

Behavior at Habitat Boundaries Can Produce Leptokurtic Movement Distributions

Juan Manuel Morales*

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269

Submitted December 4, 2001; Accepted March 13, 2002

Keywords: correlated random walk, landscape heterogeneity, movement, edge effects, diffusion, kurtosis.

There is increasing recognition that behavioral ecology should be integrated with landscape ecology for a better understanding of the effects of landscape properties on populations (Lima and Zollner 1996; Roitberg and Mangel 1997; Zollner and Lima 1999; Morales and Ellner 2002). In particular, movement behavior affects the way in which individuals redistribute themselves over space and thus has the potential to affect many ecological processes (Kareiva 1990; Tilman and Kareiva 1997; Turchin 1998). Many of these notions come from theoretical studies where the landscape is considered to be homogeneous and connectivity between habitat patches or points in space is either fixed or a simple function of distance. However, landscape ecology is rich in descriptions of land-cover types and spatial patterns that may affect movement (Turner 1989; Wiens et al. 1993; Gustafson and Gardner 1996). It is not well understood how the spatial arrangement of different habitat patches in the landscape matrix affects the movement of individuals.

Behavior at habitat boundaries further complicates modeling movement in heterogeneous landscapes. Habitat boundaries may bias turning behavior, reducing permeability of edges to dispersing animals (Stamps et al. 1987). This in turn can affect species interactions (Remer and Heard 1998; Fagan et al. 1999), corridor use, and dispersal (Tischendorf and Wissel 1997; Haddad 1999; Kindvall 1999; Schultz and Crone 2001). Understanding how habitat edges alter ecological processes is believed to be of

major importance for the scaling of spatial processes (Wiens et al. 1985, 1993).

Diffusion approximations to correlated random walks derived from field observations have successfully represented movement in heterogeneous landscapes with transparent edges (Kareiva and Odell 1987; Turchin 1991; Grünbaum 1998). The simplest diffusion model (Fickian) assumes that all individuals move independently and that the subsequent movements of an individual are uncorrelated. Although this seems unrealistic, given enough time, convergence to Fickian diffusion occurs even in the presence of inaccessible patches in the landscape and when turning angles are concentrated around 0° instead of being uniformly distributed over 360° (Skellam 1973; Johnson et al. 1992). In empirical studies we may not be able to wait until convergence happens. The important questions are then, At what scales is diffusion not a good representation of spatial redistribution? and How does the movement kernel depart from a Gaussian one?

Dispersal data from disparate taxa show that a common way to depart from a Gaussian kernel is by having a leptokurtic distribution of distance moved (Lewis 1997; Nathan 2001). These fat tails in the distribution of movement distances have been explained as the result of individuals settling at a constant rate (Okubo 1980; Turchin and Thoeny 1993) or by population heterogeneity in movement behavior (Skalski and Gilliam 2000; Fraser et al. 2001). Using computer simulations and microlandscape experiments I show how landscape structure can interact with movement behavior to produce transient leptokurtic redistribution curves that can persist for a long time, especially when individuals react to habitat boundaries.

Methods

Movement Behavior

I constructed a spatially explicit, individual-based model to simulate movement as a correlated random walk (CRW; Kareiva and Shigesada 1983; Turchin 1991, 1998). The spatial position of an organism was represented by continuous x and y coordinates that were projected onto a

* E-mail: juan.morales@uconn.edu.

binary landscape map. At every iteration of the model, individuals chose a step length and a turning angle according to the patch type in which they were located. I considered only two types of habitats and used exponential distributions for step length and wrapped normal distributions for turning angles (Fisher 1993). In all cases, mean turning angle was set to 0. The units of step length were scaled to the landscape cell size. Individuals moving in the “slow” patches had turning angles with mean cosine equal to 0.5 and average step length of 0.1. Those moving in “fast” patches had comparatively tighter turning angles (mean $\cos = 0.9$) and larger step lengths ($\bar{X} = 0.12$).

Reactions to habitat edges were incorporated as fixed probabilities of crossing a boundary between different patch types. If an animal’s next movement vector caused it to encounter a boundary between habitat types, then whether or not it crossed was determined by a coin toss with a constant crossing probability. An individual who does not make a crossing is returned to its previous location and assigned a new, random movement direction. I considered two types of edges: transparent, with probability of crossing equal to 1, and asymmetric, where the probability of crossing from a slow patch to a fast patch was equal to 0.1, and the probability of crossing from a fast patch to a slow patch was equal to 1. Note that this is not directed movement since boundary encounters are detected after the fact.

