

Simulating dispersal of reintroduced species within heterogeneous landscapes

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Abstract

This paper describes the development and application of a spatially explicit, individual based model of animal dispersal (J-walk) to determine the relative effects of landscape heterogeneity, prey availability, predation risk, and the energy requirements and behavior of dispersing organisms on dispersal success. Significant unknowns exist for the simulation of complex movement behavior within heterogeneous landscapes. Therefore, initial simulations with J-walk examined the relative effect of landscape patterns and species-specific characteristics on dispersal success. Differences in landscape pattern were simulated by random generation of fractal maps with average available energy (i.e. prey) and predation risk expressed as a function of habitat type. Variation in species-specific patterns were then simulated by a series of scenarios that varied the response of dispersing individuals to habitat heterogeneity, including: habitat selection to maximize energy intake, habitat selection to minimize predation risk, or habitat selection contingent on energy reserves. Results showed that significant shifts in dispersal could be related to (1) the unique spatial arrangement of habitat within each map, (2) changes in relative prey abundance, and (3) variation in the relationship between energy availability and predation risk. Hypothetical management scenarios were used to identify critical data needed to assure the persistence of reintroduced populations of American martens (*Martes americana*).

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1. Introduction

Dispersal is a critical process linking fragmented populations within heterogeneous landscapes (Fahrig and Merriam, 1985; Gustafson and Gardner, 1996; Schippers et al., 1996). Because dispersal connects populations that may be isolated by land-use change or habitat destruction (Bascompte and Rodriguez-Trelles,

1998; Lande, 1987; Lande et al., 1999; Peacock and Smith, 1997), the probability of metapopulation extinction may be significantly reduced by dispersal (Brown and Kodric-Brown, 1977). However, the unknowns associated with species-specific patterns of dispersal and the effects of landscape pattern on dispersal success make conservation and management recommendations (e.g. development of dispersal corridors) quite uncertain. The importance of these topics is well recognized with the relationship between dispersal and conservation design an active area of research (Banks, 1997; Bender et al., 1998; Collingham and Huntley, 2000; Dunning et al., 1995a).

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Although many studies of animal movement have been performed, much remains to be learned concerning landscape effects on dispersal success. A case in point is the American marten (*Martes americana*), which was extirpated from its former range in the north-central US in the early 1900s (Davis, 1983). Martens were successfully reintroduced into the Nicolet National Forest, Wisconsin, USA between 1975 and 1983 following the release of 172 animals. Subsequently, 85–90% of the released individuals were located within 19 km of their release sites (Bruce Kohn, personal communication). By 1994 the primary marten range was estimated to cover 775 km², with an additional 580 km² of peripheral range (James Ashenbrenner, personal communication). Although marten population densities in release areas within the Nicolet are thought to be increasing (John Wright, personal communication), the rate of range expansion has been <13 km per decade. Similar rates (8–16 km per decade) have been reported for marten refugia in Ontario (de Vos, 1951).

Understanding the reasons for these low rates of expansion may provide important insight into the dynamics of other reintroduced mammalian species. In the Nicolet case low expansion rates may be the result of spatial variability in required resources, existence of landscape barriers created by unsuitable habitat, or by the avoidance of areas occupied by potential competitors and predators such as the con-generic fisher, *Martes pennanti* (Krohn et al., 1995, 1997). If dispersal limitations for marten populations are related to habitat conditions then the spatial arrangement of habitat on the landscape may be a critical factor that must be understood to explain the population dynamics of these reintroduced species. Although dispersal is a common phenomenon in most mammalian species (Gaines and McClenaghan, 1980), successful dispersal is a relatively rare event that is difficult to observe, especially when population numbers are small. Telemetry of mobile organisms has been successful for describing movement and migration patterns of a variety of species (Baker, 1999; Gautestad and Mysterud, 1993; Siniff and Jessen, 1969) and telemetry studies of American martens have been performed in the Nicolet National Forest (Davis, 1983; Gilbert et al., 1997; Wright, 1999). However, these data have not provided adequate monitoring of the dispersal of juvenile individuals.

In spite of these unknowns and uncertainties—or perhaps because of them—a variety of simulation models has been developed to quantify the dispersal process within mammalian populations. Perhaps the simplest approach has been to ignore spatial effects by modeling movement as either a diffusive process (e.g. Andow et al., 1990; Okubo, 1980) or as simple transfer functions (e.g. Fahrig and Merriam, 1985; Murray, 1967). Although these models provide a synoptic picture of landscape dynamics without the need to consider the details of individual dispersal events—and the simplicity of these models allows analytical solutions to be developed (i.e. Waser, 1985)—they are not useful when populations are highly fragmented and dispersal success is affected by landscape patterns.

Individually based, spatially explicit models are often preferred when landscape effects dominate dispersal results (e.g. Dunning et al., 1995b; Greene and Johnson, 1992; Gustafson and Gardner, 1996; McCarthy, 1997; Wiegand et al., 1999; Schneider, 1997). Two broad categories of spatially explicit models may be identified: Those using vector-based algorithms to simulate movement as a correlated random walk (Kareiva, 1983; Lima et al., 1999; Marsh and Jones, 1988); and models using grid-based representations of landscapes to simulate the interaction of dispersing individuals with the landscape matrix (Allen et al., 1993; Gustafson and Gardner, 1996; Wiegand et al., 1999). The former category has been frequently used for organisms, such as insects, which do not continuously interact with the landscape while dispersing. The grid-based approach has been used to simulate species that move shorter distances per unit time and interact more strongly with landscape features (e.g. vertebrates and small mammals).

The objective of this paper is to present an individual-based, spatially explicit model of small mammal dispersal within heterogeneous landscapes. Our model, J-walk, considers the effects of spatial variability in habitat, variability in available energy (prey), and spatial variation in predation risk. In addition, J-walk allows a spectrum of individual dispersal strategies to be simulated with movement patterns affected by the activity level and physiological status of the dispersing individual. Because sufficient empirical information is not available for most small mammal species, J-walk was designed to evaluate the effect of alternative model assumptions on prediction results.

This paper describes the methods used in J-walk and examines the sensitivity of model results to variation in model inputs and parameters. A series of simulation experiments are then presented to identify those factors most important in determining dispersal success. Finally, simulations based on the American marten are performed to illustrate the potential of this model for management and conservation purposes.

2. Methods

2.1. Model description

2.1.1. Model overview

J-walk is a general model for simulating dispersal of a variety of vertebrate species. The following examples, and discussion of management and conservation implications, are illustrated by developing parameter values based on the dispersal of juvenile female American martens from their natal site to new, unoccupied home ranges. Simulations were initialized in J-walk by reading in a rectangular grid-cell habitat map and setting parameter variables that specified a particular dispersal scenario (Table 1). Program options allow actual landscape maps to be input or artificial landscapes to be generated. Habitat map values (sequential integers from 1 to n) were used as indices defining habitat quality, energy availability and predation risk. An ancillary map identified the location of suitable home range habitat for dispersing individuals. J-walk sequentially releases individuals from the center of the map, recording successful dispersal when the dispersing individual reached a new home range area. Interactions between dispersing individuals were not simulated in J-walk.

J-walk was written in Fortran 95 and compiled for Pentium processors running under either MS-DOS® or LINUX. Simulation of 10,000 dispersers on a 1024×1024 cell grid took between 30 min and 4 h on a 233 MHz processor. Processing time depends primarily on predation rates, with lower predation rates increasing the number of steps a disperser is likely to take.

2.1.2. Time step and movement rules

Two nested loops govern the simulated time in J-walk. The outer loop defines the number of active

hours per day, A , and the inner loop defines the maximum number of steps per hour, L . Together they determine the total number of map sites that an individual could potentially visit in a single day. The grain size of our maps was 100 m (area = 1 ha) with the default values for A and L (16 and 10, respectively; Table 1). Values for A and L were estimated from the maximum movement speed of 1 km/h for dispersing martens and set the maximum possible distance moved per day to $100 \text{ m} \times 16 \text{ h} \times 10 \text{ h}^{-1} = 16,000 \text{ m}$. Although this distance was large, it was consistent with measured movement rates: Davis (1983) found that 18% of daily movements of radio-collared martens in northern Wisconsin exceeded 3.2 km/day, with the longest movement being 22 km; and Marshall (1951) documented daily movements up to 14.5 km in Idaho.

