

Translating across scales: Simulating species distributions as the aggregate response of individuals to heterogeneity

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Received 18 April 1995; accepted 4 December 1995

Abstract

The mechanistic linkage between movement responses of animals to heterogeneity and distribution of populations provides a useful framework for investigating the extent to which fine-scale ecological information can be extrapolated across scales to explain broad-scale phenomena. We developed a simple, spatially explicit simulation model to explore whether patterns of species distributions across landscapes emerge as the aggregate response of individuals to fine-scale heterogeneity. As an empirical basis for this modelling exercise, we studied two species of acridid grasshoppers (Orthoptera) in the shortgrass prairie in northcentral Colorado, USA. Grasshopper distributions were sampled in two pastures that had been subjected to different intensities of cattle grazing. A large species, *Xanthippus corallipes* (Haldeman) was patchily distributed across this grassland, whereas the smaller *Psoloessa delicatula* (Scudder) occurred as a random distribution in both pastures. We produced a grid map of each pasture, in which each grid cell was classified according to 3 habitat types representing a gradient of forage abundance for grasshoppers. During model simulations, individuals were randomly distributed across the pasture maps and allowed to redistribute according to habitat-specific movement probabilities — the rate that an individual would leave a particular cell (habitat) type. Movement probabilities were extrapolated from observed movement rates of each species within habitats. We were initially unable to simulate realistic levels of aggregation for the two grasshopper species when extrapolated rates of movement were applied to the model. Species distributions thus do not emerge as a linear function of fine-scale movement rates, presumably because movement is constrained by different processes operating at different scales. Fine-scale movement responses to heterogeneity can be used to provide *qualitative* predictions of species' distributional patterns in different landscapes, however. For example, *P. delicatula* exhibited faster rates of movement through habitats comprising 92% of one pasture; such a high rate of turnover should lead to a random distribution, which is what we observed for this species in this system. *Xanthippus corallipes* had reduced movement in 35% of this same landscape, but was able to move rapidly across the remainder. This may enable individuals to aggregate within a minor component of the landscape and produce the clumped distributions we observed. While the general pattern of distribution can be determined from individual movement responses to heterogeneity, such information is too coarse to quantify the exact location of individuals and other statistical properties of population distributions (e.g., density).

Keywords: Landscape ecology; Microlandscapes; Movement; Populations; Spatial scale

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1. Introduction

A central issue in ecology is to what extent patterns can be extrapolated across scales. Given the fine scale at which much ecological research is conducted (Kareiva and Anderson, 1988), it would be advantageous if such information could be used to explain patterns at larger scales that are generally not amenable to the rigors of experimental manipulation (Turner et al., 1989a). Furthermore, an ability to translate fine-scale information across scales could facilitate the search for mechanistic explanations of broad-scale patterns, thus promoting a unification of pattern and process in ecology.

The study of animal movement provides a mechanistic link between ecological pattern and process (Merriam et al., 1991, Wiens et al., 1993). Spatial heterogeneity affects the movement of individuals (e.g., Smith, 1974), which in turn can influence the dispersal and distribution of animals across a landscape (Turchin, 1991; Johnson et al., 1992), affecting the stability and persistence of populations (Roff, 1974; Wiens, 1976; den Boer, 1981; Fahrig and Merriam, 1985). The linkage between fine-scale movement of individuals and the spatial dynamics of populations provides a useful framework for investigating the extent to which ecological patterns can be translated across scales.

We developed a simple simulation model to assess whether individual movement responses to habitat structure produce the patterns of species distributions observed in actual landscapes. This approach assumes that species distributional patterns emerge as the aggregate response of individuals to fine-scale heterogeneity (e.g., Turchin, 1989). To provide an empirical basis for this modelling exercise, we consider individual movement responses of two grasshopper species (Orthoptera: Acrididae) in the shortgrass prairie of northcentral Colorado, USA. The vegetation mosaic of the shortgrass prairie consists of various vegetation types (shrubs, cactus, various forbs and midgrass species) embedded within a shortgrass 'matrix' (blue grama, *Bouteloua gracilis*; buffalo grass, *Buchloe dactyloides*). The grasshopper species we studied associated primarily with the shortgrass matrix which provides their main forage (*B. gracilis*; Pfadt and Lavigne, 1982; With, 1994a). In defining the habitat structure of the short-

grass prairie, we therefore quantified forage abundance in terms of habitat heterogeneity, the degree to which the shortgrass matrix was disrupted by other vegetation types. Areas of near-uniform coverage of shortgrass were considered homogeneous, whereas at the opposite extreme, areas with little shortgrass cover that was extensively disrupted by other vegetation types were considered to be heterogeneous (see below). Movement rates of these grasshopper species were affected by habitat heterogeneity (With, 1994a). Our question is thus whether the patterns of distribution exhibited by different grasshopper species across a grassland mosaic can be explained by information on the fine-scale movement responses of individuals to heterogeneity. Our focus is restricted to a specific process movement – which is expected to have a significant effect on the redistribution of animals in space. Although other factors might also affect population dispersion or dynamics, we will not consider them in the formulation of the simple model presented in this paper. By focusing on a single process, we enhance our ability to understand how individual movement responses to habitat structure contribute to aggregative behavior at the level of populations, without being confounded by the complexities of other, potentially interacting processes. If such data were available, these other factors (e.g., habitat-specific mortality) could easily be added to the current modelling framework.