Landscapes

Two features of landscapes that may affect the spread of organisms are landscape composition (i.e., proportion of different habitat types) and the spatial distribution of patches. Movement may also be affected by the grain of habitat heterogeneity and the existence of multiple scales of variability (Gustafson and Gardner 1996). I generated artificial maps varying in composition, spatial pattern, and scales of heterogeneity (fig. 1). The simplest maps were binary random maps, where the area of the landscape

(128×128 cells) was divided into blocks of equal size, and each block was randomly assigned to a habitat type. The probabilities for each block of being one habitat type or the other were dictated by the desired proportion of habitats in the landscape. Fine-grained landscapes were constructed with single-pixel blocks, and coarse-grained landscapes with 5×5 -pixel blocks (fig. 1A, 1B). Clustered landscapes were generated as follows. Starting with a random, fine-grained, binary landscape, a pair of cells was chosen at random, and if they corresponded to different habitat types, their values were swapped and Moran’s I coefficient of spatial autocorrelation was calculated. When the new coefficient was greater, the landscape was updated; otherwise, the old landscape was kept. The process of switching values of cells continued until convergence to the desired degree of aggregation (fig. 1C). Finally, fractal landscapes were generated using the midpoint displacement algorithm and setting $H = 0.5$ (Gardner 1999).

Simulation Experiments

I performed a simulation experiment following a factorial design. I considered nine levels of landscape composition (0.1–0.9 proportion of patches of slow habitat), four types of landscapes (fine grained, coarse grained, clustered, and fractal), and two types of boundaries (transparent and asymmetric). Each combination of factors was replicated 10 times. In each replicate, a new landscape was generated and the movement of 1,000 individuals was simulated for 1,000 steps. Individuals started their movement in randomly chosen x,y coordinates within an area of 40×40 pixels in the center of the landscape. The landscape was big enough to prevent individuals reaching the limits of the landscape during the course of the simulations. I also simulated individuals moving in homogeneous landscapes, all-fast or all-slow habitats. For each replicate, I calculated changes over time in the kurtosis of the distribution of distance moved from the release point, measured in the “ x ” dimension (i.e., the “transect distribution,” according

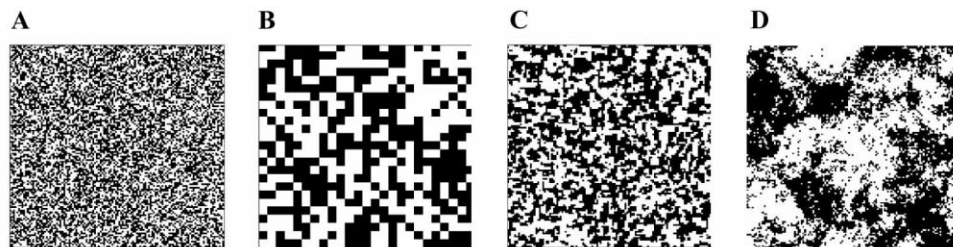


Figure 1: Examples of the types of landscapes used in the simulation experiment. A, Fine grained; B, coarse grained; C, clustered (Moran’s $I = 0.5$ for lag 1); D, fractal. These examples correspond to a proportion of slow habitat equal to 0.5.

