



A mechanistic home range model for optimal use of spatially distributed resources

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Abstract

Home ranges of animals are associated with the spatial distribution of limiting resources on a landscape, yet no mechanistic models representing this relationship exist. We present models of how animals might choose patches for their home ranges in ways that are optimal with respect to spatially distributed resources. The models assume that animals choose patches for their home ranges based on resource benefits discounted for travel costs. Animals might select patches to maximize resources within their home ranges over random use of the landscape (resource maximization), or to satisfy a minimum resource threshold needed for survival or reproduction (area minimization). We evaluated how landscape configuration structures home ranges of animals by performing individual-based, spatially explicit computer simulations using each model on simulated landscapes that differed only in the spatial continuity of resources among patches (from over-dispersed to clumped). The most important factor determining quality, efficiency, resource content, and spatial distribution of home ranges was the extent to which resources were clumped on a landscape. Characteristics of resource-maximizing home ranges were determined only by the distribution of resources, and differed from those of area-minimizing home ranges depending upon the magnitude of the resource threshold required. An increase in resource threshold increased area and total resource content for area-minimizing home ranges, but did not change their quality or efficiency. Because animals can consume or protect resources within their home ranges, they can depress the value of resources available to other animals and hence how those animals will choose their home ranges. Depression of resource values on a landscape by animals should result in different configuration and spatial distribution of home ranges on a landscape than would be predicted in its absence. We modified the two home range models to depress the value of resources available to other animals within patches selected for each home range. We generated home ranges with the new models on the simulated landscapes and evaluated how home ranges with resource depression varied with landscape configuration and with the number of home ranges on the landscape. We compared characteristics and spatial distribution of home ranges with resource depression to those of home ranges that do not. For the number of simulations we performed, resource depression resulted in home ranges that differed little in configuration and landscape interactions from those without, except that they were distributed more evenly on the landscapes and overlapped each other less. As the number of home ranges on a landscape increased, resource distributions declined in quality and heterogeneity, and home ranges became larger, less efficient, and of lower quality. Our results suggest that, in addition to landscape configuration, the extent to which animals depress resources included in their home ranges should determine the evenness of spatial dispersion, overlap, and home range structure, especially where animals select home ranges to satisfy a specific resource threshold and the density of animals is high. Because resource depression sets a limit

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on the number of home ranges a landscape with fixed resource levels can support, our models provide a means of assessing carrying capacity of a landscape.

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1. Introduction

The home ranges and territories of animals, and the spatial distribution of animals within a population, are commonly thought to reflect the distribution of one or several limiting resources on a landscape (Ebersole, 1980; Hixon, 1980; Schoener, 1981; Powers and McKee, 1994; Powell et al., 1997; Powell, 2000). A territory is that part of an animal's home range where the animal excludes conspecifics to protect resources (Ostfeld, 1990; Wolff, 1993; Powell et al., 1997; Powell, 2000) or offspring (Wolff, 1997). The relationship between resources and territories has been investigated extensively (Brown, 1969; Carpenter and McMillen, 1976; Ebersole, 1980; Gill and Wolff, 1975; Hixon, 1980; Kodric-Brown and Brown, 1978; Powers and McKee, 1994; Stenger, 1958; Schoener, 1983), primarily using economic analyses of fitness trade-offs between benefits gained from resources and costs of defending them.

In contrast, the factors structuring home ranges of animals have received little attention, partly because definitions for home ranges (and the costs and benefits that might define their structure) are imprecise. Burt (1943, p. 351) described a home range as:

... that area traversed by an individual in its normal activities of food gathering, mating, and caring for the young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range.

Burt's definition is conceptually complete but difficult to evaluate analytically because terms are vague and difficult to quantify (Powell et al., 1997; Powell, 2000). Although many studies of home ranges exist, little has been done to evaluate, quantify, or improve upon Burt's definition. Much research and debate has focused on statistical approaches to estimating home ranges from location data (Worton, 1987; Loehle, 1990; White and Garrott, 1990; Gautestad and Mysterud, 1993; Gautestad and

Mysterud, 1994; Gautestad and Mysterud, 1995; Bascompte and Vilà, 1997; Powell, 2000), but such approaches are descriptive and have limited theoretical or predictive value because they are not mechanistic (Moorcroft et al., 1999). The sole mechanistic home range model to date (Lewis and Murray, 1993; Moorcroft et al., 1999) used correlated random walk structured by scent marking to estimate home ranges of carnivores. No general, mechanistic model exists relating home ranges to the resources that structure or facilitate the "normal activities" described by Burt (1943). Although the importance of food as a limiting resource is cited in many home range studies (Harestad and Bunnell, 1979; Lindzey and Meslow, 1977; Lindstedt et al., 1986; Litvaitis et al., 1986; Jones, 1990; Holzman et al., 1992; Joshi et al., 1995), particularly for females (Young and Ruff, 1982; Ims, 1987; Powell et al., 1997), little is known about how a home range is structured with respect to these or any resources. Researchers, therefore, have had to assume that an animal's life requisites are satisfied by the resources available within its observed home range.

We hypothesize that home ranges, like territories, are structured primarily by the fitness-driven need for efficient accumulation of resources required for survival and reproduction (Powell, 2000). Because home ranges based solely on accumulating as many resources as possible would be limitless in size, it is clear that animals with defined, finite home ranges accumulate spatially distributed resources under limiting constraints. If home ranges, like territories, are a function of the availability and distribution of limiting resources, limited by the costs of resource acquisition, then the home range choices of animals seeking to maximize reproductive fitness can be modeled as an optimization function. We hypothesize that an animal maximizes resource accrual per unit area of its home range through the optimal selection of resource-bearing patches, analogous to optimal foraging for food items in a diet (Stephens and Krebs, 1986; Krebs and Kacelnik, 1991). This differs from

the common view of the home range as the sum of an animal's movements (Worton, 1987; Loehle, 1990; Gautestad and Myrsetrud, 1993; Lewis and Murray, 1993; Gautestad and Myrsetrud, 1995; Bascompte and Vilà, 1997) with a focus instead on the spatially distributed resources that structure an animal's movements (i.e., its cognitive map; Peters, 1978).

We developed spatially explicit, individual-based models for optimally selecting patches for a home range from a landscape comprising patches that contain limiting resources. Each model assumes that animals select patches of the highest quality available for their home ranges. The models differ in the point at which this patch selection would stop, i.e., when a home range contains sufficient resources. For understanding different ways animals might determine sufficiency, we envision a spectrum of behaviors. At one extreme are animals for which survival and reproduction increase monotonically with the efficient accumulation of spatially distributed resources. Such an animal would seek to balance the benefits of accumulating as many resources as possible against the costs of including the patches that contain them, causing it to seek the most efficient accumulation of resources in a home range that a resource distribution can offer. At the other extreme are animals for which survival and reproduction asymptote with the efficient accumulation of spatially distributed resources. At some point, a biological threshold is reached beyond which adding new, resource-rich patches to a home range has no benefit; such animals should seek to accumulate efficiently only the resources necessary to survive or reproduce in their home range. Based on these extremes, we modeled two alternative strategies for determining when patch selection should end in home range construction: (1) maximizing resources within a home range over random use of patches, or (2) accumulating resources sufficient to satisfy a pre-set minimum threshold. The first strategy maximizes the difference between selective and random use of a resource distribution and therefore is optimal with respect to the resources themselves. The second strategy minimizes the area needed to satisfy a resource threshold sufficient for an animal's survival and reproduction and therefore is optimal with respect to this biological threshold. We evaluated how home ranges of selective animals pursuing these strategies might differ by performing computer simulations for

each model on resource distributions of known characteristics.

In addition to strategies of patch selection by animals, spatial structure of home ranges and their distribution on a landscape should also be determined by the distribution of resource-containing patches. To evaluate this relationship, we applied our models to five simulated landscapes differing in how patches of varying resource value were distributed. From 100 simulations for each model on each landscape, we developed hypotheses about how the spatial distribution of resources should determine the structure and distribution of home ranges.

The distribution of animals on a landscape may not be solely a function of landscape structure. Other factors such as social interactions (e.g., territoriality, hierarchical antagonism) and depletion of resources by individuals using patches (e.g., consumption of foods, causing prey to be vigilant, occupation of den sites) could also strongly affect how animals are distributed in space. We hypothesized that these factors can depress the perceived value of resources contained in a patch and, thereby, affect patch selection by an animal establishing a home range. In this case, we suggest the value of resources in a patch depends on (1) the inherent quantity and quality of those resources, (2) average costs incurred in traveling to that patch, (3) the number of animals using that patch, and (4) the extent to which those animals depress the value of resources to other animals. From this it follows that use of a landscape by an animal modifies the distribution of resources available to other animals; as the number of animals using a landscape increases, the resource distribution available to successive animals changes and, therefore, the home ranges constructed on those resources and the distribution of home ranges on the landscape should also change. Consequently, on identical landscapes one would expect important differences between an equal number of home ranges with resource depression and home ranges without. Further, one would also expect important changes in characteristics of both resource distributions and home ranges as the number of animals establishing home ranges on a landscape changes.

We were interested in how resource depression in patches selected for home ranges might affect home ranges of animals pursuing both the resource-maximizing and area-minimizing home range strate-

gies we have hypothesized. To evaluate how resource depression can affect home ranges developed under each strategy and their distribution on a landscape, we modified the models so that resources in patches selected for simulated home ranges were devalued. We then used these modified models to simulate home ranges on each of five simulated landscapes differing in their distributions of resources. By comparing these home ranges to those developed using models without resource depression, we develop hypotheses about how social interactions and resource depletion, in addition to the spatial distribution of resources, affect the structure and spatial distribution of home ranges of animals inhabiting a landscape.

Our purpose was to learn how optimal use of spatially distributed resources might underlie the collection of movements and behaviors that ultimately define an animal's home range (Powell, 2000), and how effects of animals on their resource base might influence the distribution of home ranges on a landscape. Accordingly, our models emulate the selection of patches by an individual animal over a time period, and do not depict the animal's day-to-day time budget, movements, or foraging. Our models can make predictions about home ranges that differ from traditional depictions based on movements, particularly on disjunct resource distributions where selected patches may not form a contiguous area. We emphasize that our models are not intended to portray the movements of animals within their home ranges but rather the reasons for those movements, i.e., the resource-bearing patches between or within which the animals move. To that end, we defined a home range as the patches an animal selects to use (Powell, 2000). In the following sections we describe the concepts underlying our models and the resulting design of our simulations. We then present the results of our simulations, evaluate these results, and from them develop testable predictions of home range behaviors.

2. Basic model concepts

2.1. Patches

Patches can be defined in two ways. Traditional ecological understanding is that a patch is a discrete area

having some internal characteristic that distinguishes it from its surroundings (Wiens, 1995). Such patches vary in size and shape but are defined by discrete, internally homogeneous resource values. True spatial distributions of resources are often continuous, however, and defining patches through traditional patch classification can be arbitrary, if not impossible (Mitchell and Powell, 2002).

In contrast, explicitly mapping the resources available at each point in space is less arbitrary; patches are then spatial units of equal size, or cells of a grid, characterized by their resource value. The biological relevance of a relatively homogeneous, contiguous area of resources is still retained, because what might have been defined as a patch under the traditional definition remains apparent as a contiguous grouping of cells with similar values. For our models, we define patches as cells on a grid.

2.2. Currency: the value to an animal of spatially distributed resources

On a spatially heterogeneous landscape, an animal must decide which patches to use based on the benefits and costs of using each patch. We modeled the benefit of a patch to be the value of resources contained in the patch, V , set to range from 0 (low value) to 1 (high value). Assuming that predation and handling costs are negligible or implicitly included in V , we modeled the costs of including a patch in a home range as a function of the average distance that must be traveled to reach the patch. Travel costs are an important daily energy expenditure for an animal, and can influence strongly the efficient use of spatially distributed resources (Stamps and Eason, 1989). Because most animals spend much of their time in core areas roughly centered in their home ranges (Samuel et al., 1985; Samuel and Green, 1988; Seaman and Powell, 1990; Powell et al., 1997; Powell, 2000) we used the distance of a patch from the center of the core to estimate the average distance an animal travels over time to reach that patch from all other patches within its home range (Smith, 1968). We discounted the value of resources in a patch for the average cost of traveling to that patch from all other patches in the home range as

$$V' = \frac{V}{D} \quad (1)$$

where V' is the discounted resource value and D is the distance of patch from home range core. Because V' is undefined for $D = 0$ under this definition, we set D equal to 1/2 the patch width for the center patch.