2. Methods

2.1. Experimental system

We conducted our field work at the Central Plains Experimental Range (CPER), a long-term ecological research site in northcentral Colorado, USA. The CPER is characterized by semi-arid (mean annual precipitation = 324 mm) shortgrass steppe and is dominated by the perennial grasses *B. gracilis* and *B. dactyloides*. These shortgrass species produce a matrix that is disrupted by patches of bare ground and other types of vegetation including cactus (*Opuntia polyacantha*), shrubs (*Chrysothamnus nauseosus*, *Gutierrezia sarothae*), and perennial midgrasses (e.g., *Aristida longiseta*).

As part of a larger study on predator–prey interactions, the spatial dynamics of grasshopper populations were assessed within two territories of the McCown's longspur (*Calcarius mccownii*), an avian predator of grasshoppers (With, 1994b). These territories were about 1 ha in size and were located in two pastures that had been subjected to different intensities of cattle grazing. Intense grazing (> 60% of annual above-ground net primary production, ANPP, consumed) resulted in a homogeneous landscape with a 'lawn-like' physiognomy that is structurally different from that of a moderately grazed pasture (40% of annual ANPP consumed; Milchunas and Lauenroth, 1989). These two territories afforded the opportunity for model development in different grassland mosaics, and the individual territory defined the spatial extent of our sampling within each pasture. 'Territory' and 'pasture' are thus synonymous in this paper.

We adopted a 'microlandscape' approach (Johnson et al., 1992) to characterize the vegetation mosaic within individual bird territories. Territories comprised a mosaic of habitat types that varied in the abundance of shortgrass. The different habitats were quantified by visually estimating the percent cover of several vegetation types (shortgrass, midgrass, cactus, shrub, forb, and bare ground) within 39.1 m² cells (6.25 × 6.25 m²) across each territory according to a checkerboard sampling design (Fig. 1). Habitat types were classified as: (1) homogeneous (H), nearly continuous cover of shortgrass ($\bar{x} = 61.7 \pm 1.63(\text{SD})\%$ shortgrass cover, $n = 46$ of 280 cells sampled across both territories) that was disrupted by few patches of other vegetation types (number of cover types > 5% total coverage = 2.9 ± 0.07); (2) moderately heterogeneous (MH), intermediate coverage of shortgrass ($\bar{x} = 50.8 \pm 1.01\%$ shortgrass cover, \bar{x} cover types = 3.7 ± 0.04 , $n = 147$ of 280 cells sampled); (3) very heterogeneous (VH), extreme disruption of the shortgrass matrix by other cover types ($\bar{x} = 36.4 \pm 0.32\%$ shortgrass cover, $\bar{x} = 4.3 \pm 0.35$ cover types, $n = 87$ of 280 cells sampled).

We studied two grasshopper species: *Xanthippus corallipes* (Haldeman), a large (35–65 mm, Otte, 1981) species (Acrididae: Oedipodinae), and *Psoloessa delicatula* (Scudder), a smaller (16–27 mm, Otte, 1981) species (Acrididae: Gomphoceri-

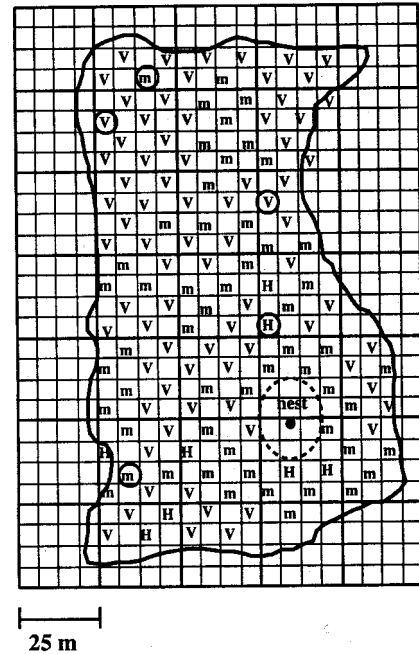


Fig. 1. Schematic representation of the spatial mosaic within a territory of a McCown's longspur. Cells (6.25 × 6.25 m²) were sampled in a checkerboard design and were classified according to the continuity of the shortgrass matrix as homogeneous (H), moderately heterogeneous (m), or very heterogeneous (V). Circled cells represent areas in which movement responses by grasshoppers to microlandscape structure were assessed. The block of cells not sampled in the lower right of the territory corresponds to the location of the active longspur nest.

nae). These two grasshopper species are abundant and are 'early season' species that are present in adult form from late April until mid to late June at the CPER (Van Horn, 1972; Welch et al., 1991). Because both species forage primarily or exclusively on *B. gracilis* (Pfadt and Lavigne, 1982), the three categories of heterogeneity (H, MH, and VH) represent a gradient in forage abundance. Defining habitat structure in terms of the relative abundance of the preferred host plant is thus relevant to how grasshoppers are interacting with heterogeneity in this system (With, 1994a).