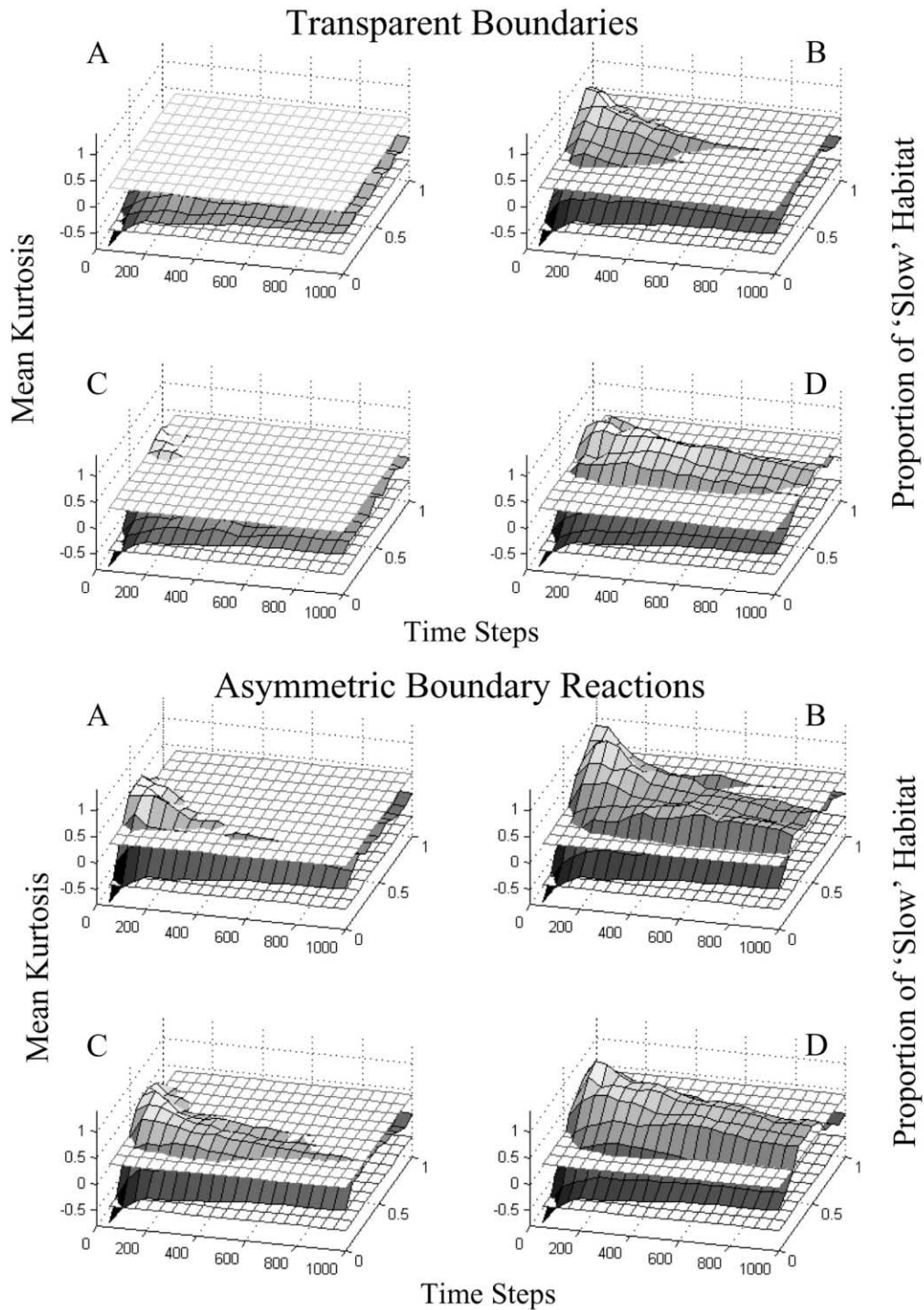


Figure 2: Changes in kurtosis with time for different landscape structure and composition for organisms crossing habitat boundaries freely (*upper panel*) and for asymmetric boundary reactions (*lower panel*). In asymmetric boundary reactions, individuals crossed freely from fast habitat to slow habitat but crossed with probability 0.1 from slow habitat to fast habitat. The values of kurtosis shown are averages of 10 replicates of each combination of landscape structure and composition. The horizontal mesh are located at the critical values of kurtosis corresponding to significant departures from normality at $P = 0.01$. A, Fine-grained landscapes; B, coarse-grained landscapes; C, clustered landscapes; D, fractal landscapes.

