for population persistence.

References

Aars, J., Johannesen, E. and Ims, R. A. 1999. Demographic consequences of movements in subdivided root vole populations. – Oikos 85: 204–216.

Åberg, J., Jansson, G., Swenson, J. E. and Angelstam, P. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. – Oecologia 103: 265–269.

Andersen, O., Crow, T. R., Lietz, S. M. and Stearns, F. 1996. Transformation of a landscape in the upper midwest, USA: the history of the lower St. Croix River Valley, 1830 to present. – Landscape Urban Plan. 35: 247–267.

Bélisle, M. and St. Clair, C. C. 2001. Cumulative effects of barriers on the movements of forest birds. – Conserv. Ecol. 5(2): 9. [online] URL: http://www.consecol.org/vol5/iss2/art9.

Bhattacharya, M., Primack, R. B. and Gerwein, J. 2003. Are roads and railroads barriers to bumblebee movement in a temperate suburban conservation area? – Biol. Conserv. 109: 37–45.

Bitterman, M. E. and Mackintosh, N. J. 1969. Habit reversal and probability learning: rats, birds, and fish. – In: Gilbert, R. M. and Sutherland, N. S. (eds), Animal discrimination learning. Academic Press, pp. 163–185.

Bowne, D. R., Peles, J. F. and Barrett, G. W. 1999. Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). – Landscape Ecol. 14: 53–65.

Bright, P. W. 1998. Behaviour of specialist species in habitat corridors: arboreal dormice avoid corridor gaps. – Anim. Behav. 56: 1485–1490.

Brooker, L., Brooker, M. and Cale, P. 1999. Animal dispersal in fragmented habitat: measuring habitat connectivity, corridor use, and dispersal mortality. – Conserv. Ecol. 3(1): 4. [online] URL: http://www.consecol.org/vol3/iss1/art4.

Calder, W. 1984. Size, function, and life history. – Harvard Univ. Press.

Collinge, S. K. 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. – Landscape Urban Plan. 36: 59–77.

Crist, T. O., Guertin, D. S., Wiens, J.A. and Milne, B. T. 1992. Animal movement in heterogeneous landscapes: an experiment with Eleodes beetles in short-grass prairie. – Funct. Ecol. 6: 536–544.

Debinski, D. M. and Holt, R. D. 2000. A survey and overview of habitat fragmentation experiments. – Conserv. Biol. 14: 342–355.

Dooley, J. L. and Bowers, M. A. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. – Ecology 79: 969–980.

Farina, A. 2000. The cultural landscape as a model for the integration of ecology and economics. – Bioscience 50: 313–320.

Fryxell, J. M. and Lundberg, P. 1998. Individual behavior and community dynamics. – Chapman and Hall.

Garland, T. 1983. The relation between maximal running speed and body mass in terrestrial mammals. – J. Zool. Lond. 199: 157–170.

Gustafson, E. J. and Gardner, R. H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. – Ecology 77: 94–107.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. – Am. Nat. 153: 215–227.

Hanski, I., Alho, J. and Moilanen, A. 2000. Estimating parameters of survival and migration of individuals in metapopulations. – Ecology 81: 239–251.

Henein, K., Wegner, J. and Merriam, G. 1998. Population effects of landscape model manipulation of two behaviourally different woodland small mammals. – Oikos 81: 168–186.

Hokit, D. G., Smith, B. M. and Branch, L. C. 1999. Effects of landscape structure in Florida scrub: a population perspective. – Ecol. Appl. 9: 124–134.

Ims, R. A. and Andreassen, H. P. 2000. Spatial synchronization of vole population dynamics by predatory birds. – Nature 9: 194–196.

Joly, P., Miaud, C., Lehmann, A. and Grolet, O. 2001. Habitat matrix effects on pond occupancy in newts. – Conserv. Biol. 15: 239–248.

Jonsen, I. D., Bourchier, R. S. and Roland, J. 2001. The influence of landscape habitat on Apthona flea beetle immigration to leafy spurge patches. – Oecologia 127: 287–294.

Kenagy, G. J. and Hoyt, D. F. 1989. Speed and time-energy budget for locomotion in golden-mantled ground squirrels. – Ecology 70: 1834–1839.

Kirk, K. L. and Bitterman, M. E. 1965. Probability-learning by the turtle. – Science 148: 1484–1485.

Kramer, D. L. and McLaughlin, R. L. 2001. The behavioral ecology of intermittent locomotion. – Am. Zool. 41: 137–153.

Lagos, V. O., Contreras, L. C., Meserve, P. L. et al. 1995. Effects of predation risk on space use by small mammals: a field experiment with a neotropical rodent. – Oikos 74: 259–264.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – Bull. Entomol. Soc. Am. 15: 237–240.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – Can. J. Zool. 68: 619–640.

Lindstet, S. L. and Boyce, M. S. 1985. Seasonality, fasting endurance and body size in mammals. – Am. Nat. 125: 873–878.

Longland, W. S. and Price, M. V. 1991. Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use? – Ecology 72: 2261–2273.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Nupp, T. E. and Swihart, R. K. 2000. Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. – J. Mammal. 81: 512–526.

Peltonen, A. and Hanski, I. 1991. Patterns of island occupancy explained by colonization and extinction rates in shrews. – Ecology 72: 1698–1708.

Pither, J. and Taylor, P. D. 1998. An experimental assessment of landscape connectivity. – Oikos 83: 166–174.

Pope, S. E., Fahrig, L. and Merriam, H. G. 2000. Landscape complementation and metapopulation effects on leopard frog populations. – Ecology 81: 2498–2508.

Rodríguez, A., Andrén, H. and Jansson, G. 2001. Habitat-mediated predation risk and decision making of small birds at forest edges. – Oikos 95: 383–396.

Saunders, D. A., Hobbs, R. J. and Margules, C. R. 1991. Biological consequences of ecosystem fragmentation: a review. – Conserv. Biol. 5: 18–32.

Schooley, R. L., Sharpe, P. B. and Van Horne, B. 1996. Can shrub cover increase predation risk for a desert rodent? – Can. J. Zool. 74: 157–163.

Sheperd, B. F. and Swihart, R. K. 1995. Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. – Can. J. Zool. 73: 2098–2105.

St. Clair, C. C., Bélisle, M., Desrochers, A. and Hannon, S. 1998. Winter responses of forest birds to habitat corridors and gaps. – Conserv. Ecol. 2(2): 13. [online] URL: http://www.consecol.org/vol2/iss2/art13.

Vandermeer, J. and Carvajal, R. 2001. Metapopulation dynamics and the quality of the landscape. – Am. Nat. 158: 211–220.

Vasquez, R. A., Ebensperger, L. A. and Bozinovic, F. 2002. The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. – Behav. Ecol. 13: 182–187.

Zollner, P. A. and Lima, S. L. 1999. Search strategies for landscape-level interpatch movements. – Ecology 80: 1019–1030.