Grasshopper populations were sampled within longspur territories by placing hoops (1 m²) in the center of the 6.25 × 6.25 m² cells according to a checkerboard design (i.e., alternate cells were sampled; Fig. 1). An observer recorded the number and species of grasshoppers flushed from each sampling

hoop with the handle of a sweep net. Total grasshopper densities within cells were estimated by multiplying the average grasshopper density within the 1 m² hoop in each cell by the total area of the cell (39.1 m²). To provide spatial maps of grasshopper density and distribution across longspur territories, grasshoppers were sampled on at least 8 occasions in each territory during the 3-week period that nests were active. Sampling was synchronous on the two territories and covered the period 13 May–2 June 1991. Because of the intensity of sampling effort, it was not feasible to sample every cell in the territory grid. A checkerboard sampling pattern was thus adopted so that the grasshopper densities within unsampled cells could be interpolated via kriging (Robertson, 1987).

2.2. Microlandscape structure of bird territories

Our premise is that animal distributions result as the aggregate response of individuals to landscape structure — the abundance and spatial patterning of habitat. To quantify the microlandscape structure of the two bird territories, we used a contagion index (D_2) that measures the extent to which different habitat types are aggregated within the landscape (Turner et al., 1989b). This is based on nearest neighbor probabilities (q_{ij}), which represent the probability that cells of habitat type i will be adjacent to habitat type j . Nearest neighbor probabilities are calculated as $q_{ij} = f_{ij}/N_i$, where f_{ij} is the frequency of cells of type i adjacent to type j , and N_i is the sum of all cells adjacent to cell type i . The formula for calculating the index of overall contagion (O'Neill et al., 1988a, modified in Li and Reynolds, 1993) for a landscape containing s habitat types is:

$$D_2 = s \ln s + \sum_{i=1}^s \sum_{j=1}^s q_{ij} \ln q_{ij}. \quad (1)$$

Values of D_2 near 1 indicate that the landscape comprises large, contiguous patches of habitat types, whereas values near 0 suggest that it is dissected into many, small patches.

A null model of how habitat distribution ought to affect animal dispersion can be devised by generating 'neutral landscapes' (sensu Gardner et al., 1987;

Gardner and O'Neill, 1991) in which habitat is randomly distributed and by observing the distributional patterns that emerge when individuals are simulated to move across such landscapes that lack explicit spatial pattern (Gardner et al., 1989; With and Crist, 1995). We compared the microlandscape structure of the bird territories with randomly generated landscapes comprising the same relative proportions of habitat types as in the birds' territories. As the proportion of the landscape occupied by a single habitat type increases, the degree of aggregation or contagion of this habitat type also increases (Gardner et al., 1987, 1989). At some threshold of relative abundance, even a random distribution of habitat will produce a high degree of contagion, resulting in a 'connected' landscape. Individuals theoretically can move in an unobstructed fashion across connected landscapes, and thus should be able to locate preferred habitat and effectively utilize resources (O'Neill et al., 1988b; With and Crist, 1995).

2.3. Model development

We designed a spatially explicit simulation model based on a grid-cell format (Kitching, 1971; Fahrig, 1988) that superimposes a grid over each bird's territory. Each cell of the grid was categorized according to one of the three habitat types (H, MH, or VH; Fig. 1). At the outset of each simulation run, we generated a random distribution of grasshoppers across the habitat map of the bird territory, based on the observed mean cell density of the actual grasshopper population, according to a Poisson distribution (Diggle, 1983). A Poisson distribution provides a random dispersion based on the expected frequency of individuals within cells. Individuals were then allowed to redistribute themselves across each territory map according to the movement rules described below and compared to the real distribution observed in that territory.

The spatial dynamics of grasshopper populations were modelled as the net change in grasshopper densities within cells of the landscape mosaic (e.g., Watt, 1968). Individual grasshoppers could be expected to move out of a particular cell with a calculated probability based on the expected residence times of individual grasshoppers within each of the three habitat types (H, MH, and VH). The expected

residence times were estimated from species-specific rates of movement through different habitats in each of the two pastures obtained from previous research (With, 1994a; Fig. 2). Movement probabilities were thus based only on species' responses to the habitat structure within the cell, and were not influenced by neighboring cells or other biotic or physical properties of the cell (e.g., density of individuals within the cell). This requires fewer assumptions in the development of the model, but certainly such complexity could be added to the model if data were available.

Grasshoppers were expected to move through a particular cell type, k , in a given pasture, l , according to the *transit rate*,

$$T_{kl} = d/r_{kl}t, \quad (2)$$

where d is a constant, the linear dimension of the cell (625 cm), t is also a constant, the average length of time per day that grasshoppers were expected to be active (5.5 h/day, see below) and r_{kl} is the average rate of movement in cell type k of pasture l