The algorithm used to generate movement is technically defined as a directionally biased, first-order correlated random walk (BCRW). Models employing simple correlated random walk (CRW), which assume independence of parameters describing distance moved and turning angle, have been shown to be adequate descriptors of movement for many species (Andow et al., 1990; Kareiva, 1983). However, because CRW are individual-based models of diffusive movement (Okubo, 1980; Turchin, 1998), and do not usually consider fine-grained variability in landscape attributes, they are not effective descriptions of organisms that perceive landscape structure and have complex strategies for foraging and dispersal (Dunning et al., 1992; Greene and Johnson, 1992). Therefore, we included in J-walk a more complex movement algorithm which consists of a four step sequence: (1) selection of the preferred direction of movement; (2) calculation at each movement step of a random angle which deflects the direction of movement; (3) calculation of the probability of movement into each adjacent cell by the habitat characteristics of those cells; and (4) the random choice of cell-to-cell movements based on these adjusted probabilities. The details of these steps are:

Step 1: Individuals were released from the center of the map with the initial movement direction, d , randomly determined from 1 of 8 cardinal directions. These cardinal directions correspond to the locations of the 8 neighboring cells (numbered clockwise with the northern neighbor: 1 to the north-western neighbor: 8).

Table 1
Model parameters and control variables

Parameter or variable	Nominal value	Range of values tested
Movement control		
<i>L</i> , maximum number of steps taken per hour	10	Constant
<i>A</i> , number of active hours per day	16	12, 16, 18
<i>B</i> , vector of bias terms affecting probabilities of movement ^a	(See text)	Constant
<i>M</i> , vector of probability of movement to 8 adjacent neighbors	(See text)	Dynamic
<i>C</i> , standard deviation of change in turning angle	0.6	0.4, 0.6, 0.8
<i>J</i> , movement decision rules: <i>e</i> : maximize energy; <i>m</i> : minimize predation; <i>c</i> : conditional between energy gain and mortality	<i>e</i>	<i>e</i> , <i>m</i> , <i>c</i>
Energy and mortality		
<i>S</i> , number of days for starvation	5.0	2.0, 5.0, 7.0
<i>P</i> , range of probabilities of predation	0.00001–0.0001	Constant
<i>E</i> , vector of mean energy availability for each habitat type	5.0	Constant
<i>F</i> , energy reserve of dispersers	0.0–1.0	Dynamic
<i>G</i> , energy gain per unit time	$G = 1.0/AL$	Dynamic
<i>R</i> , rate of energy loss per unit time	$G = E_i/AL$	Dynamic
<i>N</i> , net energy gain	$G - R$	Dynamic
<i>Q</i> , relative energy availability	E/S	(See text)
<i>Y</i> , Predation rule ^b	<i>d</i>	<i>a</i> , <i>b</i> , <i>c</i> , <i>d</i> , <i>e</i> , <i>f</i>
Landscape descriptors		
Map dimensions (number of rows and columns)	1024 × 1024	Constant
<i>H</i> , map roughness parameter for generating fractal landscapes	0.5	0.1, 0.5, 0.9
<i>k</i> , number of levels of the midpoint displacement algorithm	10	Constant
<i>n</i> , number of habitat types	10	Constant
<i>t</i> , the vector relating habitat types to probability of movement	(See text)	Constant
Number of core range areas per map	8	Constant
Program control values		
Random number seed	–18798645	na
Number of individuals simulated	10000	Constant
Maximum number of days for simulating dispersal	90	Constant
Visualization (yes, no)	Yes, no	na
Output map of habitat sites visited by dispersing individuals	Yes, no	na

^a Bias terms are a set of weights which increase the probability of movement in the selected direction. See text for values.

^b Predation function choices (*Y*) are: *a*, linear increase; *b*, quadratic increase; *c*, exponential increase; *d*, linear decrease; *e*, quadratic decrease; *f*, exponential decrease (see Fig. 1).

Step 2: At each subsequent time step the movement direction, *d*, was deflected by a random angle selected from a normal distribution with mean: 0.0 and standard deviation, *C*, of either 0.4, 0.6 or 0.8. The units for *C* are the ordinal values of the 8 cardinal directions and correspond to 18, 27 and 36°, respectively. A deflection must be as large as ±1 (±45°) to shift the direction by 1 neighbor, ±2 (±90°) to shift directions by 2 neighbors, etc. The probability of a 1 neighbor shift is approximately 0.01 when *C* = 0.4; 0.1 when *C* = 0.6; and 0.21 when *C* = 0.8. A deflection as large as ±2 neighbors never occurred when *C* = 0.4, occurred with probability <0.01 when *C* = 0.6

and occurred with probability 0.01 when *C* = 0.8. A movement deflection by as much as ±3 neighbors in a single time step is vanishingly small for all values of *C* used in these simulations. The random angle was added to *d*, with the modified value of *d* used (step 4) to bias the probability of movement, *M*.

Step 3: The values of *M_i* are determined by the movement decision rule (*J*, Table 1), the current energy reserves (*F*) of the marten (Table 1), and the surrounding habitat types. Each rule evaluates the available energy (*E_i*) and the probability of predation (*P_i*) associated with the habitat types of the 8 neighboring cells (*i*) (values of *E_i* and *P_i* were determined on input

from the relative habitat suitability indices t , Table 1). For instance, the “energy maximization” rule ($J = e$, Table 1) produces probabilities that are a linear function of available energy with predation effects set to 0.0 (i.e. predation risk is ignored). Thus, when $J = e$, $M_i = E_i$. Conversely, the “predation minimization” rule ($J = m$, Table 1) produces probabilities of movement as an inverse linear function of the probability of predation with potential energy gain or loss ignored. Thus, when $J = m$, $M_i = 1.0 - P_i$. The “conditional” rule ($J = c$, Table 1) produces probabilities of movement that vary with the current energy reserves (F) of the marten, which may range from a minimum of 0.0 (starvation) to maximum of 1.0 (satiated). As energy reserves decline, the weight for the energy terms increase, such that $M_i = (1.0 - F)E_i + (1.0 - P_i)$. For all three rules, F was also used to determine if the individual remains on the current site and continues to forage. It is assumed that individual will not move if $F < 0.5$ and E_i is >1.0 (i.e. the animal is hungry and the available energy is in excess of metabolic requirements), but would move to another cell when $F > 0.5$. This feature causes movement patterns to vary with the physiological state of the dispersing individual.

Step 4: The probabilities of movement, M_i , to the 8 adjacent sites were then multiplied by the appropriate bias terms, b_i . The initial values of b (assuming $d = 1$) were: 2.0, 1.7, 1.0, 0.29, 0.1, 0.29, 1.0, and 1.7. The current value of d sets the degree of rotation of this vector so that the maximum bias term is always associated with the current direction of movement. The final probability of movement is the product of $M_i \times b_i$, normalized so that the sum equals 1.0. Movement was then determined by comparing a uniform random number to this final probability. Although there is a finite possibility of a dispersing individual to move to any adjacent cell, the small, independent random deflections in d produce a time-dependent correlated pattern typical of dispersing organisms (Turchin, 1998). Steps 2 and 3 are repeated for each time step producing a pattern of movement that seems realistic but, because sufficient data are not available, cannot be empirically verified.

2.1.3. Energy levels, starvation and predation

Rather than measure energy availability and consumption in absolute terms, we measured energy relative to the specified metabolic rate (all parameters

used here are estimated for the American marten). Metabolic rate is estimated from the number of days (S) it takes an individual to starve with no energy intake. The energy lost per day is equal $1.0/S$, and the rate of energy lost per unit of time, R , is equal $(1/S)[1/(AL)] = 1/(SAL)$. Thus, the rate of energy loss increases as A (the number of hours active per day) and L (the number of steps per hour) decrease, but total energy loss remains constant on a per day basis no matter what the values of A or L may be.