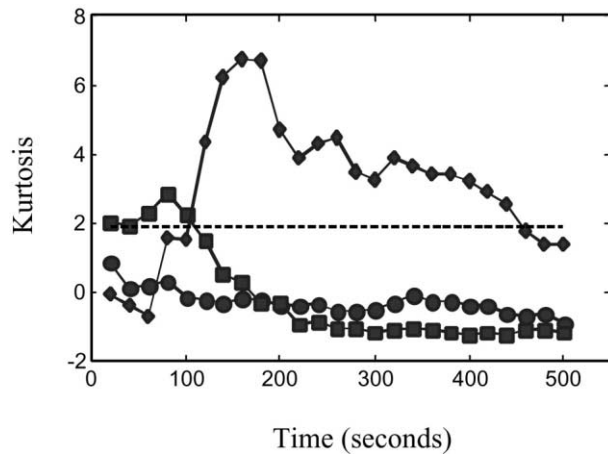


Figure 3: Temporal dynamics of the kurtosis of the distribution of movement distance for *Tribolium confusum* in experimental microlandscapes. Dots correspond to a homogeneous landscape (all “fast habitat”), squares to a random binary landscape with 20% of “slow patches,” and diamonds a random binary landscape with 20% of “slow patches” but with semipermeable edges. The dashed line corresponds to the critical value of kurtosis at $P = 0.01$ and $n = 45$.

to Metz et al. [2000]). The statistical significance of the kurtosis can be tested with a t -test with the SE for the kurtosis calculated as $(24/n)^{0.5}$ when the number of observations (n) is >150 (Sokal and Rohlf 1981). To quantify the relative effects of landscape structure and composition on the distribution of distance moved, I partitioned the variance in kurtosis measured at the end of the simulation (excluding the homogeneous landscapes). The partition was done separately for transparent boundaries and for asymmetric boundary reactions. In each case, a two-way ANOVA model with fixed effects was used.

Microlandscape Experiments

To test the general predictions of the simulations, I reanalyzed data from Morales and Ellner (2002) of adult *Tribolium confusum* beetles (Coleoptera, Tenebrionidae) walking on fast and slow artificial substrates constructed with paper and masking tape. We constructed patches of 25×25 cm of two different substrates. The fast habitat

consisted of plain paper and the slow habitat was paper where 2×2 -cm squares of masking tape were centered at 5-cm intervals along staggered rows separated by 2.5 cm. Beetles moving in the slow habitat were often faced with obstacles (pieces of tape, sticky side down) and forced to slow down and to make bigger turns. We established three different mosaic microlandscapes consisting of a 16×16 grid of habitat patches (4×4 m): homogeneous (all-fast habitat), binary random map with 20% of slow habitat patches without edges, the same as the former but with edges. Edge effects were created by pasting strips of Magic Tape at the boundaries between the slow and fast habitats. This tape has a slippery surface and served to lower the probability that a beetle would leave the habitat patch upon reaching an edge. Forty-five beetles were released one at a time in the center of each landscape, and their position was recorded every 20 s.

Results

Landscape composition and structure affected temporal changes in the kurtosis of the distribution of movement length. Long-lasting leptokurtosis was frequent when individuals reacted to habitat boundaries and when the landscape consisted of relatively large patches (i.e., coarse-grained and fractal landscapes; fig. 2). For some combinations of landscape structure and composition, the distributions of movement length at the end of the simulations often showed significant leptokurtosis. Significant values of kurtosis were more common when individuals reacted to habitat boundaries. Leptokurtosis was rare or nonexistent when the landscape composition was dominated by one of the habitat types (fig. 2). Changes in kurtosis with time for *Tribolium* beetles in the experimental landscapes showed patterns similar to those obtained though simulation (fig. 3).

Landscape structure explained slightly more than 20% of the variability in the final values of kurtosis for both types of boundaries. The relative importance of landscape composition increased from 16% for transparent boundaries to 33% for asymmetric boundary reactions. The interaction of structure and composition was important only for asymmetric boundary reactions (table 1).

Table 1: Variation partition of the final kurtosis of distance moved in different landscapes

Factor	Transparent boundaries		Asymmetric boundary reactions	
		P value		P value
Landscape structure	21.041	.000	24.175	.000
Landscape composition	15.994	.000	32.670	.000
Structure and composition	10.164	.117	16.999	.001
Error	52.801		26.156	