(cm/h). Rates of movement (r_{kl}) in the different habitat types within each pasture were obtained from previous research on the two species (With, 1994a; Fig. 2). Daily active period (t) was estimated as the average number of hours during the day that temperatures bracketed the activity range of the two grasshopper species (20–30°C; Anderson et al., 1979) throughout the sampling period ($\bar{x} = 5.5 \pm 4.66(\text{SD})$ h, $n = 21$ days). Given the transit rate, the number of iterations of the simulation model, N_{kl} , required for the individual to cross the cell was obtained as

$$N_{kl} = T_{kl}/s, \quad (3)$$

where s is the time interval per iteration (0.02 days), set to correspond with the length of the observation period (30 min = 0.02 days) upon which movement rates were based. The number of cell changes, C_{kl} , an individual with a T_{kl} transit rate could therefore make during the course of the simulation run is

$$C_{kl} = i/N_{kl}, \quad (4)$$

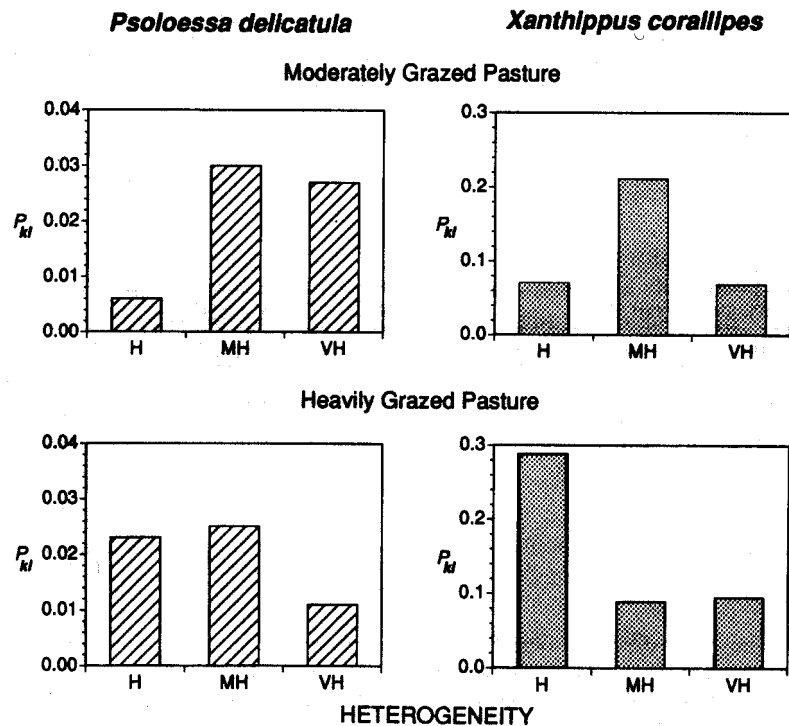


Fig. 2. Movement responses of two species of acridid grasshoppers to heterogeneity in different grassland mosaics. Response to heterogeneity is expressed as movement probabilities (P_{kl}), the probability that an individual grasshopper will move out of a particular cell type per iteration of the simulation model. Heterogeneity is defined as the relative continuity of the shortgrass matrix: H = homogeneous, MH = moderately heterogeneous, and VH = very heterogeneous.

where i is the total number of iterations in the simulation run (432 iterations). Each time step was set to the resolution at which grasshoppers were observed in the field (0.5 h), and thus the length of the simulation run equates to about a 6-week period, the approximate duration adults were present during the season $((432 \text{ iterations/run}) \times (0.5 \text{ h/iteration}) \times (1 \text{ day}/5.5 \text{ h (daily active period)}) \times (1 \text{ week}/7 \text{ days})) = 5.6 \text{ weeks/run}$). Thus, the probability of moving out of a cell, per iteration of the simulation run, is

$$P_{kl} = C_{kl}/i. \quad (5)$$

If we substitute Eq. 4 for C_{kl} , Eq. 5 becomes $P_{kl} = 1/N_{kl}$. Further substituting Eqs. 2 and 3 into modified Eq. 5 gives $P_{kl} = 1/(d/r_{kl}ts)$, or more simply,

$$P_{kl} = r_{kl}ts/d. \quad (6)$$

Movement probabilities were applied independently to each grasshopper within a cell, as opposed to the entire density of grasshoppers within each cell.

We made two assumptions regarding grasshopper movement in this model. First, direction of movement of individuals from each cell was assigned randomly into one of the immediately adjacent cells ('nearest neighbor'; Plotnick and Gardner, 1993). Each cell possessed four neighbors at most; cells on

the edge of the territory had fewer than four adjacent cells (see second point below). In the absence of information on long-term movement in these grasshopper species, we have no reason to assume that individuals exhibit directional biases in movement across more than one cell. Second, we modelled territories as closed systems, in that grasshoppers were not permitted to move outside the boundary of the territory during a simulation. Because the bird territories were imbedded in a larger spatial mosaic (e.g., pasture), it is unlikely that grasshopper movements in a real system would be bounded by the edge of the territory. We observed no 'boundary effects' (aggregation of individuals around perimeter of territory map) in our model results, however, and thus assume that a bounded system was not markedly different from an unbounded one (see Haefner et al., 1991).