The mean energy available to a foraging individual is specified by the vector E , which varies by habitat type. For the simulations reported here, the energy available to a forager within habitat type i , E_i , was calculated by assuming that the ordinal values of habitat types represent a linear ranking of energy availability. Thus, $E_i = E(i - 1)/n$, where n is the number of habitat types. Thus, habitat type 1 supplies no energy (e.g. water bodies), causing martens to always avoid these habitats, while habitat type $i = n$ has maximal available energy. If $E = S$, that is, the ratio of E to S (i.e. Q , the Energy Availability Ratio) equals 1.0, and all habitat types are equally abundant, the energy requirements of individuals will be met or exceeded on exactly 1/2 of the landscape. Energy gain per unit time (G) for a forager in habitat type i is $G = E_i/(AL)$. Net energy gain (N) was calculated at each time step by $N = G - R$. Net energy gain was added to the current energy reserve (F) of the dispersing individual at each time step. Starvation occurs whenever $F = 0.0$. Energy gain by foraging individuals does not change the amount of energy available in that cell.

Dispersing individuals are often highly susceptible to predation (Garrett and Franklin, 1988; Sakai and Noon, 1997). However, the type of predator (i.e. avian or mammalian) is often spatially variable with presence/abundance levels uncertain. Therefore, six functions were developed to represent these uncertainties by assigning predation probabilities (P_i) to each habitat type (Fig. 1): three functions positively associated predation risk with energy availability and three negatively associated predation risk with energy availability. Positive relationships describe scenarios where habitats with easily exploited prey also provide good habitat for predators. Negative relationships describe situations where habitat that lacks sufficient prey also provides good protection for predators. Mortality was randomly determined at each time step by comparing

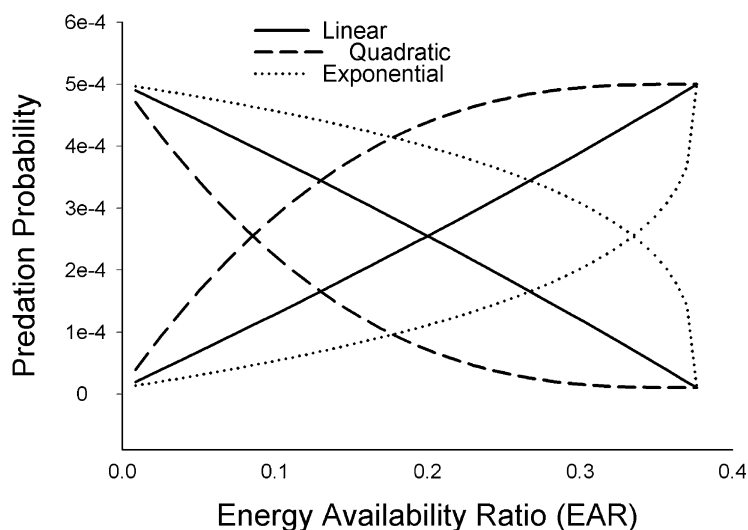


Fig. 1. Comparison of the six alternative predation rules showing the direction and rate of change in predation as a function of the energy availability of each habitat type.

a uniform random deviate to the probability of predation (P_i) associated with the habitat type (i) of the current cell.

2.1.4. Recording outcome of dispersal

The simulation of dispersal was terminated when any one of five conditions occurred: (1) the dispersing individual successfully reached a new home range area (described below), (2) the dispersing individual starved ($F = 0.0$), (3) the dispersing individual was killed by predation, (4) the dispersing individual reached the edge of the map without locating a new home range, or (5) the time limit set by the model (90 simulated days) was exceeded. For each of these conditions the model recorded: (1) the average energy values (E_i) and predation risk (P_i) of cells visited, (2) the energy reserve (F) of the dispersing individual, (3) the number of simulated days before the individual met its fate, and (4) the habitat type of starvation or predation events. For all individuals (regardless of fate) the model recorded the average distance moved per day by calculation of the straight-line distance between the disperser's location at the start and end of each day. J-walk has the capability of simulating the release and dispersal between any combination of home range areas, although results reported here only concern release from the center of the map. During

simulation, the path taken by a dispersing individual was displayed on the habitat map, and the current energy reserve (F) was graphically updated at each time step. J-walk also produced a map of the cumulative number of times each cell was visited by successfully dispersing individuals, which allows visualization of how dispersers have interacted with the landscape.

2.2. Generation of artificial landscapes

The use of artificial landscapes allows the effect of landscape heterogeneity on the pattern of movement and dispersal success to be systematically explored (Dale and Gardner, 1987; With et al., 1997). Each gridded habitat map was generated by RULE (Gardner, 1999) with 1024 rows and columns (1,048,576 total grid sites). Grid sites were assumed to be 100 m on a side (area = 1 ha each) giving a total map area of 10,486 km². Each map was composed of 10 habitat types of equal area (1048.6 km²). Habitat type 1 was assumed to be poor habitat, while type 10 was assumed to be excellent habitat. The ordinal values of the remaining habitat types were regarded as a linear ranking of habitat quality.

Fractal maps were generated by RULE by the midpoint displacement algorithm (Saupe, 1988), which created a map of real numbers by iterative interpo-

lation to locate the midpoint of a line, perturbation of the midpoint by a Gaussian random value (GRV), and successive reductions of the variance of the GRV. Three parameters are used by RULE to control the generation of fractal maps: (1) k , the “number of levels” or iterations of the midpoint displacement algorithm (the size of the map is always equal to 2^k); (2) H , the parameter which controls the rate of reduction of the GRV in successive iterations of the midpoint displacement method; and (3) the number, m , and proportion, p_i , of habitat types. For further details regarding the use of fractal maps see Plotnick and Gardner (Plotnick, 1993), Pearson and Gardner (1997) and With et al. (1997). RULE may be downloaded from <http://www.al.umces.edu/faculty/bobgardner.html>.

Maps used for these simulations were generated by setting $k = 10$, $H = 0.1, 0.5$, or 0.9 , and $m = 10$ with $p_1 \dots p_{10} = 0.1$. The value of H affects the autocorrelation of adjacent habitat types. RULE sets the variance of the GRV to 1.0, making the variance between grid points separated by distance x approximately equal to x^{2H} . When $H > 0.5$ the landscape appears quite smooth because the habitat types of adjacent map sites are positively correlated, resulting in large, contiguous habitat areas. When $H < 0.5$ the map sites are negatively correlated, and the landscapes appear rough and irregular. If the same random number seed is used to generate maps with different values of H , then the key difference between maps will be the degree of correlation, or roughness, between adjacent habitat types (Fig. 2). We have taken advantage of this property by generating maps in triplicate by selecting a unique random number seed and then set-

ting $H = 0.1, 0.5$ or 0.9 . Ten triplicate map sets (total of 30 maps) were used in the simulations reported here.

Because the spatial configuration of suitable home range habitat (core areas) has a significant effect on dispersal success (Gustafson and Gardner, 1996), the configuration of core area was held constant for all simulations. Eight core areas, square in shape and arranged in an arc equidistant from the center and edges of the map, were used as target areas for dispersal. The core areas were equal to 256 ha, the size of an average female marten home range in northern Wisconsin (Wright, 1999). For simulations reported here, all individuals were individually released from a single cell (1 ha) at the center of the map.

2.3. Simulations

2.3.1. Effect of parameter variation

A series of simulation experiments were conducted to examine the sensitivity of model predictions to a range of possible parameter values. A selected subset of model parameters that directly affect movement patterns (e.g. A , C , Q , J , and Y) were individually varied (Table 2) and the movement of 10,000 individuals were simulated on 10 fractal maps with $H = 0.5$. The percent of individuals meeting each dispersal fate, the average distance moved each day, and the average energy reserves of dispersing individuals were recorded and ANOVA used to determine the importance of landscape features and variation in model parameters on dispersal success. We also ran additional simulations to investigate possible interactions between Q and J .

2.3.2. Effect of landscape pattern

To investigate the effect of landscape pattern on marten movement, we performed a second series of simulations on 10 replicate sets of landscapes with levels of H set to 0.1, 0.5, and 0.9 (a total of 30 maps). The spatial pattern of the fractal maps was analyzed by RULE (Gardner, 1999), which identified habitat clusters using the next-nearest neighbor rule. We selected four measures of pattern that were relevant to simulated marten dispersal. The metrics were: the total number of clusters (Z) as a measure of patchiness; W , the average number of neighbors per pixel that are of a different habitat type; V , the area-weighted average

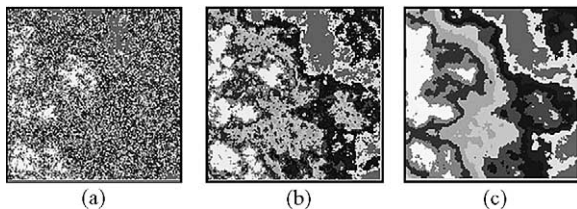


Fig. 2. Illustration of a single iteration of the three types of fractal maps used in the simulations. All maps were generated by RULE with 1024 rows and columns (1,048,576 total grid sites) using the same random number seed. Each map iteration differs only in roughness, H : (a) 0.1; (b) 0.5; and (c) 0.9. Each grid site corresponds to 1 ha, with a total of 10 replicate maps were used in the simulations.