Alternatively, this trade-off could be modeled based on energetics:

$$V' = V - cD \quad (2)$$

where c is the constant relating energy expenditure to distance traveled. Unfortunately, c is unknown for most animals and depicting costs and benefits in energetic terms for a landscape is impossible at present. Further, the value of important non-food resources such as escape cover or resting sites are not addressed in a purely energetic model; how V will lose value with distance is unknown when it is a limiting resource with a non-energetic value. Alternatively, non-energetic, comprehensive indices of habitat quality exist for many species. Most are easy to depict spatially and can be evaluated readily using Eq. (1), whereas the estimation of c and the conversion of V and D to a common currency (e.g., kcal) needed for Eq. (2) would be problematic.

2.3. Patch availability

In general, animals select patches for their home ranges from a local subset of all patches on a landscape, what we will call a neighborhood. Determining which patches constitute an animal's neighborhood is difficult because little is known about what animals perceive or how they construct cognitive maps of where they live (Powell, 2000). Nonetheless, it is logical to suppose a neighborhood beyond which an animal would not select patches because doing so would add little value to its home range. We suggest that the extent of this neighborhood is not a fixed characteristic but is instead defined by the distribution of discounted resources, V' . Our definition of V' yields a peaked spatial distribution of discounted resource values that asymptotes to 0 as D increases. Depending on the value of the resources they contain, patches have very low V' at some distance from the center of a potential home range, and these patches should have little impact on patch selection. A reasonable estimate, therefore, of the landscape neighborhood containing patches available for selection by an animal is the area that contains most of the non-negligible values of V' .

No objective means exists to determine which values are non-negligible, so we defined patch availability for our models based on a neighborhood centered on the peak of the V' distribution and containing 95% of the total value of the distribution (Mitchell, 1997).

2.4. Patch selection

We hypothesize that animals select patches for their home ranges based on the value of resources contained in the patches, discounted for travel costs, V' . We modeled this selection process for a home range by establishing a center point for a home range core on a distribution of V , using that center point to calculate V' , and selecting patches sequentially from highest to lowest V' . The assumptions of this model are:

1. An animal has complete information of all model parameters and the distribution of available patches and the resources they contain.
2. Costs of patch selection are related to average energy expended in traveling to and from selected patches within a home range and increase linearly with distance. Energetic costs of behaviors within patches are constant for all levels of patch quality and abundance.
3. Resources are fixed in time and space and their value does not change during patch selection.

3. Models

3.1. Model M_R , maximizing resource density

Animals that use patches randomly on a landscape will, on the average, accrue resources within a home range at a rate proportional to the mean availability of resources per patch for that landscape. A reasonable hypothesis is that a selective animal should choose high quality patches for its home range, exceeding mean availability of resources by as much as possible, until adding more patches begins to reduce this difference. Therefore, a home range that maximizes the density (V'/area) of resources within a home range can be modeled as one maximizing the difference (Fig. 1A, difference d) between accumulated resources, V' , within the home range of a selective animal (Fig. 1A, Patch Selectivity line) and

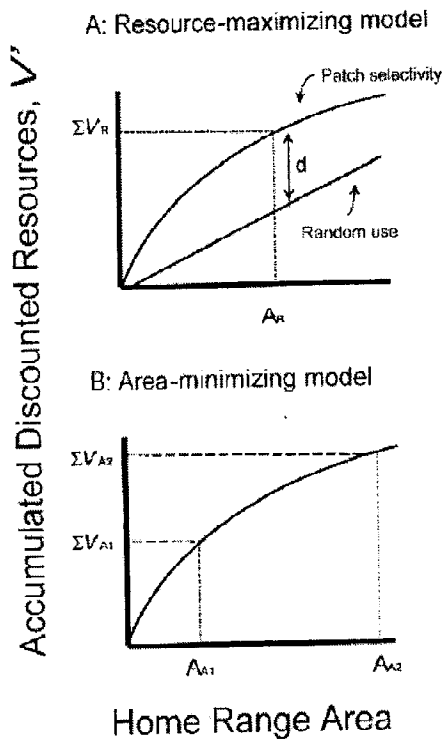


Fig. 1. Conceptual models for constructing optimal home ranges based on selecting patches containing high quality resources. In both models an animal selects patches in order of their resource value (V'), discounted for travel costs required to reach the patches. Under Model M_R (A): an animal would stop selecting patches once the difference between random and selective use of the landscape, d , was maximized, representing the optimal balance between costs and benefits of patch ownership that can be obtained from the landscape. Under Model M_A (B): an animal would stop selecting patches when a minimum threshold necessary for survival and reproduction is reached. (A) Shows the resource-maximizing home range defined by resource accumulation $\Sigma V'_R$ and area A_R . (B) Shows two possible area-minimizing home ranges, defined by $\Sigma V'_{A1}$ and area A_{A1} and $\Sigma V'_{A2}$ and area A_{A2} , respectively, based upon meeting a required minimum resource threshold.

those accumulated by animals wandering randomly on the landscape (Fig. 1A, *Random Use* line). This is equivalent to energy-maximizing models of optimal foraging (Charnov, 1976; Stephens and Krebs, 1986; Krebs and Kacelnik, 1991).

This model constructs home ranges that maximizes resource accumulation over random use by selecting patches in order of quality until the rate of resource accumulation per area of home range and the average rate for all available patches are equal; that is, from n available patches, in descending order of V' add each patch i that satisfies the condition:

$$V'_i > \frac{\sum_{i=1}^n V'_i}{n}$$

where V'_i is the discounted resource value of patch i .

3.2. Model M_A , minimizing area needed to satisfy a resource threshold

Home ranges of animals might contain only the minimum levels of resources necessary to survive or to reproduce successfully. Thus an optimal home range would be one that meets the required minimum in as small an area as possible. We modeled such survival or reproductive thresholds as a constant (Fig. 1B). The point at which the resource accumulation curve of a selective animal meets the minimum resource threshold represents the home range that satisfies the resource needs of the animal in as small an area as possible, equivalent to time-minimizing in optimal foraging models (Stephens and Krebs, 1986; Krebs and Kacelnik, 1991; Fig. 1B).

3.3. Models M_{RD} and M_{AD} , modifications for resource depression

Home ranges predicted under each of the two models should respond differently to depression of resource values in patches selected for home ranges (Fig. 2). As more animals establish home ranges on a landscape and depress resource values, both the *Patch Selectivity* lines and the *Random Use* lines become more shallow, changing the structure of predicted home ranges (e.g., Fig. 2). Because resource-maximizing home ranges maximize the difference between selective and random resource accumulation (d , Fig. 2A), and the point at which d is maximized does not change with proportional changes in the curves, home range area, A_R , does not change with resource depression, but accumulated resources (V') decline (from $\Sigma V'_{R1}$ to $\Sigma V'_{R2}$ in Fig. 2A). For area-minimizing home ranges, accumulated resources (V') do not change with resource depression ($\Sigma V'_A$), but area increases (from A_{A1} to A_{A2} in Fig. 2B).

We modified both models M_R and M_A so that after a simulated home range was generated by the models, resource values of patches included in the home range were reduced for any subsequent home ranges. We designated the new models as M_{RD} and M_{AD} , re-

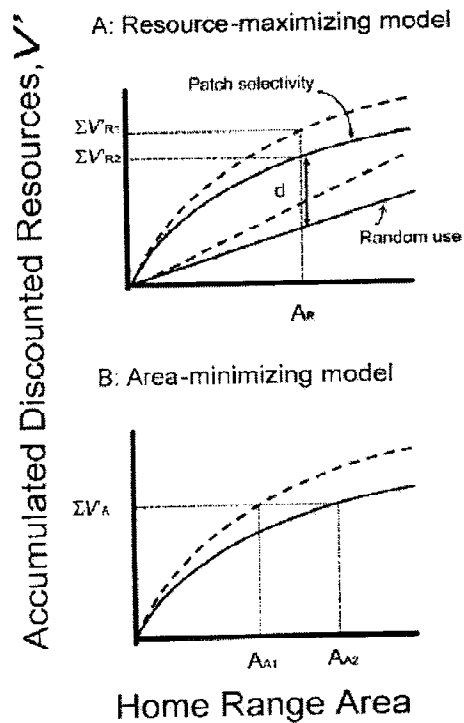


Fig. 2. Conceptual model for how resource depression by animals affects the construction of home ranges under two models of optimal patch selection. The *Patch Selectivity* line in Fig. 1A and B indicate how a selective animal would accumulate resources by choosing patches for its home range in order of their resource value (V), discounted for travel costs required to reach the patches. The *Random Use* line in Fig. 1A indicates how an animal using the landscape randomly would accumulate resources. Dashed lines indicate resource accumulation for selective and random use prior to resource depression, solid lines indicate resource accumulation after resource depression. Because resource-maximizing home ranges maximize the difference between selective and random resource accumulation (d , Fig. 1A), and the point at which d is maximized does not change with proportional changes in the curves, home range area, A_R , does not change with resource depression, but accumulated resources (V') decline from $\Sigma V'_{R1}$ to $\Sigma V'_{R2}$. For area-minimizing home ranges, accumulated resources (V') do not change with resource depression ($\Sigma V'_A$), but area increases from A_{A1} to A_{A2} .

spectively. For simplicity, we modeled resource depression in patches selected for each simulated home range as a uniform reduction of V across all patches. The extent of the reduction could theoretically vary from almost none, resulting in home ranges closely resembling those constructed under M_R and M_A , to complete, resulting in exclusive home ranges, or territories. For both home range models on each simulated landscape, we constructed the first home range, re-

duced V for all subsequent home ranges on the patches included in the first, then constructed a second home range, reduced V for its patches, and so forth. Biologically, this sequence could represent either a social hierarchy where dominant animals have priority use of patches or sequence of arrival on a landscape.

4. Methods

4.1. Landscapes

We simulated five landscapes on a 109×131 matrix of cells, or patches. V for each patch was a value between 0 and 1 inclusive, and the means and standard deviations of V for the five landscapes were approximately equal (Table 1), although maintaining the same variance for highly clumped values of V was not possible. We constructed the landscapes to differ in spatial continuity (i.e., covariability between neighboring patches), which we quantified using Moran's I (Cliff and Ord, 1981). Moran's I provides an estimate of interdependence among spatial data analogous to Pearson's correlation coefficient and ranges from -1 for over-dispersed distributions in which neighboring cells have no similarity, through 0 for a random distribution, to 1 for clumped distributions where cell values correlate completely with neighbors (Fig. 3). We designed the simulated landscapes to range from over-dispersed resources (Landscape OD, Fig. 2A), through randomly distributed resources (Landscape R, Fig. 2B), to increasingly clumped resources (Landscape SC [slightly clumped], MC [moderately clumped], and HC [highly clumped], Fig. 2C through E, Table 1).