2.4. Evaluation of model behavior

To evaluate the ability of our simulation model to produce distributional patterns matching those of the sampled grasshopper populations, we calculated Morisita's index (J_m), an index of contagion which measures the likelihood that two individuals, drawn at random, came from the same cell. For example,

Table 1
Mosaic composition of two pastures

Landscape type	Proportion of cell types			Nearest neighbor probabilities ^a			D_2 ^a
	VH	MH	H	q_{11}	q_{22}	q_{33}	
moderately grazed pasture							
Territory	0.27	0.65	0.08	0.42	0.72	0.20	0.77
Random	0.27	0.65	0.08	0.28 (0.028)	0.66 (0.013)	0.08 (0.034)	0.83 (0.072)
heavily grazed pasture							
Territory	0.26	0.53	0.21	0.52	0.62	0.46	0.68
Random	0.26	0.53	0.21	0.24 (0.036)	0.53 (0.022)	0.20 (0.034)	0.27 (0.022)

'Territory' refers to the spatial extent of each pasture that we sampled grasshopper populations. 'Random' refers to an artificial landscape in which the habitat types were randomly allocated to cells according to the relative abundance of each habitat type within the territory. Nearest neighbor probability is the probability that a given cell type is adjacent to a like cell: q_{11} = probability that very heterogeneous (VH) cells are adjacent, q_{22} = probability that moderately heterogeneous (MH) cells are adjacent, and q_{33} = probability that homogeneous (H) cells are adjacent. Contagion (D_2) is the overall degree of habitat aggregation across the mosaic and provides a measure of landscape connectance.

^a Values for random landscape mosaics are the mean (SD) from 10 runs.

$I_m = 2.5$ indicates that it is 2.5 times more likely that two randomly selected individuals are in the same cell compared to that in a randomly distributed population. Morisita's index is preferred to other distribution indices (e.g., variance-to-mean ratio) because it is not influenced by sample size and is more sensitive to departures from randomness ($I_m = 1.0$, Hurlbert, 1990). The resulting degree of aggregation (I_m) of the simulated distribution (average of 5 runs, see below) was compared to the extreme values of I_m observed in the empirical grasshopper distributions. We considered the model fit to be successful if the I_m value of the simulated distribution fell between the extreme I_m values for the observed grasshopper distribution because this represented the range of variability exhibited by natural populations.

To understand the full behavior of our model, we explored model state space to assess how changes in habitat-specific movement probabilities affected distributional patterns. We simultaneously varied movement probabilities for all three habitat types (H, MH, and VH) across a range from $1/200$ (*X. corallipes*) or $1/100$ (*P. delicatula*) of the initial calculated P_{kl} (Fig. 2) to $100P_{kl}$ at the other extreme. This method of extrapolation occasionally inflated $P_{kl} > 1.0$ (e.g., *X. corallipes* at $100P_{kl}$ for H cells of the heavily grazed pasture, Fig. 2). This is an artifact and operationally had no effect on model behavior because individuals could move only 1 cell/iteration ($P_{kl} = 1.0$). We additionally assessed the consequences of independently changing P_{kl} for a single habitat type on the resulting species distribution because this permitted an assessment of the relative importance of the species' response to each habitat type on its pattern of distribution across the landscape (e.g., Fahrig, 1991). Five simulation runs were performed for each level of P_{kl} (e.g., $(1/100)P_{kl}$) in each of these sensitivity analyses (Table 1); simulation results were extremely consistent among runs within a series.

3. Results

3.1. Microlandscape structure of bird territories

The moderately grazed landscape was comprised mostly (65%) of moderately heterogeneous (MH)

cells, so it was highly likely that MH cells were adjacent (probability that nearest neighbor was a MH cell = 0.72, Table 1). Very heterogeneous (VH) cells were 50% more likely to be adjacent than expected in a randomly generated mosaic with the same overall proportion of these three cell types as in the actual landscape (Table 1). The probability that homogeneous (H) cells were adjacent was 2.5 times greater in the real landscape than in a randomly assembled one (nearest neighbor probability = 0.20 in the territory versus 0.08 in the random landscape, Table 1). The high degree of overall contagion in this landscape was attributable to the large MH component.

In the heavily grazed landscape, there were nearly equal proportions of VH and H cells; the spatial mosaic of this landscape differed from that of the moderately grazed one in having 2.6 times more H cells (Table 1). Because MH cells made up half of this landscape, there was a high probability (0.62) that MH cells were adjacent. VH and H cells exhibited about twice the degree of aggregation expressed in a random mosaic (Table 1). This landscape was 2.5 times more clumped than a random landscape, but nevertheless had a high degree of connectivity similar to that of the moderately grazed pasture.

3.2. Empirical distributions of grasshoppers

The two grasshopper species in this grassland system exhibited different patterns of distribution. *Psoloessa delicatula* had distributions that were slightly more aggregated than a random distribution in both the heavily grazed ($I_m = 1.5$ – 1.7) and moderately grazed pastures ($I_m = 1.9$ – 2.1). The larger *X. corallipes* exhibited a more clumped distribution than *P. delicatula* on the two pastures, ranging from about 2.5 times more aggregated than a random distribution on the heavily grazed pasture to 4 times more aggregated than random on the moderately grazed pasture. The larger species thus had a more patchy distribution across these grassland mosaics than the smaller one.