Table 2

Mean and coefficient of variation (in parenthesis) of the effect of individual parameter perturbations on percent starved (%Starved), percent killed (%Killed), percent successfully dispersed (%Dispersed), the mean daily displacement (mean displace), and the mean energy level (mean energy) of dispersing juveniles

Simulation case ^a	%Starved	%Killed	%Dispersed	Mean displace	Mean energy
Base case	22.6 (109.0)	25.9 (3.0)	6.9 (74.2)	1458.4 (38.8)	0.75 (34.5)
A = 12	25.8 (109.6)	20.6 (35.6)	4.3 (73.5)	1295.0 (37.7)	0.75 (35.7)
A = 18	21.7 (107.8)	28.3 (32.1)	8.4 (70.7)	1534.2 (39.2)	0.75 (33.8)
J = M	31.2 (94.3)	24.6 (38.5)	6.6 (84.9)	1447.8 (36.9)	0.72 (36.4)
J = C	29.7 (95.1)	25.0 (38.4)	6.6 (85.0)	1431.8 (36.9)	0.72 (36.3)
Q = 1.4	10.2 (129.3)	38.9 (16.4)	10.3 (26.9)	1900.0 (5.7)	0.91 (11.7)
Q = 0.4	97.5 (0.5)	2.5 (19.1)	0	1866.8 (5.8)	0.34 (21.8)
C = 0.4	24.4 (95.4)	24.9 (31.8)	13.8 (72.5)	1769.5 (39.1)	0.74 (33.3)
C = 0.8	21.9 (115.5)	26.0 (34.4)	4.4 (71.5)	1316.5 (38.9)	0.76 (34.9)
Y = a	23.9 (113.4)	36.6 (80.7)	4.6 (64.8)	1444.9 (39.5)	0.75 (35.1)
Y = b	22.7 (114.9)	49.1 (56.9)	3.8 (69.1)	1444.8 (40.0)	0.75 (35.1)
Y = c	25.2 (109.4)	30.4 (68.2)	6.0 (66.7)	1448.7 (39.3)	0.75 (34.5)
Y = e	25.2 (109.4)	30.4 (68.2)	6.0 (66.8)	1448.7 (39.3)	0.75 (34.5)
Y = f	24.1 (106.6)	14.3 (32.2)	8.3 (75.1)	1453.9 (39.1)	0.75 (34.6)

^a Base case refers to a simulation with all parameters set at their nominal value. J and Y refer to decision and predation rule, respectively. All perturbation experiments were performed on random fractal maps with $H = 0.5$. See Table 1 for parameter and variable definitions.

size of each habitat patch; and X, the average correlation length of each habitat cluster (Gardner, 1999). Z and W estimate of the frequency with which dispersing individuals encounter different habitat types while V and X estimate differences in the size of these clusters between map types. Ten thousand individuals were simulated on each landscape and the percent of individuals meeting each dispersal fate, the mean distance moved each day, and the mean energy reserves of dispersing individuals were recorded. Simple correlations between descriptors of landscape pattern and model predictions of dispersal were calculated, and the effect of landscape pattern on dispersal success analyzed using ANOVA. All statistical analyses were conducted using SAS (SAS, 2001).

2.3.3. A management scenario

An example of the use of J-walk for a hypothetical forest management scenario was constructed by creating a marten habitat map for part of Wisconsin's Nicolet National Forest (NNF). An index of habitat suitability was generated from logistic regression of marten radio telemetry data collected by Wright (1999) on the NNF. The logistic regression estimated the probability of marten use of forest stands as a function of forest type, mean tree size (dbh), and degree of canopy closure. These data were obtained

from stand records maintained by the NNF. Marten presence/absence data were collected in 1016 separate forest stands within the NNF: martens were never observed in 715 of these stands, while 301 stands had at least one marten observation. The fit of the logistic model was satisfactory ($-2 \log \text{Likelihood ratio}$; $\chi^2 = 107.5$), with 6 degrees of freedom and $P < 0.0001$. The logistic equation was then applied to each 1 ha cell of the 58,596 ha portion of the NNF to create 61 classes of habitat suitability. Patches of suitable habitat (i.e. marten core areas) were arbitrarily identified as sites where the probability of marten observance, as estimated by the logistic equation, exceeded 0.54.

A second map, simulating management modification of 2 marten core areas, was created by reducing the habitat quality within 2 core areas (i.e. Q, the relative energy availability) to less than 0.1. The unmodified and modified forest scenario maps had 27.1 and 24%, respectively, sites with a Q value greater than 0.5. Simulations were performed on both maps by the release of 10,000 martens from a central core area. With the exception of the map alterations, all other parameters were as given in Table 1. The proportion of martens successfully emigrating to other core areas was recorded, and the visualization of the simulations was used to inspect the spatial details of marten movement.

3. Results

3.1. Effect of parameter variation

Table 2 reports changes in the percent of dispersing juveniles that starved (%Starved), were killed (%Killed), successfully dispersed (%Dispersed), as well as the mean distance moved per day and mean energy reserves as a consequence of individual perturbations of model parameters (Table 1). The base case (all parameters set to their nominal value) resulted in 25.9% of the simulated dispersers killed by predation, 22.6% starved and 6.9% successfully dispersed (Table 2). Very few individuals (<0.02%) reached the edge of the map during the 90-day simulations. The remaining simulations (45.6%) were terminated after 90 days. The percentage of individuals starving was most affected by Q , the energy availability ratio. When $Q = 1.4$, the percent starvation was the lowest of all cases (10.2%), but when $Q = 0.4$, the percent starvation was the highest (97.5%) of all cases (Table 2). All other parameter perturbations increased the starvation rate over the base case. The percent starvation was highly variable across all perturbation experiments (i.e. the coefficient of variation: 100%), except when $Q = 0.4$ and most individuals starved (coefficient of variation: 0.5%).

The percent of individuals killed was lowest when starvation was highest ($Q = 0.4$) and highest when $Q = 1.4$ (Table 2), reflecting the assumed independence of these two processes. The rule $Y = b$, representing a quadratic increase in the probability of predation with greater probability of prey availability (Fig. 1), results in greatest percentage of individuals killed (49.1%).

The percent of individuals successfully dispersing was at a minimum when $Q = 0.4$ and at a maximum when $C = 0.4$. Inspection of the visualization of movement of dispersers showed that lower values of C , which governs the degree of change in movement direction (Table 1), results in a tendency for dispersers to ignore the fine-grained details of the map and simply “forge ahead” even though local landscape characteristics may be unsuitable. The percentage of simulated dispersers that successfully dispersed was also higher than the base case when $Q = 1.4$, $Y = f$ and $A = 18$ (Table 2). Longer activity periods, greater landscape productivity relative to marten star-

vation rates, and predation rates inversely related to habitat suitability all favor higher average daily displacement and consequently greater rate of successful dispersal.