Table 1

Summary statistics for simulated landscapes consisting of spatially explicit distributions of resources used to evaluate home range models. V = value of limiting resource (ranging from 0 to 1) assigned to a cell in a simulated landscape; Moran's I is an index of spatial continuity

Simulated landscape	Mean V	S.D. of V	Moran's I	Description
1	0.46	0.26	-0.80	Over-dispersed V
2	0.46	0.28	0.00	Randomly dispersed V
3	0.46	0.16	0.35	Slightly clumped V
4	0.46	0.12	0.71	Moderately clumped V
5	0.46	0.11	0.89	Highly clumped V

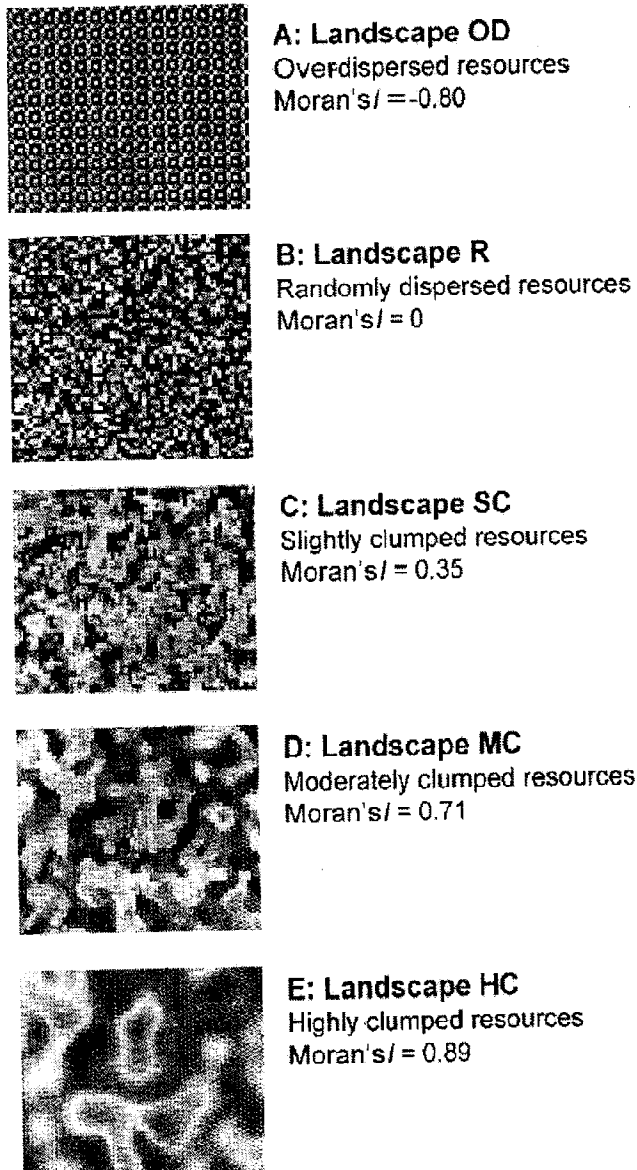


Fig. 3. Simulated landscapes of resource values (V , ranging from 0, dark hues, to 1, light hues) used to evaluate home range models which optimize use of spatially distributed resources. Mean and standard deviation for V was approximately equal across all landscapes (0.46 ± 0.20); each landscape differed in the spatial continuity of V , indexed using the Moran's I statistic, which ranges from -1 (over-dispersed) to 1 (highly continuous).

4.2. Home ranges

4.2.1. Models without resource depression

On each of the simulated landscapes, we selected 100 random starting points for home ranges generated

under model M_R , each separated from the edges of the landscape by a buffer of ca. 12 patches to preclude an edge effect.

Whereas each resulting home range under model M_R was efficient for its center point, it might not have been for the immediate distribution of resources. To allow patch selection to adapt to the local V distribution, we calculated the geographic center (weighted for V) of the home range and calculated the difference between the original starting point and the weighted center. If the difference were ≥ 1 cell, we discarded the original home range and built a new one using the weighted center as the starting point. We repeated this process until the weighted center point of the home range stabilized. This allowed patch selection to be efficient over a neighborhood of patches within the landscape and eliminated the arbitrary effects of random starting points. Allowing patch selection to adapt to the immediate landscape emulates a decision-making process coarser than patch selection, analogous to the learning process by which an animal using a landscape would adapt to new information about the distribution of across its home range.

We generated home ranges under M_A using three different thresholds for accumulated resources to evaluate how area-minimizing home ranges might vary across different thresholds. To set the three thresholds, we first summed V for each home range created using M_R and constructed the frequency distribution for these sums. We then chose the 25th, 33rd, and 50th percentiles as thresholds 1, 2, and 3. Using the final center points for the 100 home ranges constructed by M_R on each of the five landscapes, we constructed home ranges under M_A at each center point for each of the three thresholds.

4.2.2. Models with resource depression

We arbitrarily set the amount by which V was reduced for patches selected for home ranges to 0.15. V for each patch was reduced each time it was included in a home range, thereby setting a maximum number of home ranges that could use each patch, depending on its original value of V (e.g., a patch with an original value of 0.6 for V could be included in 4 home ranges at most). We set minimum V for reduced patches to 0. For Model M_{AD} , which depends on achieving a set resource threshold for termination of patch selection, we used the arbitrary Threshold two defined above

(the 33rd percentile of the distribution of summed V' for home ranges created on the same landscapes under M_R , without effects of resource depression).

Unlike the simulations we performed with models M_R and M_A , we did not use random starting points for constructing home ranges under M_{RD} and M_{AD} because home ranges constructed with resource depression are not independent of each other. A randomly located starting point might fall within an isolated neighborhood of high home range density and therefore heavy resource depression. Even though iterative patch selection for our models can adapt to local landscape configuration, the number of iterations required to move patch selection away from a highly depressed neighborhood would be truncated by reasonable limits on the number of iterations allowed in the simulations. To avoid this possible bias to our modeling results, we selected starting points for each home range generated by models M_{RD} and M_{AD} using moving windows analysis of the V distribution (Isaaks and Srivastava, 1989) on each simulated landscape. For each home range on each of the five landscapes, we calculated mean V for each 20×20 patch window (each window overlapped neighboring windows by 20×10 patches). Within the window with the highest mean, the moving windows analysis was repeated on increasingly smaller scales until the 4×4 window with the highest mean V was identified. The starting patch for home range construction was selected randomly from the patches with the highest value in this window. After each home range was constructed, we reduced V for patches included in the home range, then selected the starting patch for the next home range using moving windows analysis, and so on, until we had 100 home ranges for each model on each of the five simulated landscapes, for a total of 1000 simulated home ranges with resource depression.

4.3. Simulations

We created 100 home ranges under M_R , M_{RD} , and M_{AD} , and 300 under M_A , on each of the five simulated landscapes for a total of 3,000 simulated home ranges. For each home range, we calculated mean and sum for V of chosen cells. Although patches were selected for home ranges based on V' , the summary statistics for V represent traditional measures of habitat quality that might be estimated for home ranges based on their

resource content. We also calculated mean, standard deviation, and Moran's I for the distribution of V in the home range's neighborhood.

We evaluated the fragmentation of patches selected for each home range using the index, F :

$$F = 1 - \frac{\sum_{i=1}^n N_i}{N_{\max}}$$

where n is the number of cells selected to be in the home range, N_i the number of selected patches adjacent to patch i (maximum = 8), and N_{\max} is the sum of the number of patches adjacent to each patch in a circle of the same area as the home range. Because maximum of $\sum N_i$ increases with n , we standardized the index by dividing by N_{\max} . F values range from 0, indicating low fragmentation, to 1, indicating high fragmentation (Mitchell, 1997).

The spatial dispersion of home ranges on each simulated landscape also interested us, and we used an overlap index, O , to evaluate the overlap of one simulated home range with all other home ranges. We defined O for each home range as:

$$O = \frac{C_{\text{shared}}}{C_{\text{total}}} \times \bar{S}$$

where C_{shared} is the number of cells in a home range shared with at least one other home range, C_{total} the total number of cells in the home range, and \bar{S} is the mean number of home ranges incorporating each shared cell. Low values of O indicate little overlap, high values indicate high overlap (Mitchell, 1997).

4.4. Analyses

We excluded from analysis home ranges for which the iterations of patch selection were arbitrarily truncated by computing constraints and all home ranges exceeding 1,000 patches. To understand how patch selection and resource distributions interacted, we analyzed graphically how parameters for home ranges (area, mean V , summed V , fragmentation) and neighborhood V and V' (mean, standard deviation, spatial continuity) varied across the simulated landscapes from overdispersed to highly clumped. We compared home range parameters between all models graphically. To evaluate effects of resource depression, we compared the home ranges generated under M_{RD} and M_{AD} to those generated under M_R . We used only M_R

home ranges for comparison because they differed little from M_A home ranges generated with the resource threshold we used for M_{AD} home ranges (Threshold 2). We log-transformed all non-linear data for linear analyses.

We defined efficiency for a home range as the extent to which the resource content, V , of the home range was greater than what would be realized from a random use of the neighborhood (i.e., the magnitude of d in Fig. 1A). To distinguish how the spatial distribution of resources might affect the efficiency of home ranges, and to determine the extent to which the two home range strategies might vary in efficiency, we compared graphically efficiency of home ranges among the two home range models plotted against the simulated landscapes.

Even though starting points for our home ranges were randomly selected, the adaptability of the patch selection process to the local resource distribution meant that home range overlap and the dispersion of home ranges on a landscape should depend on the selection of patches by individuals and the distribution of resources on a landscape, and the number of home ranges on a landscape. With the number of home ranges on each landscape constant ($n = 100$), we addressed the first two factors by evaluating graphically how home range overlap generated by each model varied across the simulated landscapes. To identify patterns in spatial dispersion of home ranges, we used a moving windows analysis (Isaaks and Srivastava, 1989) of centers of simulated home ranges created under M_R , M_{RD} , and M_{AD} (M_A home ranges had the same center points as M_R) to estimate the mean number of home range centers contained in each 20×20 -patch window on each simulated landscape (each window overlapped each neighboring windows by 20×10 patches). The ratio of variance in number of centers/window to its mean indicates the degree to which home range centers are clumped on the landscape ($1 =$ consistent with random dispersal, $>1 =$ clumped dispersal, $<1 =$ even). We calculated this index of spatial dispersion for home range centers on each landscape and evaluated its variation across the landscapes graphically.

Because both home ranges and landscapes changed as M_{RD} or M_{AD} home ranges were added to a landscape, we believed the most interesting effects of resource depression would be found in changes within

home range and neighborhood parameters as the number of home ranges on a landscape increased. To evaluate these relationships, and to distinguish how these changes differed between resource-maximizing (M_{RD}) and area-minimizing (M_{AD}) home range strategies, we regressed parameters for models M_{RD} and M_{AD} and their neighborhoods on number of home ranges and compared the slopes of the relationships (PROC GLM, SAS Institute Inc, 1990). In the absence of complete territoriality, home range overlap should increase as home ranges are added to a landscape, but the rate of increase should be lower where resources are depressed (M_{RD} and M_{AD}) than where they are not (M_R). To assess how increase in overlap differed between home ranges with and without resource depression, we used tested O against sequence of construction and home range models M_{RD} , M_{AD} and M_R (PROC GLM, SAS Institute, Inc., 1990).

5. Results and discussion

We discarded 117 of the 3,000 simulated home ranges because they exceeded the size or iteration limits; the number of home ranges discarded did not vary consistently across simulated landscapes or home range models (Mitchell, 1997). For all home range parameters we discuss, the magnitude of differences between resource-maximizing (M_R and M_{RD}) and area-minimizing (M_A and M_{AD}) home ranges depended on the arbitrarily-set minimum resource threshold. Changing the threshold alters how home ranges compare between models within each landscape, but patterns of home ranges across landscapes remain consistent for each model. Similarly, rates of change in home range and neighborhood parameters as home ranges increased on a landscape depended on the magnitude of the arbitrarily-set level of resource depression for patches used in a home range. Changing the level of resource depression, however, should change only the magnitude of trends without reversing them and should affect both home range models equally.

5.1. Home ranges

5.1.1. Models without resource depression

Model M_R created home ranges that maximized resource accumulation over random use of each simu-

lated landscape (i.e., resource maximization). Model M_A created home ranges of minimal size that contained a threshold level of resources necessary for survival or reproduction (i.e., area minimization). Home ranges produced by both models were generally similar in fragmentation, quality and efficiency (compare Figs. 4 and 5); differences between M_R and M_A home ranges in area and resource accumulation were a func-

tion of the magnitude of required resource thresholds defined for M_A home ranges.