3.3. Results of the simulation model

When the initially calculated movement probabilities (P_{kl}) for all three habitat types were applied to

the simulations, the model failed to generate levels of aggregation that matched grasshopper distributions in either landscape (compare points for x with the I_m lines in Fig. 3). The best fit of the model was obtained for *P. delicatula* in the moderately grazed landscape, in which a level of aggregation similar to that of the observed population (Fig. 3) was achieved at $10P_{kl}$ ($10x$). Although this type of simulation did not produce the exact degree of aggregation observed in natural populations, maximum clumping occurred when values near initially calculated transition rates were used (i.e., peak of curves occurs at x or $10x$, Fig. 3). Otherwise, simultaneously changing values of P_{kl} for all three cell types resulted in an essentially random distribution of individuals ($I_m \rightarrow 1.0$) across both landscapes for the two grasshopper species (Fig. 3).

The relative effect that individual responses to each habitat type in the landscape had in producing

different distributional patterns can be assessed by comparing the slopes of the response curves in Fig. 4. Because H cells were a very minor component of the moderately grazed landscape (< 10%, Table 1), both species had the potential to attain extremely clumped distributions (Fig. 4) because P_{kl} values were lowest in this habitat type for each species (Fig. 2). Reduced movement in a rare component of the landscape promotes aggregation if the organism is able to move readily across the remainder of the landscape and is able to locate and settle within the scarce habitat. Aggregation can also be achieved to a lesser degree by reduced movement in VH cells (points to the left of x for VH-curve fall below those of H-curve, Fig. 4), which comprised less than a third of the moderately grazed landscape (Table 1). In the heavily grazed landscape, the highest levels of aggregation in both species were produced by reduced movement in VH cells (Fig. 4). This cell type

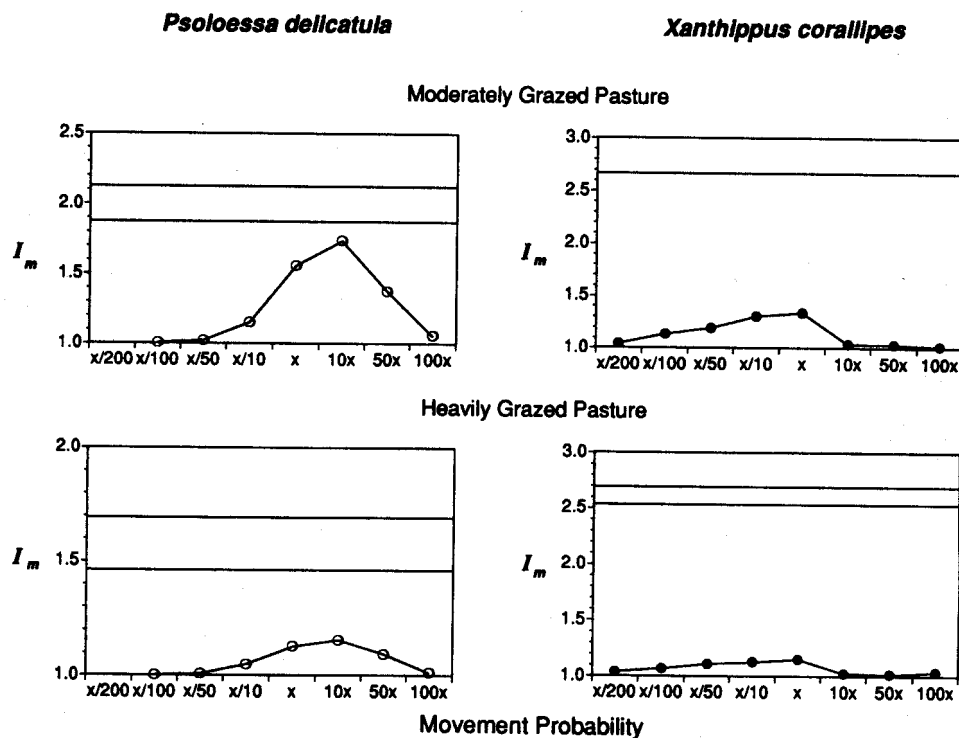


Fig. 3. Analysis of simulation models in which movement rates in all three habitat types were changed simultaneously. Horizontal lines across panels represent the range of aggregation (Morisita's index, I_m) exhibited by the population. The upper level of aggregation (I_m) for *Xanthippus corallipes* in the moderately grazed pasture was 4.1. Error bars ($\pm 2SE$) generally fell within symbols and therefore are not displayed. For movement rates, $x = P_{kl}$ of Fig. 2.

is not rare (Table 1), but it is still a minor component (less than a third) of the landscape and is the one in which both species had the highest residence times (Fig. 2).