The percentage of dispersers that either starved, were killed, or successfully dispersed exhibited a threshold effect when $Q \approx 0.5$ (Fig. 3). Variability in

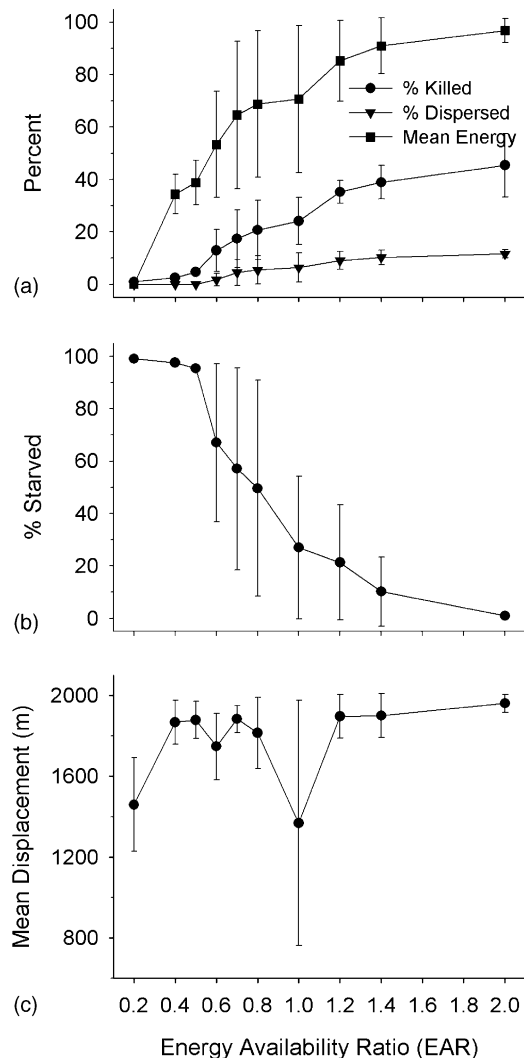


Fig. 3. Changes in the percentage of simulated dispersers either killed or dispersed (a), or starved (b) as a function of the energy availability ratio (Q) when model parameters were set at base case levels (Table 1). Part (a) shows the change in the mean energy reserves of dispersing individuals and (c) shows the mean distance moved per day as a function of Q .

each dispersal fate was high when $0.6 < Q < 1.2$ and the average energy reserves of dispersers increased rapidly over this interval. The average distance moved per day was relatively stable when $Q > 0.4$ except for a curious drop associated with high variability when $Q = 1.0$ (Fig. 3). Taken together it would appear that movement patterns below an Q of 1.0 are directed toward energy acquisition, while above 1.0 individuals are dispersing—and also experiencing a greater risk of predation. The reason for the high variability in dispersal success when $Q = 1.0$ (Fig. 3c) is uncertain, but possibly reflects interactions between variable energy supplies and the switch from energy acquisition to dispersal that occur at this point.

The predation rule, Y , had a profound effect on the predicted fate of dispersing individuals. The most straightforward comparison was between the linear functions (Y : a , linear increase; d , linear decrease, Fig. 4). A linear decrease in the risk of predation within more suitable habitat resulted in greater dispersal and fewer individuals killed by predation. When predation risk was positively associated with energy availability (“increasing” functions, Fig. 1), dispersal success was generally less and predation higher (Fig. 4). Note that the “quadratic increasing” and “exponential decreasing” functions (Fig. 1) produce relatively high predation probabilities over a broader range of energy availability values, resulting in higher mean predation rates (Fig. 4). The effect of movement decision rule, J , varied by fate (Fig. 4). As expected, the “maximize energy” rule resulted in the lowest starvation rates and the “minimize mortality” rule produced the lowest predation rates (marginally). When J was set to the “conditional” rule there was less starvation than the “minimize predation” rule ($J = m$, Table 1), but dispersal success did not increase and lower average energy reserves were observed than for the “minimize predation” rule, which ignores energy status entirely. Different movement decision rules produced only marginally different dispersal success rates. Average energy reserves were highest when J was set to e , the “maximize energy” rule.

3.2. Patterns of simulated landscapes and their effect on dispersal

The four landscape metrics (Table 3) show that the fractal maps have substantially different patterns. The

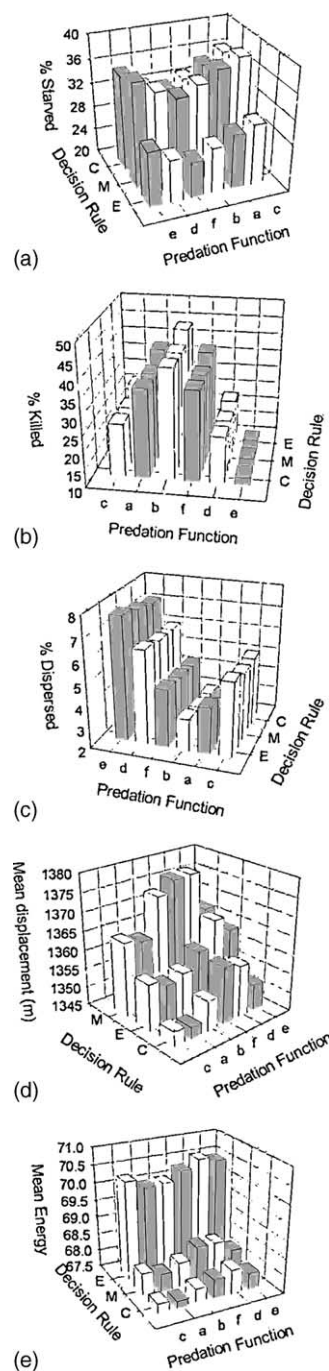


Fig. 4. Changes in the percentage of simulated dispersers that either starved (a), were killed (b) or successfully dispersed (c) as a function of the movement decision rule (E , M , or C) or the predation function (see Table 1). The mean energy reserves (d) and the mean distance moved per day (e) are also illustrated.

Table 3
Characterization of spatial pattern of landscape maps used in the simulations^a

Index ^b	Mean	Standard deviation	Coefficient of variation	Minimum	Maximum
<i>H</i> = 0.1					
Z	272695.7	25647.5	9.4	240540.0	304646.0
W	5.40	0.14	2.66	5.22	5.60
V	2001.9	1121.1	56.0	386.9	4020.9
X	20.9	4.8	23.2	12.2	28.0
<i>H</i> = 0.5					
Z	22948.7	4454.6	19.4	16692.0	30075.0
W	1.69	0.32	18.5	1.26	2.21
V	35732.6	13189.7	36.9	17313.9	55574.7
X	207.9	40.7	19.5	153.2	257.9
<i>H</i> = 0.9					
Z	1547.9	290.9	18.8	947.0	2014.0
W	0.28	0.04	15.6	0.21	0.36
V	68793.0	9630.9	13.9	555048.2	81837.7
X	243.2	18.0	7.4	213.7	262.5

^a Ten fractal maps with *H* = 0.1, 0.5 and 0.9 were generated and analyzed using RULE (Gardner, 1999). Each map had 10 habitat types of equal abundance. Map dimensions were 1024 rows and columns. See text for additional details.

^b Pattern indices are: Z: total number of habitat clusters per map; W: average amount of edge per pixel; V: area-weighted average cluster size; X: correlation length. Statistics are reported in map units, with each map unit (pixel) equal to 1 ha.

total number of clusters (*Z*) and the amount of edge per pixel (*W*) decrease by a factor of 176 and 19, respectively, from *H* = 0.1 to 0.9 (Table 3). Conversely, the area-weighted average size (*V*) and the correlation length of the clusters (*X*) increase by factors of 34 and 11 from *H* = 0.1 to 0.9. Because *H* controls the degree of autocorrelation of landscape pattern, maps with higher values of *H* have fewer clusters of larger size and less edge than maps with lower values of *H* (Fig. 2). As expected, all four landscape metrics are highly correlated with *H* (*Z*: *r* = −0.89; *W*: *r* = −0.96; *V*: *r* = 0.95; and *X*: *r* = 0.9). Most landscape indices are correlated with one another (Riitters et al., 1995). Therefore, it is not surprising that the correlation among these four indices was also high.

The results presented in Table 4 show that starvation was lowest (0.5%) and the percent killed was highest (37.6%) when *H* = 0.1. Percent starvation increased to 33.9% and the percent killed decreased to 23.7% when *H* = 0.9. Because map patterns are rougher (i.e. negatively correlated) when *H* < 0.5, a dispersing individual was more likely to encounter a variety of habitat types within a short distance than when *H* > 0.5. Clearly, the differences in roughness between map types affects, in turn, the fate of dispers-

ing individuals. Surprisingly the degree of success of dispersing individuals was not related to *H* (Table 4). Although the average displacement of a dispersing individual was highest when *H* = 0.9, this attribute is highly variable between map types and these small differences did not appear to be significant. The average energy reserves of dispersing individuals decreases by 14% from *H* = 0.1 to 0.9 (Table 4).