Unlike M_R home ranges whose sizes varied little across the landscape types, M_A home ranges were largest on landscapes with low to moderately clumped resources, with the difference becoming more pronounced as the resource threshold increased (Fig. 5A). The decrease in resource (V) accumulation in M_A

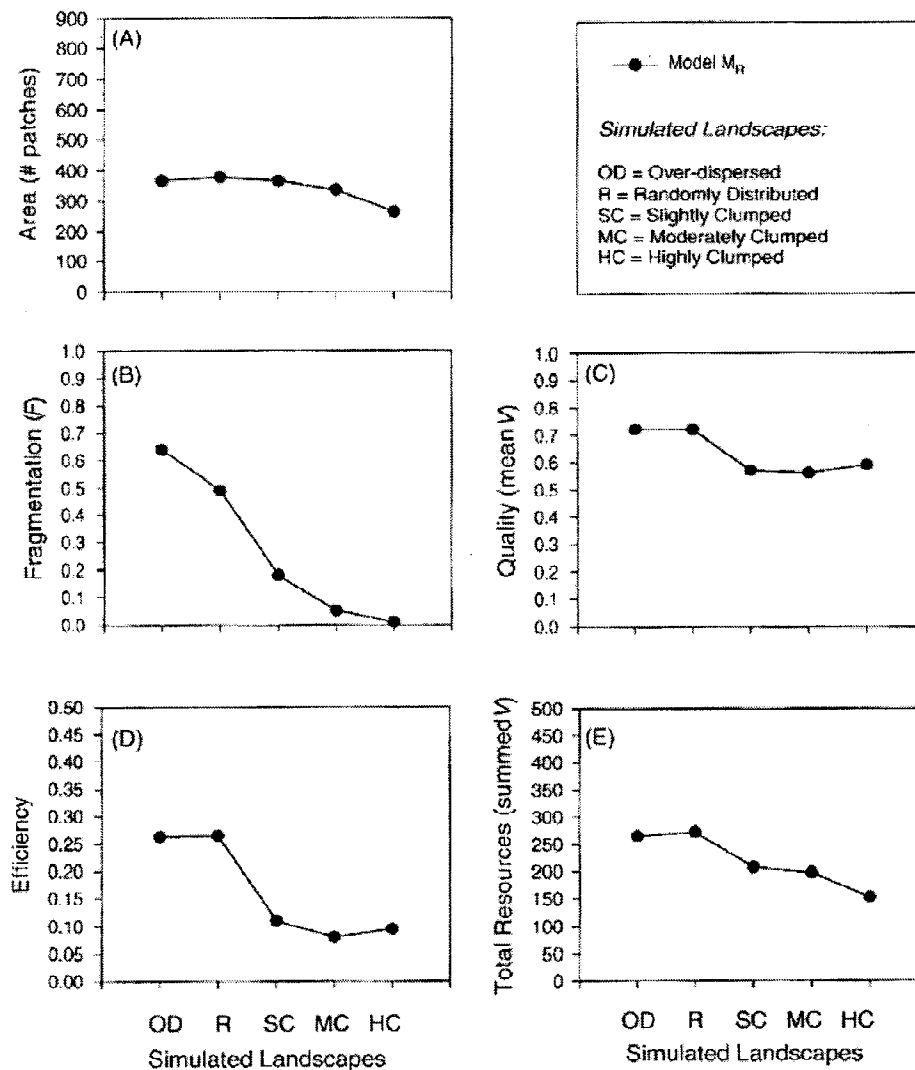


Fig. 4. Relationships of simulated home ranges created using patch selection designed to maximize resource density (Model M_R) with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. On each of the five landscapes 100 simulated home ranges were created under model M_R which selects patches to maximize resource accumulation of V discounted for travel costs (V') over random use of the landscape. (A) depicts area of home ranges (number of patches of equal size), (B) depicts fragmentation of home ranges (fragmentation index F , see text), (C) depicts quality of home ranges (mean V), (D) depicts efficiency of home ranges (the extent that resource accumulation in home ranges exceeded that for random use), and (E) depicts total resources contained in the home ranges (summed V). Means for home ranges generated under each model are shown.

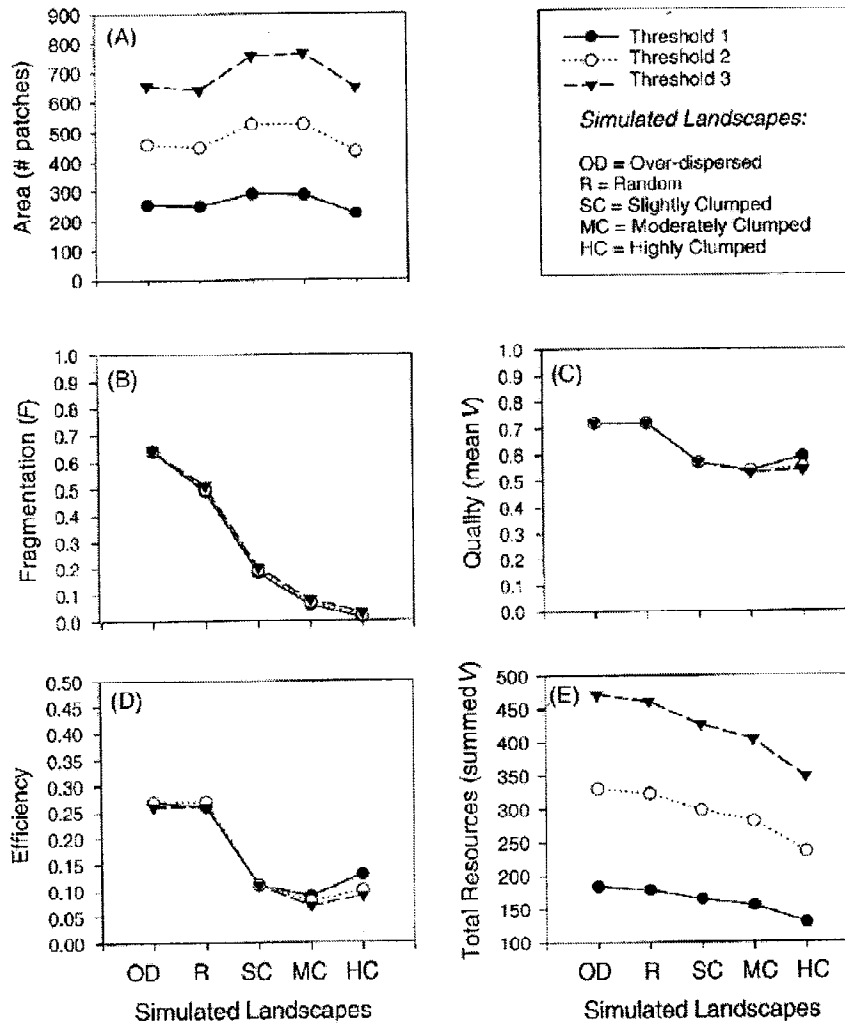


Fig. 5. Relationships of simulated home ranges created using patch selection designed to optimally satisfy a minimum resource threshold for survival and reproduction (Model M_A) with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. One-hundred simulated home ranges were created under model M_A for each of three minimum resource thresholds on each of the five simulated landscapes. (A) depicts area of home ranges (number of patches of equal size), (B) depicts fragmentation of home ranges (fragmentation index F , see text), (C) depicts quality of home ranges (mean V), (D) depicts efficiency of home ranges (the extent that home ranges exceeded resource accumulation over random use), and (E) depicts total resources contained in the home ranges (summed V). Means for home ranges generated under each model are shown.

home ranges with increased clumping of resources on the landscape also became more pronounced with an increase in resource threshold (Fig. 5E). Differences among landscapes in M_A home ranges areas and accumulated resources were most pronounced for the largest threshold (Fig. 5A and E). Area and accumulated resources increased proportionally with threshold, however, causing quality and efficiency of home ranges (Fig. 5C and D) to be similar for all

thresholds for each simulated landscape. The only exception to this pattern was a slight divergence where resources were most clumped; home ranges built with low thresholds had relatively high quality and efficiency because they could meet threshold requirements with a small number of highly aggregated patches of high quality (Fig. 5C). Intuitively, home range overlap increased with the size of the minimum resource threshold used in the model (Fig. 6).

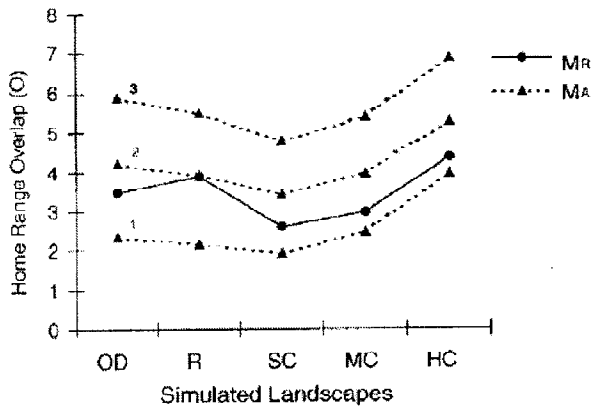


Fig. 6. Relationships of overlap (overlap index O) among simulated home ranges with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. One-hundred simulated home ranges were created under resource-maximizing model M_R and area-minimizing model M_A on each of the five simulated landscapes. M_A home ranges were generated under three different minimum resource thresholds (100 home ranges each) and share a common symbol and dashed line in the figure (labels 1, 2, and 3 associated with each M_A line indicate thresholds 1 [low] to 3 [high]). The overlap index, O , is a measure of home range overlap that includes the number of cells shared within each home range, as well as the number of home ranges sharing those cells, at the time the home range was constructed. High values of O indicate high overlap. Means for home ranges generated under each model are shown.

5.2. Models with resource depression

Home ranges produced by models M_{RD} and M_{AD} were generally similar in area, fragmentation, quality, efficiency, resource content (Fig. 7) and overlap (Fig. 8). Although differences between landscape-optimizing and area-minimizing home ranges are largely due to the resource threshold that must be satisfied in the latter case, it is informative that, on the average, resource depression did not affect the two strategies differently for these parameters across the different landscapes. Home ranges under M_{RD} and M_{AD} exhibited relationships with landscape characteristics similar to the same number of home ranges where resource values were not depressed (M_R), with some differences. M_{RD} and M_{AD} home ranges were smaller (Fig. 7A), of lower quality (mean V , Fig. 7C) and contained fewer resources (summed V , Fig. 7E) than M_R home ranges across all landscapes. M_{RD}

and M_{AD} home ranges were also slightly less fragmented (Fig. 7B) and less efficient (Fig. 7D) than M_R home ranges on landscapes with little or no clumping of resources. These patterns, however, are specific to the number of simulated home ranges placed on each landscape (100 for these simulations). Because resource values are depressed for every home range under M_{RD} and M_{AD} , increasing the number of home ranges over 100 on a landscape would likely increase differences observed between home ranges with and without resource depression.