Although each species exhibited different fine-scale responses to heterogeneity within each pasture (Fig. 2), the rank importance of each habitat response in contributing to population aggregation was the same for both species (compare response curves for each species within a pasture, Fig. 4). For example, reduced movement in H cells produced extremely aggregated distributions for both species in the moderately grazed pasture, whereas reduced movement in VH cells had the most potential to create patchy distributions in the heavily grazed pasture. Landscape composition may thus be primarily responsible for the resulting pattern of distribution,

but the degree of aggregation that can be attained by the population is still a function of the species-specific rules of movement in different habitats. Interestingly, as the relative rate of movement in MH cells is increased for *P. delicatula* in both pastures, the simulated populations became aggregated (points to the right of x for the MH-curve, Fig. 4). This effect was more pronounced in the moderately grazed than in the heavily grazed one (maximum $I_m = 4.8$ versus 2.3). Nearly two-thirds of the moderately grazed pasture is comprised of MH cells; as movement is enhanced across a major portion of the landscape, individuals settle within the remaining cell types (VH and H) that occupy a small percentage of the landscape, thus increasing the level of aggregation attained by the population. Populations in the heavily grazed pasture were unable to attain

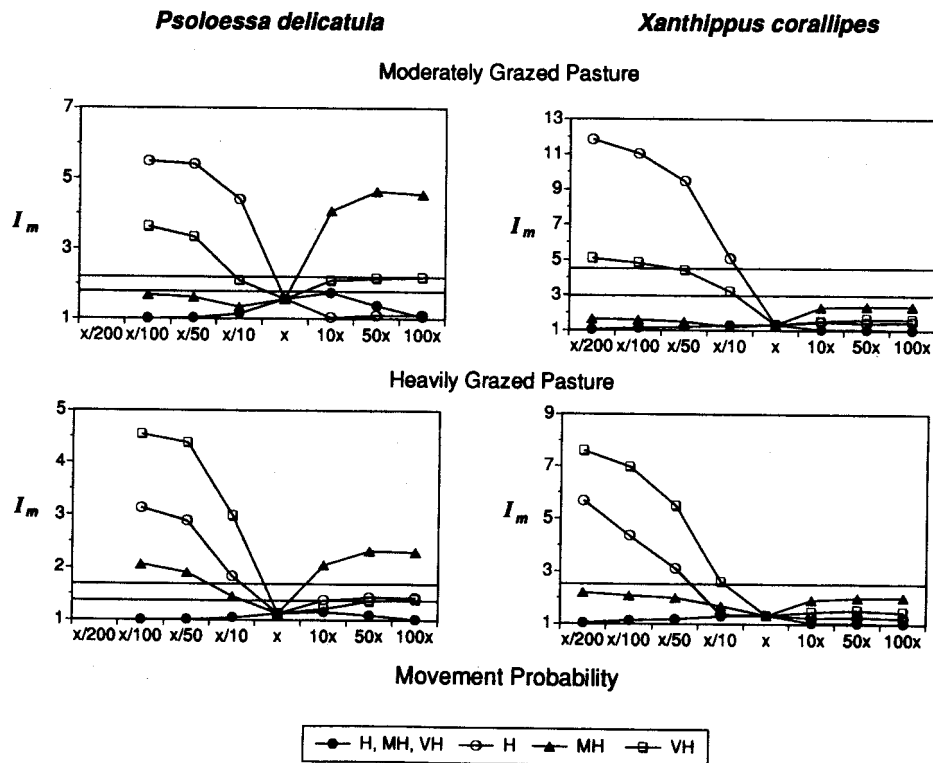


Fig. 4. Analysis of simulation models in which the movement rate was varied for a single habitat type at a time. Horizontal lines across panels represent the range of aggregation (Morisita's index, I_m) for the population. H, MH, VH = response of model when movement probabilities for all three cell types were changed simultaneously (Fig. 3), H = only the movement rate for homogeneous cells were changed, MH = only the movement probabilities for moderately heterogeneous cells were changed, and VH = only the movement probabilities for very heterogeneous cells were changed. Error bars ($\pm 2SE$) generally fell within symbols and therefore are not displayed. For movement rates, $x = P_{ki}$ of Fig. 2.

such high levels of aggregation because MH cells occupied about half of the landscape.

4. Discussion

This paper illustrates how difficult it is to recover the statistical properties of species' distributions from the averages of first-order individual behavior. The two species of grasshoppers that we studied exhibited fundamentally different patterns of distribution: *Xanthippus corallipes* occurred in clumped distributions that were 2.5 to 4 times more clumped than a random distribution, whereas the smaller *Psoloessa delicatula* had a pattern of distribution that was closer to random. The inability of the model to simulate observed levels of aggregation for these mosaic species as a linear function of calculated movement rates in different microlandscape types (e.g., Fig. 2) indicates that the emergence and maintenance of population structure within a landscape is not simply a direct extrapolation of the fine-scale movements of individuals to heterogeneity.

In attempting to extrapolate fine-scale information across scales, one assumes either that the process of interest is unaffected by changes in scale or that the change can be expressed as a simple monotonic function of observations obtained at finer scales (Gardner et al., 1989; Wiens et al., 1993). One of the simplifying assumptions of our model is that the spatial dynamics of populations result from the direct extrapolation of *average* individual response to landscape structure. This may propagate the 'fallacy of averages' (Welsh et al., 1988) that stems from modelling broad-scale system behavior as an aggregate of fine-scale responses (King et al., 1991; Rastetter et al., 1992). The proportionate scaling of all three transition rates in our model thus may have compounded aggregation error. If maintaining individual variation in an ecological model is deemed important in explaining the dynamics of the system (e.g., O'Neill, 1979), then parameter values are best obtained as random draws from the observed distribution of individual movement rates via Monte Carlo simulations (King et al., 1991). Spatially explicit population models, in general, are potentially vulnerable to the 'propagation of model uncertainty' (Conroy et al., 1995, p. 18).