Discussion

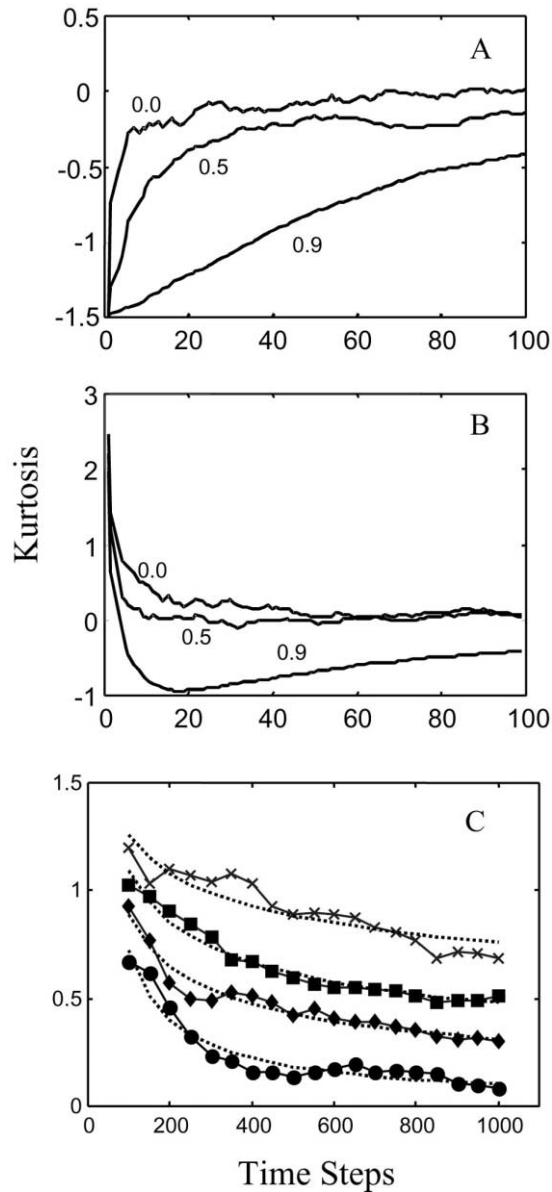


Figure 4: Changes with time in the kurtosis of the distribution of movement distance. *A*, Correlated random walk (CRW) in homogeneous landscapes and with the step length fixed at 1 unit of distance. *B*, CRW in homogeneous landscapes with exponentially distributed step length ($\bar{X} = 0.12$). The numbers next to the curves indicate the corresponding mean cosine of turning angle. Each curve is the average of 30 replicates of the movement of a noninteractive population of 200 individuals. *C*, CRW in heterogeneous landscapes with different structure (note change in the scale of the X-axis). Dots correspond to fine-grained landscapes; diamonds to clustered, squares to coarse-grained, and crosses to fractal landscapes (see fig. 1). The composition of all the landscapes is 50% fast patches and 50% slow patches. Dotted lines correspond to best-fit power laws ($y = ax^b$). Fine-grained: $a = 35.71$, $b = -0.85$, $R^2 = 0.93$; coarse grained: $a = 5.69$, $b = -0.36$, $R^2 = 0.97$; clustered: $a = 7.22$, $b = -0.45$, $R^2 = 0.95$; fractal: $a = 3.45$, $b = -0.22$, $R^2 = 0.83$.

The main components of this simulation work are features commonly found in studies of insects moving in natural or manipulated landscapes. Analysis of movement paths have usually found habitat-dependent movement parameters (Kareiva 1982; Odendaal et al. 1989; Turchin 1991; Crist et al. 1992; McIntyre and Wiens 1999; With et al. 1999), and several empirical studies have underscored the importance of boundary permeability (Haddad 1999; Kindvall 1999; Kindvall et al. 2000; Martin et al. 2001; Schultz and Crone 2001). Landscape composition and structure can affect different aspects of individual movement paths such as net displacement and tortuosity (Crist et al. 1992; McIntyre and Wiens 1999; With et al. 1999), but I am not aware of any empirical study of the effect of landscape properties on kurtosis or other descriptors of the shape of the redistribution kernel. Some suggestive evidence can be found in Donocaster et al. (2001, fig. 2 therein) in which they report normal probability plots of maximum distance moved for hedgehogs (*Erinaceus europaeus*) that look skewed and somewhat leptokurtic for releases in highly fragmented “unsuitable habitats” compared to more normal-looking plots for releases in relatively unfragmented “favorable habitats.” Although limited to a few patches per landscape, Kindvall (1999) released bush crickets (*Metrioptera bicolor*) in four landscapes differing in the abundance and distribution of suitable habitat (grassland patches) and found different frequency distribution of net displacement for each landscape. Interestingly, both studies also found important effects of habitat boundaries. The lack of empirical evidence is probably due to the lack of a theory to relate movement behavior and landscape heterogeneity to redistribution kernels.