Table 5 presents an ANOVA of the individual parameter perturbation experiments. The variance in model predictions accounted for by the parameters we varied (*Q*, map replicate, *C*, *A* and *Y*) ranged from a minimum of 66% (percent killed) to a maximum of 84% (percent starved and mean energy level). *Q*, the energy availability ratio, was the most important variable in the ANOVA for percent starved, percent dispersed and the mean energy level. Map replicate, which measures map-to-map differences in landscape pattern, was the next most important determinant of variability in dispersal success. *C*, the standard deviation of the turning angle, which affects the pattern of tortuosity of the movement pattern across the landscape, was also significantly related to mean daily displacement and dispersal success. The predation rule (Fig. 1) affected the percent of individuals either killed or successfully dispersing, but was not related

Table 4

Results of 10,000 simulated individuals within three different types of random landscapes^a

Model predictions ^b	Mean	Standard deviation	Coefficient of variation	Minimum	Maximum
<i>H</i> = 0.1					
%Starved	0.5	0.739	148.4	0	1.8
%Killed	37.6	5.76	15.3	25.5	45.1
%Dispersed	6.84	2.90	42.5	1.68	10.8
%Edge	0.03	0.013	47.0	0	0.04
Mean displace	1503.2	417.0	27.7	752.0	1950.0
Mean energy	0.836	0.148	17.7	0.58	0.987
<i>H</i> = 0.5					
%Starved	22.6	24.7	109.0	0.87	66.9
%Killed	25.9	8.56	33.0	14.3	37.0
%Dispersed	6.92	5.14	74.2	0.16	12.7
%Edge	0.02	0.014	63.6	0	0.04
Mean displace	1458.0	566.4	38.8	761.2	1983.0
Mean energy	0.751	0.259	34.4	0.441	0.991
<i>H</i> = 0.9					
%Starved	33.9	36.0	106.2	0.94	90.6
%Killed	23.7	9.89	41.7	9.35	38.9
%Dispersed	6.79	6.26	92.0	0	13.4
%Edge	0.03	0.02	84.9	0	0.07
Mean displace	1592.7	491.1	30.8	903.9	1990.3
Mean energy	0.701	0.303	43.21	0.367	0.993

^a Ten fractal maps with *H* = 0.1, 0.5 and 0.9 generated with RULE (Gardner, 1999) were used in the simulations. The patterns of these landscapes are reported in Table 3.

^b The recorded fates of dispersing individuals were: %Starved: percent of individuals starving; %Killed: percent of individuals dying by predation; %Dispersed: percent of individuals successfully dispersing; %Edge: percent of individuals reaching edge of map. The average displacement (mean displace) and average energy level (mean energy) were also recorded.

Table 5

F-values from an analysis of variance of dispersal success

Source of variation ^a	d.f.	Dependent variables ^b				
		%Starved	%Killed	%Dispersed	Mean displace	Mean energy
Map replicate	9	103.8***	12.1***	46.2***	110.1***	186.7***
<i>Q</i>	2	661.5***	27.5***	49.2***	48.9***	221.1***
<i>A</i>	2	0.9	2.6*	7.3***	5.2**	0.1
<i>C</i>	2	0.9	1.4	52.1***	18.5***	0.4
<i>Y</i>	4	0.8	13.1***	4.8***	0.0	0.2
<i>J</i>	2	3.2*	0.0	0.1	0.1	0.7
Error ^c	129	(2.06E1)	(1.47E–2)	(5.77E–4)	(3.18E4)	(4.16E–3)
<i>R</i> ²		0.95	0.66	0.85	0.91	0.95

Results are based on 10,000 simulated martens on 10 fractal maps with *H* = 0.5. The asterisks by the *F*-values indicate the level of significance: **P* ≤ 0.05; ***P* ≤ 0.01 and ****P* ≤ 0.001.

^a The dependent variables in the ANOVA are: map replicate: the iteration number of the randomly generated maps; definitions of other parameters may be found in Table 1.

^b The recorded fates of dispersing martens were: %Starved (percent of individuals starving), %Killed (percent of individuals dying by predation), and %Dispersed (percent of individuals successfully dispersing) were arcsine transformed before analysis by the SAS GLM procedure (SAS, 2001). The average displacement (mean displace) and average energy level (mean energy) were also recorded.

^c The mean squared error is shown in parenthesis.

Table 6

Correlations between landscape descriptors and dispersal for 10,000 simulations on 10 replicates each of maps with $H = 0.1$, 0.5 and 0.9

Model predictions	Landscape descriptors ^a				
	Z	W	V	X	H
%Starved	−0.47**	−0.51**	0.59***	0.53**	0.49**
%Killed	0.64***	0.64***	−0.63***	−0.66***	−0.57***
%Dispersed	0.007	0.02	−0.13	−0.07	−0.002
Mean displace	0.003	−0.02	−0.03	−0.03	0.08
Mean energy	0.25	0.26	−0.36*	−0.30	−0.23

^a Pattern indices are: Z: total number of habitat clusters per map; W: average amount of edge per pixel; V: area-weighted average cluster size; X: average correlation length of all habitat patches. Significance values of correlation coefficients are indicated by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

to the other model predictions (Table 5). J , the movement decision rule that governs the habitat choices of the dispersing individuals was weakly related to the percentage starved, and not significantly related to any of the other model predictors. Surprisingly, A , the number of hours that individuals were active, was not significantly related to any of the model predictions.

The ANOVA results reported in Table 5 show that systematic differences in maps (e.g. map replicate) were significantly related to model predictions (Table 5). The individual parameter perturbation experiments reported in this ANOVA were performed on 10 replicates of a single map type (i.e. a fractal

map with $H = 0.5$). To test the effect on dispersal of different spatial arrangements of habitat within fractal maps, a second set of simulations was performed with 10 map replicates with H set to 0.1 and 0.9 with all parameters set to their nominal values (Table 1). A comparison of the individual landscape metrics showed that the percent of dispersing individuals starved or killed was significantly related to differences in landscape patterns but dispersal success and mean daily displacement were unrelated to any of the landscape metrics (Table 6). This result is surprising because the algorithm used in the model simulates movement steps that are biased by local habitat characteristics. One might assume, therefore, that the size and arrangement of habitat, which varies with H , would significantly affect dispersal as well as mortality.

An ANOVA of the simulations performed on the three types of fractal maps (Table 7) provides additional insight into this apparent contradiction. Indeed, individual differences between maps (i.e. differences between map triplicates) was the most significant variable predicting dispersal success. However, when a landscape metric was added to the ANOVA (e.g. the total number of habitat clusters on the map), landscape pattern, adjusted for differences in map replicate, was also significant. These two variables, map replicate and total clusters, clearly indicate that the success of dispersing individuals is dependent on landscape pattern. However, although mortality (percent starved and

Table 7

F-values from an analysis of variation of landscape effects on dispersal success

Source of variation ^a	d.f.	Dependent variables ^b				
		%Starved	%Killed	%Dispersed	Mean displace	Mean energy
H	2	8.8**	15.1***	0.0	0.6	3.3
Map replicate	9	3.8**	3.5**	12.8***	7.7***	10.5***
Z	1	3.4	0.0	9.4***	0.8	1.6
Error ^c	17	(4.17E−2)	(4.1E−7)	(4.73E−4)	(7.64E4)	(1.42E2)
R^2		0.76	0.78	0.88	0.80	0.85

ANOVA results were performed using a general linear model (SAS, 2001) on the simulated dispersal of 10,000 martens on 10 replicate fractal maps with H set to 0.1, 0.5 and 0.9 (total of 30 maps) and all model parameters set to their nominal value (Table 1). The asterisks by the F-values indicate the level of significance: * $P \leq 0.05$; ** $P \leq 0.01$ and *** $P \leq 0.001$.

^a The dependent variables in the ANOVA are: map replicate: the iteration number of the randomly generated maps; H : the roughness parameter used to generated the fractal maps; and Z: the total number of habitat clusters on the map.

^b The recorded fates of dispersing martens were: %Starved (percent of individuals starving). %Killed (percent of individuals dying by predation), and %Dispersed (percent of individuals successfully dispersing) were arcsine transformed before analysis by the SAS GLM procedure (SAS, 2001). The average displacement (mean displace) and average energy level (mean energy) were also recorded.

^c The mean squared error is shown in parenthesis.