Furthermore, scale-dependent shifts may occur in the process that is primarily responsible for the pattern (Gardner et al., 1989; Wiens et al., 1993). Extrapolation from fine-scale information would then be risky or inappropriate. Modelling such 'spatial transmutations' (O'Neill, 1979; King et al., 1991) involves the incorporation of nonlinear responses to heterogeneity. Animal dispersal may well exhibit a nonlinear response to heterogeneity across spatial scales. Individual movement is constrained by processes operating at different scales, which might affect the movement response of individuals to landscape structure across these range of scales or spatial 'domains' (sensu Wiens, 1989). For example, grasshoppers do not exhibit unbounded movement across a landscape; maximum dispersal for several acridids in a grassland was less than 100 m (Joern, 1983). The search for scale-dependency in patterns is one area of ecology that should receive high research priority (Wiens, 1989; Levin, 1993), but it must be recognized that spatial transmutations represent but an extreme case of scale dependency.

The question, then, is whether or not the process remains *qualitatively* similar across scales or whether it in fact becomes subsumed by some other process at broader scales, as when spatial transmutations occur. If the former were true, individual responses to fine-scale heterogeneity would be fundamentally responsible for the resulting spatial structure of the population, but additional processes and constraints would add 'noise'. Fine-scale information could then explain much, but not all, of the variance of the large-scale pattern (Gardner et al., 1989). Given a particular landscape, is it possible to predict the patterns of species' distributions based on the fine-scale movement responses of individuals to heterogeneity? The spatial mosaics of the two landscapes in this study bear a resemblance to percolating networks (e.g., Gardner et al., 1987) in that both mosaics are comprised primarily of a single cell type (MH) that spans the map (proportion of MH cell type approaches or exceeds 0.5928, the critical threshold at which a single habitat type is expected to 'percolate' on a randomly distributed landscape; Stauffer, 1985). The high degree of overall contagion (Table 1) for both mosaics also suggests that there is a high degree of connectivity within these landscapes. Thus, a species that exhibits a high rate of

movement through MH microlandscapes would be expected to move very rapidly across these grassland mosaics. For example, *P. delicatula* exhibits the highest rate of movement through 92% of the moderately grazed pasture (MH and VH cells; Fig. 2). Because individuals are not being retained in a particular component of the landscape, a random distribution is more likely, which matches the observed distribution of this species (With and Crist, 1995).

By way of comparison, *X. corallipes* exhibits extremely high rates of movement through two-thirds of the moderately grazed landscape (Fig. 2). Although percolation theory predicts that an individual should be able to traverse the entire landscape when a preferred habitat type comprises about 60% of a random mosaic, this critical threshold does not apply to heterogeneous landscapes comprised of multiple habitat types as in these grassland mosaics (With and Crist, 1995; With et al., in press). The uncertainty regarding the precise distributional pattern to be expected under these conditions suggests that, for a given response of a species to heterogeneity (e.g., Fig. 2), there should exist some critical threshold in the mosaic composition of a landscape that gives rise to different patterns of distribution (With and Crist, 1995). The results of our model clearly demonstrate that when movement is accelerated through a major component of a landscape and substantially reduced in a minor component, extreme levels of aggregation can occur. The clumped distribution of *X. corallipes* in the moderately grazed pasture may thus result from the high turnover of individuals in a major component of the mosaic (MH cells), coupled with reduced turnover in the remainder of the landscape.

This modelling exercise, based on a real system, has illustrated some of the pitfalls involved in the extrapolation of fine-scale information across scales. Animal movement is likely constrained by processes operating at different scales and thus extrapolation of information on fine-scale movement across broad scales may provide a poor quantitative prediction of the spatial dynamics of populations. Nevertheless, movement is the mechanism by which animals interact with heterogeneity and thus an understanding of species' responses to landscape structure, even at fine scales, may provide *qualitative* predictions about patterns of species distributions in different landscapes. Even the most-detailed spatially explicit pop-

ulation models cannot predict the exact location of individuals across a landscape, or reproduce precise statistical properties of population distributions (Dunning et al., 1995). The best application of this type of modelling approach is "in making comparative and qualitative statements about the likely population responses to a set of potential or real landscape" scenarios (Dunning et al., 1995, p. 9). As we have demonstrated in this paper, such spatially explicit models can be especially useful in assessing the extent to which fine-scale processes, based on field experiments, produce broad-scale distributional patterns.

Acknowledgements

R. Gardner, A. Joern, B. Kondratieff, R. O'Neill, D. Steingraeber, M. Turner, B. Van Horne, J. Wiens and two anonymous reviewers commented on various versions of this manuscript. We thank K. Rhoads, W. Sievertson, D. Wilson, and J. LaFleur for assistance in obtaining the fine-scale movement responses by these two grasshopper species to heterogeneity, and K. Rhoads and D. Wilson for their help in sampling grasshopper distributions. K.A.W. was supported by research grants from the Program for Ecological Studies at Colorado State University, NSF funding through the Long-Term Ecological Research site at the Central Plains Experimental Range (BSR-8612105), and by NSF grant BSR-880529. T.O.C. was also funded through NSF grant BSR-880529.

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