Population heterogeneity produces leptokurtic distributions of distance moved when a subset of the individuals consistently moves longer distance than others (Skalski and Gilliam 2000; Fraser et al. 2001). When the heterogeneity is in the landscape, not in the individuals, the departures from a Gaussian kernel will eventually be washed out because a particular individual will switch its movement behavior as it encounters patches of different habitats. The patch structure of the landscape and the behavioral reactions to habitat boundaries affect the rate of switching and, hence, the time needed to reach normality. Both population and landscape heterogeneity are likely to be important for accurate representations of movement. Note that Morales and Ellner (2002) found that behavioral heterogeneity between individuals and within individuals over time had to be included in their random walk models in order to fit observed patterns of spread. However, despite differences in movement behavior between individuals, the effect of landscape hetero-

geneity and habitat boundaries on kurtosis was conspicuous (fig. 3).

The central limit theorem states that the sum of n independent and identically distributed random variables with finite variance will approach a Gaussian distribution as n increases. If all individuals in a population move according to the same stochastic process, we would expect that at some time after the initiation of movement, the distribution of distance moved becomes Gaussian because the distance traveled is the sum of movement vectors. Individual behavior and landscape structure impose autocorrelation on the displacement vectors. As long as the autocorrelation decays quickly enough over time, there will be convergence toward a Gaussian distribution and the spread of individuals over space can be described on this longer time scale by a diffusion model.

For CRW in homogeneous landscapes, the direction of a movement vector is correlated with the previous one. This autocorrelation initially produces platykurtic distributions, but the autocorrelation dies off exponentially and convergence to a Gaussian is relatively fast. The speed of convergence is related to how fast the individuals "forget" their previous direction (fig. 4A). Furthermore, the distribution of step vectors affects not only the rate of convergence but also the way in which convergence is achieved (fig. 4B). A formal treatment of the rate of convergence to a Gaussian in heterogeneous landscapes is beyond the scope of this note, but an inspection of the simulation results showed that the decay of kurtosis with time may be described as a power law (fig. 4C). The rate of convergence to a Gaussian will also be affected by skewness in the movement vectors. In this work, the occurrence of skewed distributions of distance moved was minimized since there was no persistent bias in movement direction and because all the landscapes were isotropic.

A central issue in spatial ecology is the extrapolation of ecological information across scales (Turner 1989; Levin 1992; Wiens et al. 1993). For animal movements, the hope is to be able to use information collected at patch scale to gain insights into the spatial population dynamics at the landscape scale. The results presented here show that the shape of the redistribution function in heterogeneous landscapes may be dynamical, depending on details of individual behavior and landscape composition and structure. For organisms that freely cross patch boundaries and move as CRW, a simple diffusion model would capture the main features of dispersal if the grain of landscape heterogeneity is not too large compared to the movement rate of the individuals, that is, if the movement paths of individuals often encounter different habitat types. When organisms react to habitat boundaries, or when the structure of the landscape results in individuals moving mostly in one habitat type, a detailed landscape structure is likely

to be necessary in scaling up from individual movement rules to landscape redistribution.

Acknowledgments

Thanks to R. Dunn, S. P. Ellner, J. F. Gilliam, M. Groom, D. Haydon, G. T. Skalski, P. Turchin, and two anonymous reviewers for comments on early versions of the note. This work was supported in part by a Fulbright fellowship to J.M.M. and by National Science Foundation grant 0078130.

Literature Cited

- Crist, T. O., D. S. Guertin, J. A. Wiens, and B. T. Milne. 1992. Animal movement in heterogeneous landscapes: an experiment with *Eleodes* beetles in shortgrass prairie. *Functional Ecology* 6:536–544.
- Donocaster, P. C., C. Rondini, and P. C. D. Johnson. 2001. Field test for environmental correlates of dispersal in hedgehogs *Erinaceus europaeus*. *Journal of Animal Ecology* 70:33–46.
- Fagan, W. F., R. S. Cantrell, and C. Cosner. 1999. How habitat edges change species interactions. *American Naturalist* 153:165–182.
- Fisher, N. I. 1993. *Statistical analysis of circular data*. Cambridge University Press, New York.
- Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G. T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist* 158:124–135.
- Gardner, R. H. 1999. RULE: map generation and a spatial analysis program. Pages 280–303 in J. M. Klopatek and R. H. Gardner, eds. *Landscape ecological analysis: issues and applications*. Springer, New York.
- Grünbaum, D. 1998. Using spatially explicit models to characterize foraging performance in heterogeneous landscapes. *American Naturalist* 151:97–115.
- Gustafson, E. J., and R. H. Gardner. 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. *American Naturalist* 153: 215–227.
- Johnson, A. R., B. T. Milne, and J. A. Wiens. 1992. Diffusion in fractal landscapes: simulations and experimental studies of tenebrionid beetle movements. *Ecology* 73:1968–1983.
- Kareiva, P. 1982. Experimental and mathematical analyses of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261–282.
- . 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transac-*