Table 8

Simulation changes in marten percent dispersal success and percent mortality in the Nicolet National Forest due to habitat modification

Core area ^a	Percent dispersal success	
	Unmodified habitat map	Modified habitat map ^b
1	0.01	0.0
2	2.2	12.7
3	6.9	9.0
4	0.6	5.9
5	33.8	–
6	0.01	0.0
7	6.3	7.6
9	0.8	9.9
10	22.0	–
11	0.07	3.0
12	1.7	2.0
Total	74.2	50.2
Percent mortality		
%Starved	2.7	5.6
%Killed	11.9	21.7
Total	14.6	27.3

^a Virtual martens were released from core area 8 and the percentage of martens successfully reaching other core areas were recorded.

^b The habitat quality of core areas 5 and 10 was modified making them unsuitable for marten residence. See text for additional details.

killed) was significantly related to H , there was very little difference in dispersal success simply due to the roughness of the maps (Table 4). We also examined the possibility that H , when corrected for the effect of map replicate and Z , might be significant. The corrected sum of squares (SAS, 2001) was significant at $P < 0.05$, indicating a modest contribution of map roughness to dispersal success that was independent of the unique features of each map replicate or the total number of clusters found on the map.

The results of the management scenario simulations (Table 8) show that the modifications of the marten habitat map resulted in a 24% decline in dispersal success. This dramatic change is largely attributable to spatial effects because the modified map has nearly as much core marten habitat (24%) as the unmodified map (27.1%). Because removal of the 2 core sites nearest the release point (sites 5 and 10, Table 8) caused dispersing martens to take 84% more dispersal steps within the modified map, these martens ex-

perienced a higher rate of mortality (27.3%) than on the unmodified map (14.6%, Table 8). Spatial effects are also apparent in the changing pattern of immigration success: core areas 3, 7, and 12 were nearly unchanged between the modified and unmodified maps while core areas 4, 9, and 11 experienced more than an order of magnitude increase in immigration success (Table 8).

4. Discussion

Spatially explicit population models, or SPEMs (Dunning et al., 1995a,b), have become important tools for species management, preservation, and protection (den Boer, 1981; Fahrig, 2001; Tester et al., 1997). The use of SPEMs has increased our awareness of the importance of dispersal success for predicting population expansion and persistence (e.g. Bascompte and Sole, 1998; Fahrig, 1998; Wiegand et al., 1999). Consequently a wide variety of models have been developed to characterize dispersal at landscape scales (see review by Zabel, 1994). Among the most influential have been the reaction-diffusion equations introduced to ecologists by Skellam in his seminal paper (Skellam, 1951). Reaction-diffusion models, which usually assume a homogeneous landscape (but see Flather and Bevers, 2002), have been responsible for the development of a comprehensive theory of population movement and spread (Okubo, 1980; Turchin, 1998). However, the assumption of homogeneity becomes inadequate when landscapes are highly fragmented (Johst and Brandl, 1997; Gustafson and Gardner, 1996; Hof and Flather, 1996; King and With, 2002).

Models that explicitly consider the effect of habitat heterogeneity on movement patterns often replace equations for diffusion with an individual-based modeling approach (Zabel, 1994). Individual based models allow the details of animal movement and interaction with the environment to be explicitly simulated, although analytical solutions for these movement algorithms have not been developed (Grimm et al., 1999). Landscape heterogeneity may be represented in a variety of forms in these models, with simple 2-phase maps (e.g. King and With, 2002; Turner et al., 1993; Hiebeler, 2000) or corridors linking adjacent habitat patches (e.g. Bunn et al., 2000; Anderson and

Danielson, 1997; Henein and Merriam, 1990; Tischendorf et al., 1998) being the most common formulations.

Martens are highly active animals that move and forage over very large areas. Because marten dispersal events result in diverse habitats being encountered, simple representations of landscapes are inadequate. J-walk is the first model to simultaneously consider the effects of multiple habitat types, the energetic constraints of dispersing organisms and habitat-specific variation of predation risk on successful range expansion of a reintroduced species. The advantage of this approach is that these multiple factors, and their interactions, may be quantified. The primary disadvantage is the increased model complexity the numerous parameters that must be estimated and the need for complex simulations, rather than analytical solutions, to characterize results (Grimm et al., 1999). Nevertheless, the modeling framework of J-walk provides a foundation for empirical studies to identify key parameters and processes which must be measured, and provide sufficient data to test these predictions in the field.

The simulations with J-walk reported here are based on data and observations of the reintroduction of 172 American martens (*M. americana*) into the Nicolet National Forest, Wisconsin, USA between 1975 and 1983. Because of the broad range of uncertainties considered, sets of simulations were performed to investigate the impact of unknowns on the behavior and fate of marten dispersal. The results indicate that variation in dispersal success is best explained by both the landscape features (i.e. the spatial arrangement of suitable habitat and the spatial variation in prey availability) as well as parameters that modify species-specific descriptors of dispersal.

In the experiments that varied the degree of habitat roughness (parameter H , Table 1), the arrangement of habitat was similar at broad scales, but differed in the roughness of the pattern at fine scales (see Fig. 2). Although H results in significant changes in map pattern (Table 3), the analysis of variance showed that “map replicate” (i.e. map-to-map variation in pattern) was more important than variation in roughness produced by H (Table 7). This result was unexpected and implies that differences in pattern, as revealed by a variety of landscape indices, were unimportant while the peculiar arrangement of habitat of each map triplicate was an important determinant of dispersal suc-

cess. Visual inspection of simulation results indicated that this effect was probably due to the broad-scale variation in habitat near the center of each map where individuals were released. Large unsuitable areas (i.e. regions dominated by habitat type 1) in the center of the map reduce overall dispersal success while large suitable regions enhance it. Bear in mind that if one tried to select natural areas for an empirical study so that landscape replicates were as similar as possible, the degree of difference between maps would be much greater than that between replicates of the 10 artificially generated maps. Even if similar natural areas could be selected, the results of these simulations indicate that the idiosyncratic nature of each landscape will play a significant role in the fate of dispersing animals.

The variation in energy availability (i.e. prey abundance) within different habitats and the energy requirements of dispersing organisms is another important unknown. The expression of these two variables as a ratio (Q) allowed a parsimonious representation of the relative variation in the prey abundance as a function of the metabolic requirements of dispersing martens. The three fates of dispersing individuals measured by J-walk (dispersers either starve, are killed by predators, or fail to find suitable habitat within 90 days) showed that variation in Q had a significant impact on each dispersal fate (Table 5). With higher relative energy availability, fewer dispersers starved, but because individuals were able to move over a longer period of time they were more susceptible to being killed by predators. A threshold in dispersal outcome may exist when the average level of landscape productivity is approximately 50% of that required by dispersing martens ($Q \sim 0.5$, Fig. 3a and b). The existence of this threshold implies that a lowered relative energy availability caused dispersing individuals to “switch” behavior from a high dispersal mode to a more intense pattern of foraging for prey as the risk of starvation increased (Fig. 3b). The high metabolic rate of martens would seem to play an important role in dispersal within natural systems. But equally important is the assessment of prey availability within the landscape. Knowledge of both variables will be required to adequately assess the dispersal potential of martens residing in real landscapes.

The specification of a variety of predation functions (Y) allowed us to also evaluate the effect of different

assumptions about the interaction between prey abundance and predation risk on dispersal. Variation in the predation functions produced significant changes in the percent killed and percent successfully dispersing (Table 5). The interaction of the predation rules with the energy availability ratio was also important: the quadratic increase and exponential decrease functions produced relatively high mortality rates over a broader range of Q values. These results suggest that increased predation risk in energy-rich habitats (i.e. the “increasing” Y cases) reduced dispersal success (compare “linear increase” to “linear decrease” in Fig. 4). Assumptions regarding both the shape and slope (increase or decrease) of the predation function seem to be equally important in determining dispersal outcome (Fig. 4). It is obvious that when dispersers avoid predation (e.g. $Y = f$, Table 2) they are more likely to successfully disperse.