5.3. Relationships between home ranges and landscapes

5.3.1. Models without resource depression

The ability of our home range models to adapt to landscape configuration because home range centers moved during successive iterations of patch selection represented habitat selection at a neighborhood level, as opposed to a patch level. Neighborhoods selected by home ranges did not differ across landscape types in mean resource quality or variability, nor did the neighborhoods differ in quality and variability from landscape averages (Table 1; Fig. 9A and B). Neighborhoods did, however, differ from their respective landscape averages in spatial variability. Except for the over-dispersed landscape (Landscape OD), which was homogenous on a broad scale, home range centers settled on neighborhoods with relatively high spatial continuity of resources on each landscape (Table 1, Fig. 9C). Neighborhoods tended to be largest where resources were slightly to moderately clumped (Fig. 9D), reflecting the size of the area needed to capture 95% of the variability in V on these distributions. The relatively large size of the neighborhoods on landscapes with slightly to moderately clumped resources (Fig. 9D), paired with the size of the M_A home ranges on those landscapes (Fig. 5A), suggests an effect of grain of heterogeneity on a landscape important to the configuration of home ranges. Home ranges should be relatively small where resource distributions are homogeneous or heterogeneous on a fine grain. Where clumping begins to result in small to moderate aggregations of both high and low quality patches, an area-minimizing animal would be required to include aggregations of low quality patches in its home range, even in a high quality neighborhood, and

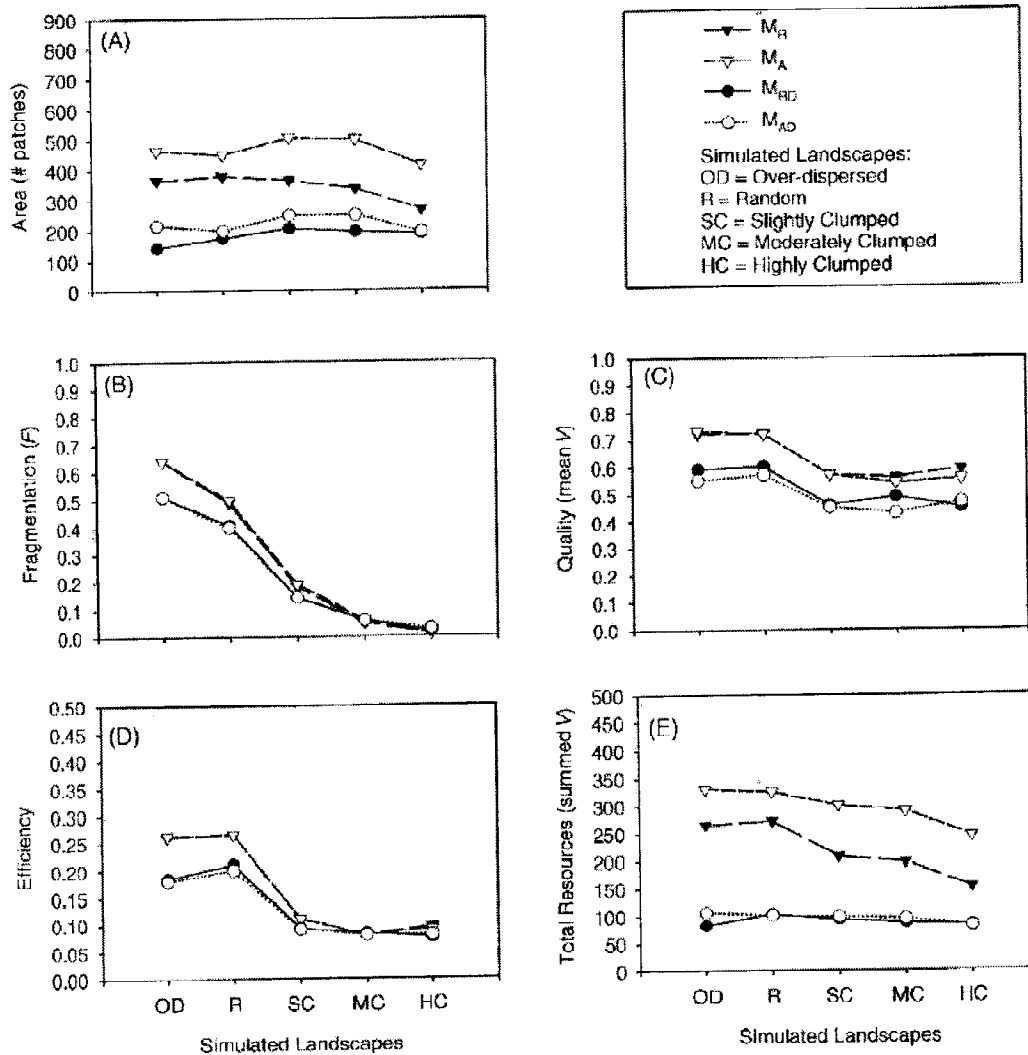


Fig. 7. Relationships of simulated home ranges with resource depression (Models M_{RD} and M_{AD}) with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. On each of the five landscapes 100 simulated home ranges were created under models M_{RD} and M_{AD} which selected patches to maximize resource accumulation of V discounted for travel costs (V) over random use of the landscape and to meet a set resource threshold, respectively. Parameters observed for home ranges created without resource depression (model M_R) are displayed for comparison. (A) depicts areas of home ranges (number of patches of equal size), (B) depicts fragmentation of home ranges (fragmentation index F , see text), (C) depicts quality of home ranges (mean V), (D) depicts the efficiency of home ranges (the extent that resource accumulation in home ranges exceeded that for random use), and (E) depicts the total resources contained in the home ranges (summed V). Means for home ranges generated under each model are shown.

therefore would require a larger home range to reach its threshold.

Landscape configuration had important effects on characteristics of simulated home ranges resulting from habitat selection at the patch level (e.g., Fig. 10). Overall, home range area (defined as the number of patches of equal area included in a home range)

remained relatively consistent across simulated landscapes for both models (Figs. 4A and 5A), decreasing only where spatial continuity of resources was highest. This suggests there should be little relationship between the spatial dispersion of resources (V) and home range size (measured in quantity of equally sized patches selected), except where resources are

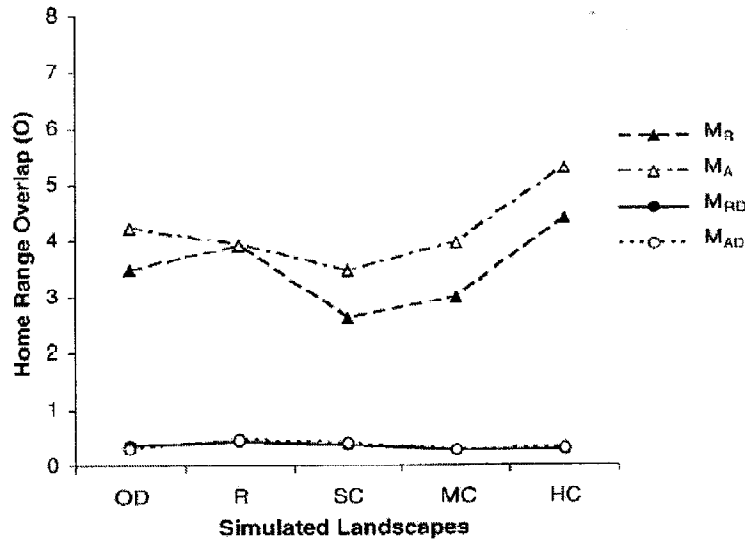


Fig. 8. Relations of overlap (overlap index O) among simulated home ranges with resource depression with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. One-hundred simulated home ranges with resource depression were created under landscape-optimizing model M_{RD} and area-minimizing model M_{AD} on each of the five simulated landscapes. Overlap of home ranges created without resource depression (models M_R and M_A) are displayed for comparison. The overlap index, O , is a measure of home range overlap that includes the number of cells shared within each home range, as well as the number of home ranges sharing those cells, at the time the home range was constructed. High values of O indicate high overlap. Means for home ranges generated under each model are shown.

both rich and highly clumped and home ranges are relatively small and conform closely in shape to clumps of patches. The size of an animal's home range, therefore, should be almost entirely determined by the distribution of resources weighted for travel costs (V'), and secondarily by the behavioral strategy underlying its selection of patches.

Conversely, the distribution of resources strongly affected the spatial structure of simulated home ranges. Fragmentation of home ranges (F) decreased for both models as spatial continuity of resources increased (Figs. 4B and 5B). This pattern is intuitive: where resources are widely dispersed, so should be patches selected for a home range. By valuing resources for their proximity, an animal can select patches that balance costs and benefits of resource ownership, and non-selected patches will be largely irrelevant (presuming they do not bar access to selected patches). Hence, on a landscape with even or randomly-distributed resources, much of an animal's perception of its home range might consist of empty, or useless, space separating areas of importance (Powell, 2000). Whereas an animal may need to cross non-selected, interstitial

patches to reach those it has selected, such use would have little to do with patch characteristics and therefore would be largely irrelevant to understanding why the animal has the home range it does. Comparing predictions of a patch-selection model to observed home ranges based on animal movements therefore can be problematic where resources are broadly distributed.

Unlike home range area, the quality (mean V) of simulated home ranges varied across simulated landscapes. Counter-intuitively, quality was highest where spatial continuity of resources was low, decreasing as spatial continuity increased, except where clumping of resources was greatest (Landscape HC; Figs. 4C and 5C). Efficiency (the extent the home range of a selective animal improves over random use of the landscape) of home ranges across landscapes demonstrates the same pattern (Figs. 4D and 5D). This suggests that animals can make good use of an even or random distribution of resources (what might strike an observer as marginal habitat), by selecting few high quality patches while ignoring the equally available patches of poor quality. Selectivity pays its highest rewards where high quality resources are well-dispersed.

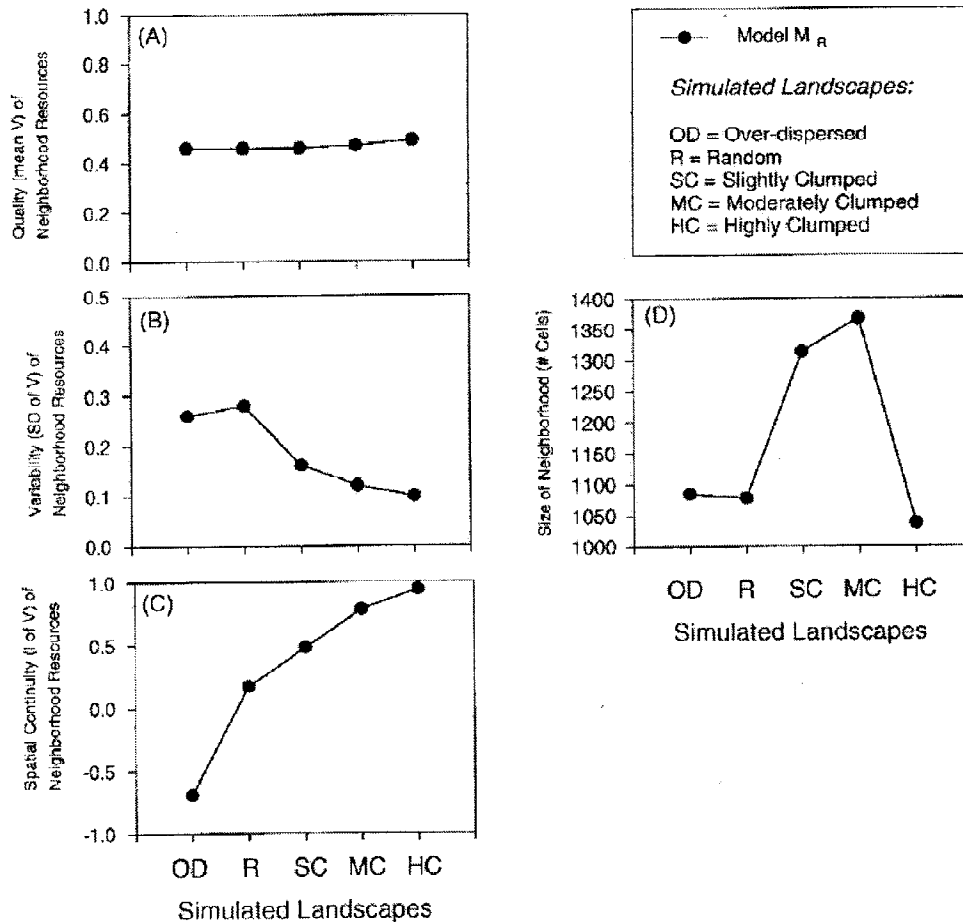


Fig. 9. Relationship of quality, variability, and spatial continuity of resources (mean, standard deviation and Moran's I of resource value, V , respectively) within neighborhoods of simulated home ranges with the simulated landscapes on which the home ranges were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. 100 simulated home ranges were created under model M_R based on optimal selection of patches containing these resources, and a neighborhood consisted of that portions of the landscape from which patches were selected for each home range. Means for neighborhoods associated with home ranges generated are shown.