- tions of the Royal Society of London B, Biological Sciences 330:175–190.
- Kareiva, P., and G. Odell. 1987. Swarms of predators exhibit “preytaxis” if individual predators use area-restricted search. *American Naturalist* 130:233–270.
- Kareiva, P., and N. Shigesada. 1983. Analyzing insect movement as a correlated random walk. *Oecologia* (Berlin) 56:234–238.
- Kindvall, O. 1999. Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera: Tettigoniidae). *Journal of Animal Ecology* 68:172–185.
- Kindvall, O., G. Nordlander, and H. Nordenhem. 2000. Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. *Entomologia Experimentalis et Applicata* 95:53–61.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 75:1943–1967.
- Lewis, M. A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. Pages 46–69 in D. Tilman and P. Kareiva, eds. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11:131–135.
- Martin, M., F. Bastardie, D. Richard, and F. Burel. 2001. Studying boundary effects on animal movement in heterogeneous landscapes: the case of *Abax ater* (Coleoptera: Carabidae) in hedgerow network landscapes. *Comptes Rendus de l'Academie des Sciences Serie III Sciences de la Vie* 324:1029–1035.
- McIntyre, N. E., and J. A. Wiens. 1999. Interactions between landscape structure and animal behavior: the roles of heterogeneously distributed resources and food deprivation on movement patterns. *Landscape Ecology* 14:437–447.
- Metz, J. A. J., D. Mollison, and F. van den Bosch. 2000. The dynamics of invasion waves. Pages 482–512 in U. Dieckmann, R. Law, and J. A. J. Metz, eds. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge Studies in Adaptive Dynamics. Cambridge University Press, Cambridge.
- Morales, J. M., and S. P. Ellner. 2002. Scaling up movement in heterogeneous landscapes: the importance of behavior. *Ecology* 83:2240–2247.
- Nathan, R. 2001. The challenges of studying dispersal. *Trends in Ecology & Evolution* 16:481–483.
- Odendaal, F. J., P. Turchin, and F. R. Stermitz. 1989. Influence of host-plant density and male harassment on the distribution of female *Euphydryas anicia* (Nymphalidae). *Oecologia* (Berlin) 78:283–288.
- Okubo, A. 1980. *Diffusion and ecological problems*. Springer, New York.
- Remer, L. C., and S. B. Heard. 1998. Local movement and edge effects on competition and coexistence in ephemeral-patch models. *American Naturalist* 152:896–904.
- Roitberg, B. D., and M. Mangel. 1997. Individuals on the landscape: behavior can mitigate landscape differences among habitats. *Oikos* 80:234–240.
- Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892.
- Skalski, G. T., and J. F. Gilliam. 2000. Modeling diffusive spread in a heterogeneous population: a movement study with stream fish. *Ecology* 81:1685–1700.
- Skellam, J. G. 1973. The formulation and interpretation of mathematical models of diffusionary processes in population biology. Pages 63–85 in M. S. Barlett and R. W. Hiorns, eds. *The mathematical theory of the dynamics of biological populations*. Academic Press, London.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. W. H. Freeman, San Francisco.
- Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist* 129:533–552.
- Tilman, D., and P. Kareiva. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, N.J.
- Tischendorf, L., and C. Wissel. 1997. Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. *Oikos* 79:603–611.
- Turchin, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253–1266.
- . 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Mass.
- Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications* 3:187–198.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171–197.
- Wiens, J. A., C. S. Crawford, and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421–427.
- Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims.

1993. Ecological mechanisms and landscape ecology. *Oikos* 66:369–380.
- With, K. A., S. J. Cadaret, and C. Davis. 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology* 80:1340–1353.
- Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030.

Associate Editor: Nicolas Perrin