Rather than select a single decision rule for dispersal, J-walk implements three sets of alternative assumptions (J , Table 1) which alter the movement decision criteria based on the energy requirements of the dispersing animal ($J = e$), the risk of predation ($J = m$), or a “conditional” rule which attempts to balance energy gain with reducing predation risk ($J = c$). Although a significant interaction between behavior and habitat pattern was expected, simulation results demonstrated that dispersal outcomes did not differ significantly as a result of the different J cases (Table 5 and Fig. 4). The “conditional” rule generally had the same effect as the “minimize predation” rule on the percent successful dispersal. However, because the “conditional rule” switches to the “maximize energy” rule when energy reserves were low, a decrease in the percent of dispersers that starved resulted. Because percent killed and percent dispersed are only marginally higher under the “conditional” rule compared to the “minimize predation” rule, the dispersers that were saved from starvation by the “conditional” rule apparently experienced the other dispersal fates in relatively equal proportions.

The overall direction of dispersal is controlled by the variability in the turning angle, C . Increases in C result in more tortuous pattern of movement and a decline in the average distance moved per day (Table 2). Decreases in C significantly increased dispersal success (Table 5) because the pattern of movement becomes more directional allowing martens to explore a

larger area in less time and, on average, more quickly finding a suitable habitat patch. Because predation is simulated at each time step, less wandering means less exposure to predation. This effect of the turning angle is well known from other studies that have simulated dispersal as a correlated random walk (Kareiva, 1983; Siniff and Jessen, 1969). However, information regarding the estimation of C for dispersing martens is not currently available (John Wright, personal communication).

The movement algorithm within J-walk is a complex formulation that considers the variation in habitat pattern, the physiological status of dispersers, and a variety of assumptions regarding predation and movement. Nevertheless, J-walk still simplifies many aspects of movement that may significantly impact dispersal success. Examples of such factors include the long-range perception of habitat quality, species interactions including avoidance of predators and con-specifics, and the time-dependent modification of movement through learning. Although not specifically modeled, the current version of J-walk provides some insight into each of these factors. For example, simulation results indicate that variation in the risk of predation significantly affects dispersal success (Table 5). This result implies that the slow rate of range expansion within the Nicolet National Forest may be the result of martens avoiding the abundant and widespread fisher. However, estimates of average predation mortality of dispersing martens in the Nicolet are unavailable. It is possible that martens are able to avoid fishers by detection of their scent trails. Inclusion of this dynamic within J-walk would be relatively straight forward, but requires extensive data regarding fisher abundance and movement as well as fisher–marten interactions. Because martens are highly active, and have a keen sense of smell, they may have a greater perceptual range than we have simulated (100 m). A greater perceptual range may significantly enhance dispersal success (Lima et al., 1999), making experiments similar to those recommended by Lima and Zollner (1996) of value. Although learning has been simulated in other models (Saarenmaa et al., 1988), the empirical information required to estimate parameters for these algorithms is unavailable for martens.

The simulation methods implemented in J-walk were specifically designed to simulate dispersal on

very large landscapes. The landscape extent for the simulations reported here was set to 10,486 km² to minimize the number of dispersers (<0.02%) reaching the edge of the map before the simulation was concluded. Marten movements of this extent are consistent with empirical studies (Gilbert et al., 1997) that have documented movements in excess of 64 km from their initial capture site. Although simulated landscapes were constrained to have equal levels of habitat availability, the spatial pattern of the generated landscapes covered a wide range of spatial heterogeneity (Table 3). However, the patterns of patch (stand) size and edge per pixel generated with $H = 0.1$ most closely resembles the pattern found in the Fisher/marten Management Unit of the Nicolet National Forest (Wright, 1999). Simulation results also indicate that dispersing martens had the highest energy levels and experienced the greatest level of predation on landscapes with $H = 0.1$ (Table 4).

It is premature to use the results reported here as guidance for developing specific plans to assure the growth and sustainability of marten populations or to identify general principles. It is interesting, however, that our simulations result are generally consistent with several common axioms of wildlife management: (1) Food availability is critical for dispersing organisms who must sustain themselves by finding sufficient energy within novel habitats; (2) variability in exposure to predation (either real or perceived) is an important determinant of dispersal success; and (3) the spatial pattern of habitat features may either enhance or diminish the probabilities of survival and dispersal. The unknown parameters that must be estimated empirically to use J-walk as a predictive tool are substantial, although we have work currently under way to provide some of these values for martens in Wisconsin. The most important unknowns are: (1) an improved understanding of the energy budgets of dispersers in various habitats. Energy availability is presumably a function of prey population densities and the micro-habitat structure that allows martens to capture prey. (2) Quantitative estimates of predation risk and energy availability in habitats outside of core range areas are also needed. Predation during dispersal is important, suggesting that information on habitat-specific mortality rates would help in the management of landscapes for marten dispersal. (3) Empirical estimates of the degree of route tortuosity during dispersal (i.e.

estimates of C) are needed to realistically simulate movement. (4) A more precise determination of habitat pattern on dispersal behavior must be determined. Although dispersal did not differ between map types (i.e. degree of roughness as modified by H), the specific patterns of each map triplicate (i.e. map replicate in Table 5) did significantly affect dispersal success.

Our results also suggest that dispersal success is relatively insensitive to variation in a number of model parameters. The parameter perturbation experiments showed that changes in the number of hours a disperser was active (A) from 12 to 18 h had a small effect, increasing dispersal from 4.3 to 8.4% (Table 2). However, when all parameters were simultaneously varied the activity parameter was even less important in explaining overall dispersal success (Table 5). The movement decision rule (J , Table 1), which modifies fine-grained movement patterns, did not significantly affect landscape-scale dispersal success. Although individual martens certainly do have behavioral characteristics that may modify fine-grained movement patterns, our results suggest that other factors are more important in determining dispersal outcome.

Simple models of dispersal have been shown to be extremely sensitive to small changes in parameters that affect the rate of mortality of dispersing organisms (Kareiva et al., 1997; Mooij and DeAngelis, 1999; Ruckelshaus et al., 1999). Not surprisingly, predictions of population persistence based on these models of dispersal are extremely sensitive to the assumed rate of mortality (South, 1999). However, simulations with J-walk do not confirm these results. It appears that the spatial variation in predation risk within J-walk allows dispersing organisms to avoid predation (especially when energy levels are high) resulting in relatively minor consequences when there is wide variation in predation-induced mortality. Evidently, the simulation of multiple processes affecting mortality (rather than its representation by a single, fixed parameter) dramatically alters the sensitivity of model results to mortality rates.

In spite of the large uncertainties associated with the process of dispersal, simulations with models such as J-walk may assist the development of strategies for managing the establishment of reintroduced populations such as the American marten. In our hypothetical management scenario, the map modifications simulated change in habitat quality as a result

of natural disturbance, forest harvesting or, perhaps, the presence of resident martens within those core areas. The distance moved by martens increased by 84% on the modified maps, resulting in a 25% decline in dispersal success and a 12.7% increase in mortality from starvation and predation. Because the simulations with J-walk are spatially explicit, it is possible to view the details of the simulations and locate sites that either block dispersal or produce unusually high rates of mortality. Such results might suggest relatively inexpensive modifications that would significantly enhance dispersal success.

We present these management simulations as a heuristic tool to evaluate relative changes in dispersal success as a function of particular changes in model inputs and parameters. Simulations to address a variety of other management issues can be constructed for J-walk, and might include: (1) Investigations of the relative effect of landscape alterations on dispersal success. Proposed landscape plans (i.e. the development of dispersal corridors, the construction of roads, etc.) might serve as a template for model simulations to evaluate the relative merits of each plan. (2) An assessment of cost-efficient strategies for enhancing the establishment and persistence of reintroduced species. For instance, would a decrease in mortality due to the removal of predators provide a significant advantage to newly released marten populations? (3) Determination of the effects of land use change due to natural or anthropogenic disturbances on dispersal. Comparison of maps of forest disturbance against undisturbed systems might reveal important aspects of dispersal success similar to that represented by the “map replicate” variable in Table 5. (4) The effect of habitat improvement, especially improvement that results in an increased production of prey species, might be systematically explored. In the absence of additional data, such simulations must be based on hypotheses relating forest age and structure to the production of prey.

We believe that the simulations with models such as J-walk may assist the design and implementation of empirical studies to reduce uncertainties associated with the reintroduction of a variety of threatened and endangered species. Even when models have significant unknowns, as is the case here, they provide a quantitative means of assessing the importance of potential studies to increase understanding and improve

prediction accuracy. We are currently using these modeling results to design and undertake such studies.

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