Where resources are clumped, the potential to improve over random use of the landscape (i.e., the magnitude of d , Fig. 1) declines because as resources become more clumped in distribution, the aggregation of like-valued patches increases for both high and low quality patches. Unable to select only small, high quality patches within a reasonable distance, an animal must therefore include larger, more marginal patches in its home range (e.g., a nearby patch of low quality will have a higher value than a distant patch of high quality). This trend continues as clumping increases until aggregations of high quality patches converge in size with the neighborhood defining patch availability for an animal, beyond which resources have little value.

At this point, an aggregation of high quality patches can support an entire home range, requiring the animal to select few, if any, marginal patches and resulting in a nearly homogeneous, high quality home range. We would expect the increasing trend in quality and efficiency seen for Landscape HC to continue for resource distributions that are even more clumped than those we evaluated.

Accumulation of resources (summed V) generally declined as spatial continuity of resources increased (Figs. 4E and 5E). Like the pattern for home range quality, this at first appears counterintuitive. Again, the increased scale of patchiness with slight to moderate clumping of resources (e.g., Landscapes SC and MC)

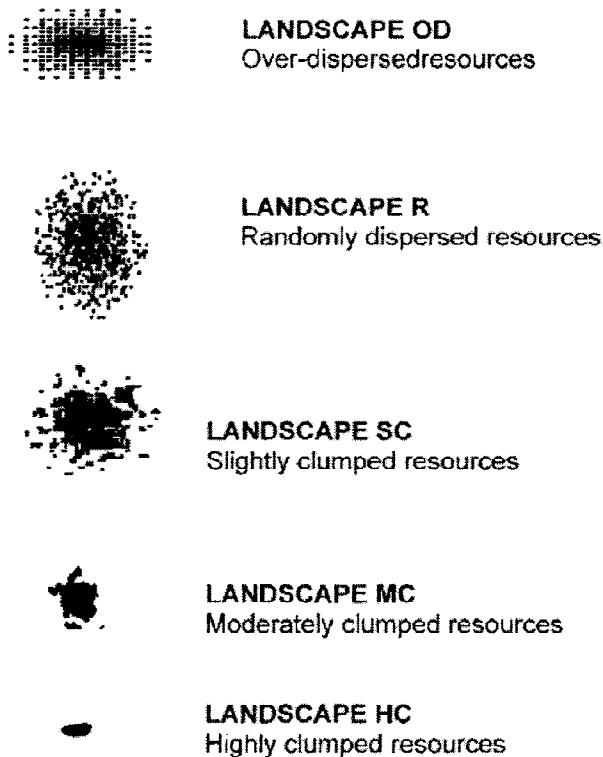


Fig. 10. Examples of simulated home ranges generated under home range model M_R on five different simulated landscapes consisting of spatial distributions of resource values, V , and that differed only in the spatial continuity. Spatial continuity of the landscapes was indexed using the Moran's I statistic, which ranges from -1 (over-dispersed) to 1 (highly continuous). Scale of depiction is the same for all home ranges.

should require an animal to include more marginal cells in its home range on these landscapes than on evenly or randomly distributed landscapes, reducing the total accumulation of resources per unit area within its home range. This cannot hold true, however, where clumping is great because an animal on a large aggregation of high quality patches will not need to include many marginal cells in its home range. Our models portray an animal selecting patches based on their resource value adjusted for travel costs (V' instead of V). An animal making these decisions in a large patch of high quality should perceive a relatively small neighborhood comprising relatively high values of V' . In this case, maximizing the efficient use of resources (represented in V') differs from simply maximizing their accumulation (summed V); an animal might have the capacity to garner many resources but at some point

begins to suffer a decrease in efficiency by doing so. On a rich, highly clumped landscape, relative efficiency of a home range can be very high, satisfying an animal's needs with fewer resources than required on a more heterogeneous landscape.

The spatial distributions of simulated home ranges depended strongly on how resources were distributed on the simulated landscapes. Overlap of home ranges was highest where spatial continuity of resources was either low (because evenly-spaced, high-value cells were incorporated into many spatially diffuse home ranges) or very high (because home ranges clustered on large patches of high-value cells); overlap was lowest where clumping of resources was slight to moderate because home ranges were more contiguous than those on evenly-distributed resource distributions, but less clustered than those on highly clumped distributions (Fig. 6). The centers of home ranges tended to be clumped on all landscapes, but clumping of home ranges increased with clumping of resources on a landscape (Fig. 11). These results suggest home ranges of animals in a population on a diffuse landscape will be widely and evenly distributed, with all high quality patches shared among several home ranges. Where resources are highly clumped, home ranges within a population will aggregate on high quality ecological patches with extensive sharing of cells. In the mid-range, where resources are less clumped and animals make more use of relatively poor-quality patches (see above), sharing of marginal patches by animals will be less consistent than sharing of high-quality patches on landscapes with evenly distributed or highly clumped resources. Whereas a high-value patch might be valuable to numerous nearby animals in its vicinity and included in as many home ranges, a low-value patch will be valuable only to animals in its immediate vicinity and therefore included in fewer home ranges.

5.3.2. Models with resource depression

The spatial distributions of M_{RD} and M_{AD} home ranges on the simulated landscapes differed considerably from M_R home ranges. Home range overlap was much lower for M_{RD} and M_{AD} home ranges than for M_R home ranges, and varied little with landscape configuration (Fig. 8). Spatial dispersion of home ranges (the variance to mean ratio of home range centers) differed, however, among all three home range models ($F_{2,12} = 36.98$, $P < 0.01$; Fig. 11). The spatial distri-

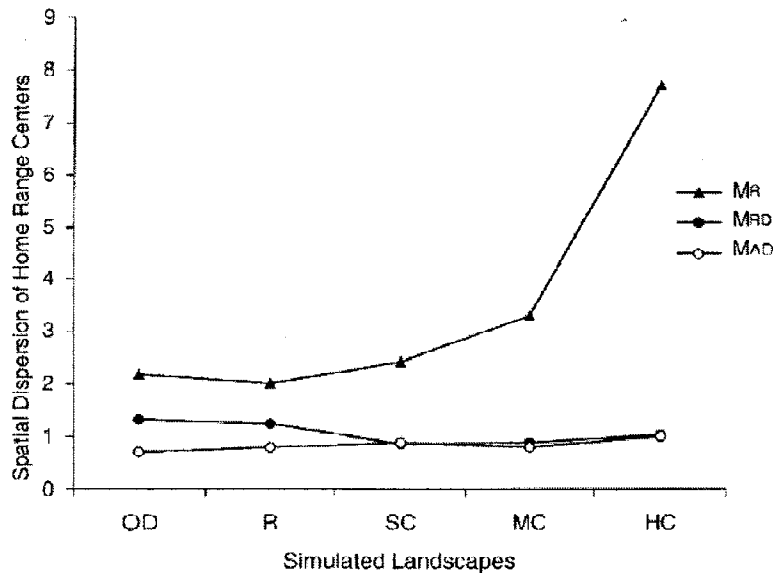


Fig. 11. Relationships of spatial dispersion of centers among simulated home ranges (models M_R , M_{RD} and M_{AD}) with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V ranging from over-dispersion to highly clumped. One-hundred simulated home ranges each were generated each model on each of the five simulated landscapes. Home ranges generated by model M_A are not presented because they had the same centers as those created under M_R . Spatial dispersion of home range centers was evaluated using a moving windows analysis of the ratio of mean number of home range centers to its variance for every 20×20 cell window for each landscape. A ratio <1 indicates an even dispersion, a ratio >1 indicates a clumped dispersion. A ratio of 1 indicates a dispersion that can not be distinguished from random. Means for home ranges are shown.

butions of home ranges with resource depression were more evenly distributed than those without and could not be distinguished from random across all landscapes (Fig. 11). The difference between home ranges with and without resource depression was most pronounced where resources were most clumped, whereas M_R home ranges were strongly clumped on landscape HC, the distribution M_{RD} and M_{AD} home ranges was not distinguishable from random. These results suggest that whereas home ranges of animals that protect or consume resources may be structurally similar to those of animals who do not, they will be distributed more evenly on the landscape and overlap each other less, potentially showing little relationship to the distribution of resources.

Models M_{RD} and M_{AD} emulate the situation where new animals making use of a landscape perceive a different distribution of resources than do their predecessors. In our simulations, characteristics of home ranges where animals deplete resources depended on the number of simulated home ranges created on a given landscape. Therefore, exploring how home

ranges change as the number of home ranges on a landscape increases clarifies the effects of resource depression and contrasts alternative home range strategies.

Initial home ranges placed on each landscape encountered few or no patches included in other home ranges and were generally indistinguishable from home ranges constructed by models that do not incorporate resource depression. As the number of home ranges on a landscape increased, however, home range area increased and quality (mean V) decreased for both resource-maximizing (M_{RD}) and area-minimizing (M_{AD}) home ranges. Theoretically, area should not have changed at all for resource-maximizing home ranges (Fig. 1A) and, indeed, did so at a much lower rate ($F_{2,960} = 256.21$, $P < 0.01$) than for M_{AD} home ranges (Fig. 12A). The slight though statistically significant increase in area for M_{RD} home ranges may be due to the heterogeneous way in which resource values declined across a landscape as home ranges were added. Because resource values did not decline uniformly across landscapes,

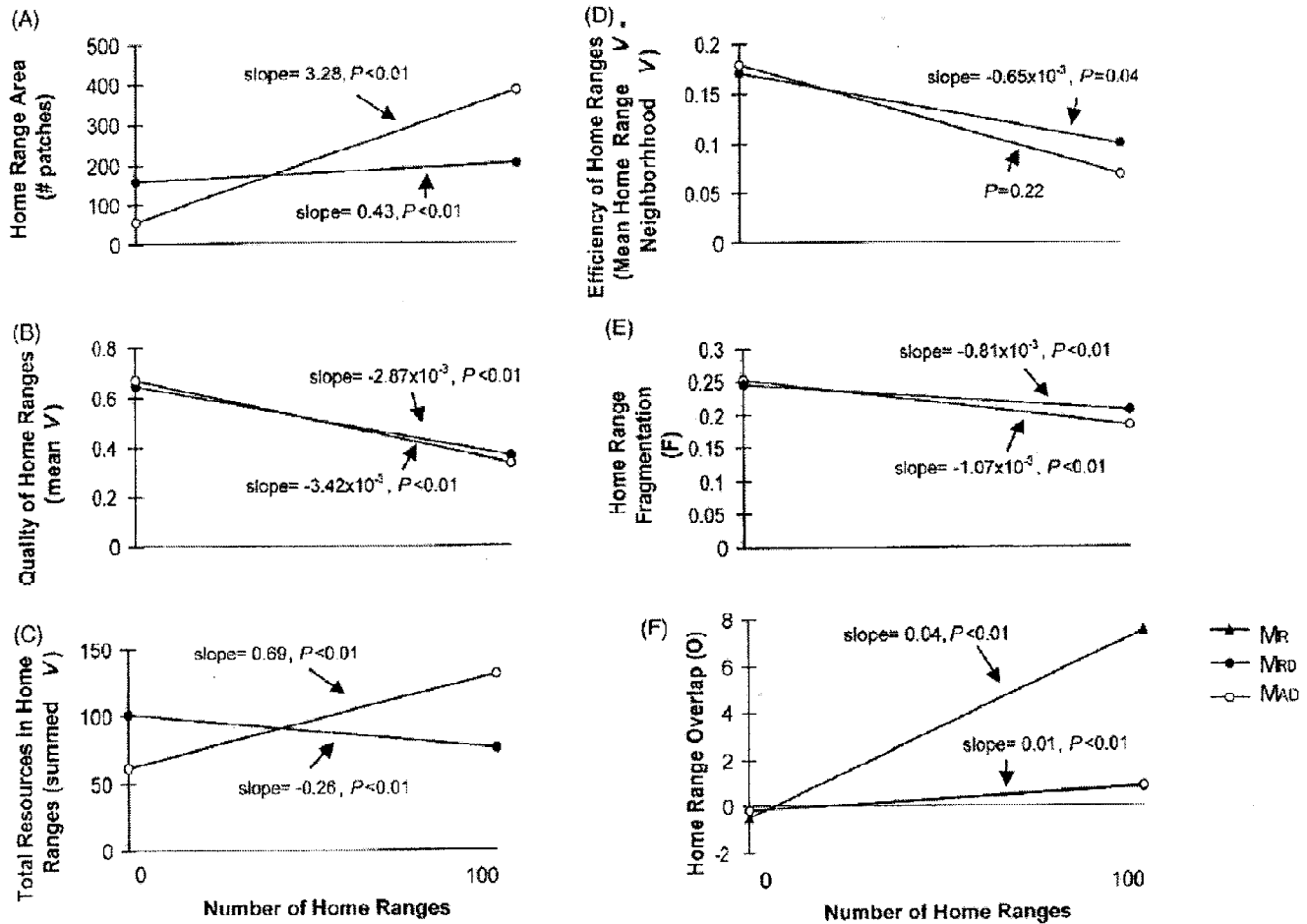


Fig. 12. Linear regressions of changes in home range parameters of simulated home ranges generated using models M_{RD} and M_{AD} as the number of home ranges added to landscapes increased. One-hundred simulated home ranges were performed under each of the two home range models on each of five simulated landscapes (spatially explicit distributions of resource values, V) differing only in spatial continuity of V , ranging from over-dispersion (Landscape OD) to highly clumped (Landscape HC). Fig. 13A depicts changes in home range area (number of selected patches of equal size), 13B depicts changes in home range quality (mean V), 13C depicts changes in total resources contained in home ranges (summed V), 13D depicts changes in fragmentation (F) of home ranges, 13E depicts changes in efficiency of home ranges (the extent that resource accumulation in home ranges exceeded that for random use), 13F depicts changes in home range overlap (O). Changes in overlap for home ranges created without resource depression (model M_R) are displayed in 13F for comparison (note: lines for M_{RD} and M_{AD} are identical).

rates of resource accumulation (summed V) through efficient patch selection did not decline as quickly as did those for random patch selection, in effect shifting A_R in Fig. 1B to the right. Quality of M_{AD} home ranges was initially higher than that for M_{RD} home ranges, but as home ranges were added quality decreased faster ($F_{2,960} = 617.63$, $P < 0.01$) for M_{AD} home ranges than for M_{RD} home ranges (Fig. 12B). In addition, resource accumulation (summed V , as opposed to V') decreased for M_{RD} home ranges as

home ranges were added but increased for M_{AD} home ranges ($F_{2,960} = 61.38$, $P < 0.01$; Fig. 12C). Efficiency of both M_{RD} and M_{AD} home ranges declined as home ranges were added. Efficiency of M_{AD} home ranges was initially higher than that for M_{RD} home ranges but decreased faster as home ranges were added ($F_{2,960} = 88.73$, $P < 0.01$; Fig. 12D). Home range fragmentation decreased slightly for both models as home ranges were added and the difference between the models was marginal ($F_{2,960} = 2.84$,

$P = 0.06$; Fig. 12E). Increase in home range overlap as home ranges were added differed over all home range models ($F_{5,2373} = 491.12$, $P < 0.01$). Increase in overlap as home ranges were added to a landscape was high for home ranges without resource depression whereas overlap increased only slightly for models that did (Fig. 12F).

Changes in home ranges as more were added to a landscape were brought about by changes in the distributions of resources due to resource depression in home ranges. Quality of resources (mean V) in neighborhoods of home ranges decreased for both M_{RD} and M_{AD} home ranges as more were added, declining at a slightly faster rate ($F_{2,960} = 1970.97$, $P < 0.01$) for M_{AD} home ranges (Fig. 13A). The variability of neighborhood resources decreased for both M_{RD} and M_{AD} home ranges as home ranges were added, again at a slightly greater rate ($F_{2,960} = 77.08$, $P < 0.01$) for M_{AD} home ranges (Fig. 13B). M_{RD} and M_{AD} home ranges differed in their effects on the spatial continuity (Moran's I) of resources in neighborhoods ($F_{2,960} = 3.06$, $P = 0.04$); M_{RD} home ranges did not significantly affect spatial continuity of resources as home ranges were added, but M_{AD} home ranges tended to increase spatial continuity (Fig. 13C).

Our simulations suggest that resource depression by animals can have a strong effect on the landscape, which in turn can strongly affect the use of space by animals. As more animals use a landscape, they sequester the best resources first and thereby diminish and homogenize the resources available to subsequent animals, reducing the quality and variability of resources while increasing their spatial continuity. How animals respond to these changes in habitat will depend on strategies they might use to establish their home ranges.

Home ranges chosen by resource-maximizing animals will be relatively unaffected by resource depression because, as we modeled them, they do not have to satisfy a minimum resource threshold within their home ranges. As habitat declines in quality for them (Fig. 13A), so does the resource content of their home ranges (Fig. 12C) because patches are selected based only on maximizing resource density over random use of the landscape. Theoretically, a landscape can support a very large number of these home ranges, each a selection of the best patches available from an increasingly marginal landscape. Obviously,

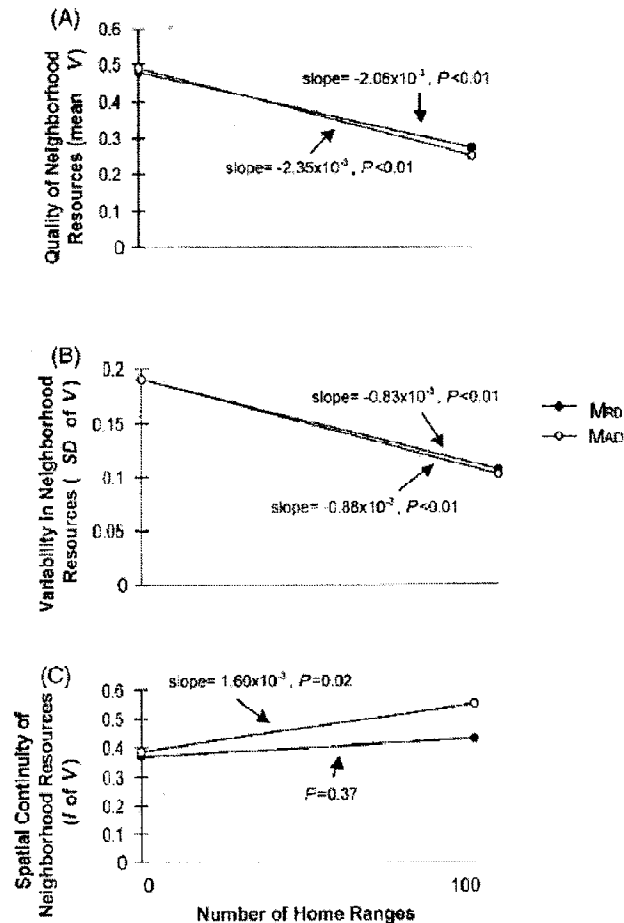


Fig. 13. Linear regressions of changes in parameters of neighborhood resource values (V) associated with simulated home ranges generated using models M_{RD} and M_{AD} as the number of home ranges added to landscapes increased. One-hundred simulated home ranges were performed under each of the two home range models on each of five simulated landscapes (spatially explicit distributions of resource values, V) differing only in spatial continuity of V , ranging from over-dispersion (Landscape OD) to highly clumped (Landscape HC). Fig. 14A depicts changes in quality of neighborhood resource values (mean V), 14B depicts changes in variability of the quality of neighborhood resources (standard deviation of V), 14C depicts changes in the spatial continuity of resources (Moran's I of V).

a more realistic portrayal of the choices made by a resource-maximizing animal would include some resource threshold below which the animal could not survive, requiring a shift in strategies (e.g., to area-minimization) to meet at least this minimum.

The home ranges of area-minimizing animals will react the most strongly to changes in a landscape. Colonizing or dominant individuals with primacy of

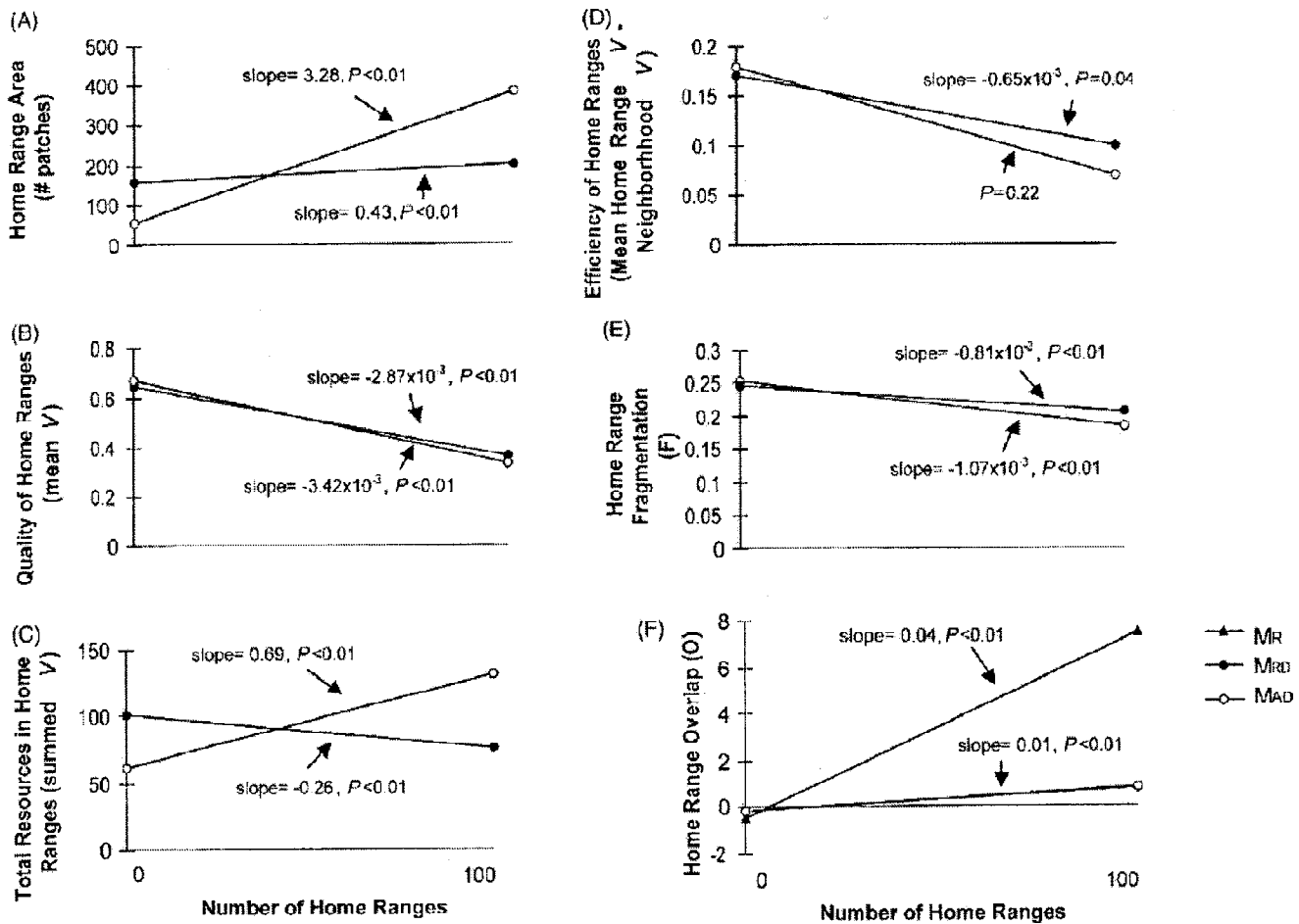


Fig. 12. Linear regressions of changes in home range parameters of simulated home ranges generated using models M_{RD} and M_{AD} as the number of home ranges added to landscapes increased. One-hundred simulated home ranges were performed under each of the two home range models on each of five simulated landscapes (spatially explicit distributions of resource values, V) differing only in spatial continuity of V , ranging from over-dispersion (Landscape OD) to highly clumped (Landscape HC). Fig. 13A depicts changes in home range area (number of selected patches of equal size), 13B depicts changes in home range quality (mean V), 13C depicts changes in total resources contained in home ranges (summed V), 13D depicts changes in fragmentation (F) of home ranges, 13E depicts changes in efficiency of home ranges (the extent that resource accumulation in home ranges exceeded that for random use), 13F depicts changes in home range overlap (O). Changes in overlap for home ranges created without resource depression (model M_R) are displayed in 13F for comparison (note: lines for M_{RD} and M_{AD} are identical).

rates of resource accumulation (summed V') through efficient patch selection did not decline as quickly as did those for random patch selection, in effect shifting A_R in Fig. 1B to the right. Quality of M_{AD} home ranges was initially higher than that for M_{RD} home ranges, but as home ranges were added quality decreased faster ($F_{2,960} = 617.63$, $P < 0.01$) for M_{AD} home ranges than for M_{RD} home ranges (Fig. 12B). In addition, resource accumulation (summed V , as opposed to V') decreased for M_{RD} home ranges as

home ranges were added but increased for M_{AD} home ranges ($F_{2,960} = 61.38$, $P < 0.01$; Fig. 12C). Efficiency of both M_{RD} and M_{AD} home ranges declined as home ranges were added. Efficiency of M_{AD} home ranges was initially higher than that for M_{RD} home ranges but decreased faster as home ranges were added ($F_{2,960} = 88.73$, $P < 0.01$; Fig. 12D). Home range fragmentation decreased slightly for both models as home ranges were added and the difference between the models was marginal ($F_{2,960} = 2.84$,

$P = 0.06$; Fig. 12E). Increase in home range overlap as home ranges were added differed over all home range models ($F_{5,2373} = 491.12$, $P < 0.01$). Increase in overlap as home ranges were added to a landscape was high for home ranges without resource depression whereas overlap increased only slightly for models that did (Fig. 12F).

Changes in home ranges as more were added to a landscape were brought about by changes in the distributions of resources due to resource depression in home ranges. Quality of resources (mean V) in neighborhoods of home ranges decreased for both M_{RD} and M_{AD} home ranges as more were added, declining at a slightly faster rate ($F_{2,960} = 1970.97$, $P < 0.01$) for M_{AD} home ranges (Fig. 13A). The variability of neighborhood resources decreased for both M_{RD} and M_{AD} home ranges as home ranges were added, again at a slightly greater rate ($F_{2,960} = 77.08$, $P < 0.01$) for M_{AD} home ranges (Fig. 13B). M_{RD} and M_{AD} home ranges differed in their effects on the spatial continuity (Moran's I) of resources in neighborhoods ($F_{2,960} = 3.06$, $P = 0.04$); M_{RD} home ranges did not significantly affect spatial continuity of resources as home ranges were added, but M_{AD} home ranges tended to increase spatial continuity (Fig. 13C).

Our simulations suggest that resource depression by animals can have a strong effect on the landscape, which in turn can strongly affect the use of space by animals. As more animals use a landscape, they sequester the best resources first and thereby diminish and homogenize the resources available to subsequent animals, reducing the quality and variability of resources while increasing their spatial continuity. How animals respond to these changes in habitat will depend on strategies they might use to establish their home ranges.

Home ranges chosen by resource-maximizing animals will be relatively unaffected by resource depression because, as we modeled them, they do not have to satisfy a minimum resource threshold within their home ranges. As habitat declines in quality for them (Fig. 13A), so does the resource content of their home ranges (Fig. 12C) because patches are selected based only on maximizing resource density over random use of the landscape. Theoretically, a landscape can support a very large number of these home ranges, each a selection of the best patches available from an increasingly marginal landscape. Obviously,

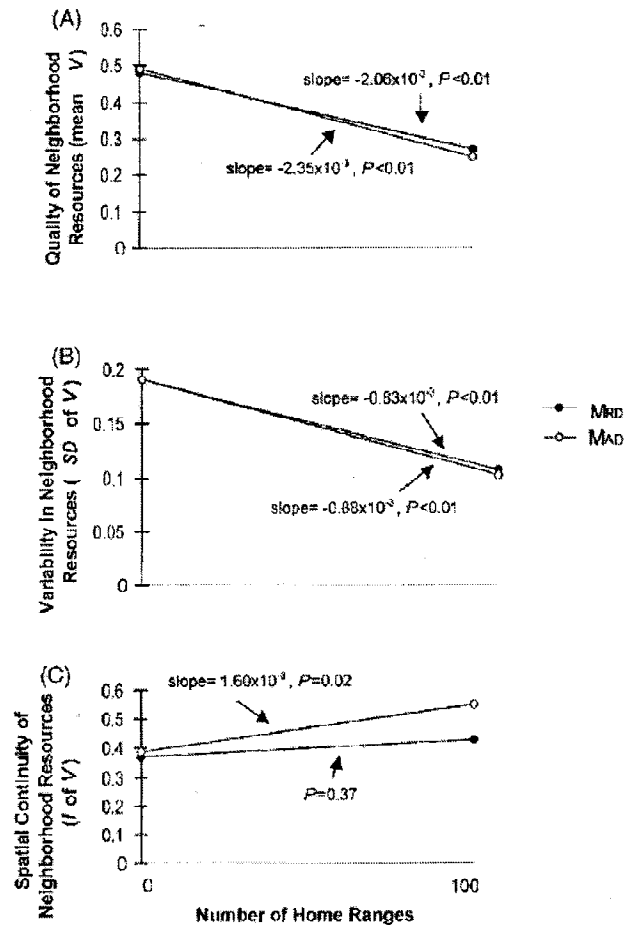


Fig. 13. Linear regressions of changes in parameters of neighborhood resource values (V) associated with simulated home ranges generated using models M_{RD} and M_{AD} as the number of home ranges added to landscapes increased. One-hundred simulated home ranges were performed under each of the two home range models on each of five simulated landscapes (spatially explicit distributions of resource values, V) differing only in spatial continuity of V , ranging from over-dispersion (Landscape OD) to highly clumped (Landscape HC). Fig. 14A depicts changes in quality of neighborhood resource values (mean V), 14B depicts changes in variability of the quality of neighborhood resources (standard deviation of V), 14C depicts changes in the spatial continuity of resources (Moran's I of V).

a more realistic portrayal of the choices made by a resource-maximizing animal would include some resource threshold below which the animal could not survive, requiring a shift in strategies (e.g., to area minimization) to meet at least this minimum.

The home ranges of area-minimizing animals will react the most strongly to changes in a landscape. Colonizing or dominant individuals with primacy of

place will enjoy small, highly efficient home ranges. At some point, subsequent or subordinate animals will require increasingly larger home ranges to satisfy the same resource requirements (Fig. 12A). The efficiency of new home ranges will continually decline as more remote and poor quality (Fig. 12B) patches are included in home ranges. Total resource content of home ranges will increase (Fig. 12C), but the costs in terms of travel distance would strongly offset the value of so many resources. Unlike for the resource-maximizing model, the requirement of a home range to meet an absolute resource minimum sets a limit on the number of viable home ranges a landscape can support. At some point as a population grows, a landscape becomes unable to support any more home ranges that meet the minimum resource requirement, setting a carrying capacity for that landscape.

Our results suggest resource depression also strongly affects how a population of animals can be distributed on a landscape. Intuitively, animals that consume or protect key resources should be more widely dispersed on a landscape than those that do not, and our simulations support this. Models that included resource depression created a spatial pattern of home ranges on landscapes different from that seen for those that did not (Figs. 11 and 12F). In the absence of resource depression, nothing constrained the clustering of home range centers, particularly for highly clumped distributions, and overlap was high. The homogenizing effects of resource depression on the spatial distribution of resources (Fig. 13), however, resulted in more evenly dispersed home ranges (Fig. 11). Interestingly, the spatial distribution of resources did not affect home range overlap among home ranges with resource depression and those that did not (Fig. 8). This suggests that, for equal numbers of animals that consume or protect resources on different landscapes, the distribution of resources has no predictive value for the overlap of home ranges.

5.4. *Insights and general predictions*

Ours are the first mechanistic home range models based on optimal use of resources distributed on a landscape. Our models differ from the only other mechanistic home range model of which we know (Lewis and Murray, 1993; Moorcroft et al., 1999) in important ways. The model of Lewis and Murray

(1993) was based on movement, using correlated random walk models structured according to the location of scent markings, it did not relate home ranges to resources and it was limited to carnivores. By contrast, our models are based on optimal selection of resource-bearing patches, presumably the foundation (i.e., the cognitive map, Peters, 1978) underlying the movements of animals. Further, our models are general and can be applied to any taxonomic group for which the spatial distribution of resources or habitat quality can be quantified, and are particularly well suited for application to the large number of species for which habitat suitability indices (HSI) have been developed. Because our models are both mechanistic and founded on ecological theory (Stephens and Krebs, 1986; Krebs and Kacelnik, 1991), they allow the development of biologically credible predictions about home ranges and spatial distributions of animals that can be tested empirically. Application of our models to the study of home ranges in real animals will, therefore, advance both the understanding of the species studied as well as the theoretical foundations for home range behavior. We present general, testable predictions for home ranges proceeding from our models below, although we emphasize that this list is not exhaustive. Because of the generality of our models, their potential for developing insights into home range behavior is proportional to the diversity of empirical applications to which they can be applied.

If, as we hypothesize, animals select resource-bearing patches for their home ranges optimally, the size of a home range may not be an indicator of efficiency, or how well the home range sequesters resources. Home ranges on evenly- or randomly-dispersed resource distributions should be relatively evenly spaced, having large areas of overlap shared by relatively few home ranges. Patches actually selected for these home ranges could be widely dispersed but of relatively high quality, resulting in a highly fragmented, but also highly efficient home ranges. Field evaluations relying solely on movements to identify selected patches could erroneously conclude that such home ranges were of poor quality. Home ranges in areas with poor resource quality, should also be large, evenly spaced, and broadly overlapping, even where spatial continuity of resources is high. The patches actually selected for these home ranges should be contiguous over broad areas, resulting in unfragmented

but relatively poor quality home ranges. Without a spatially explicit depiction of resources and highly resolved observations of patch use, differences in the underlying structures of these two types of apparently similar home ranges would be difficult to distinguish with field data.

Home ranges on slightly to moderately clumped resource distributions should be highly variable in size, shape and resource content, and generally larger than those observed on resource distributions that are homogeneous or heterogeneous on a fine grain. Home range overlap should be low, and patterns of home range aggregations on relatively clumped resources should be apparent only where a large number of home ranges are studied. Home ranges on highly clumped resource distributions should be aggregated on large resource clumps, should be relatively small, and should vary little in size, continuity, or resource content. Quality of home ranges should be moderately high. Home range overlap should be high with extensive areas of overlap shared by many home ranges.

The distribution of discounted resource value (V') was the predominant factor structuring home ranges of both of our models, causing resource-maximizing and area-minimizing home ranges to be similar in many of our simulations. This suggests an overriding influence of landscape structure on home ranges, and animals practicing either strategy (or perhaps any other) will have home ranges that are similar in many ways unless individuals have very small or large resource requirements relative to the productivity of the landscape.

Which model should be applied to understanding the home range of any given animal is a biological question, but our models provide the opportunity for making contrasting predictions that can be tested for any animal. Our models suggest that home ranges of animals that maximize resource density and those that satisfy a threshold in a minimum area could be distinguished in three ways. First, resource-maximizing and area-minimizing home ranges should respond differently to changes in resource productivity on a landscape. For example, a uniform decrease in resource quality across a landscape will not affect the size of resource-maximizing home ranges because rates of resource accumulation from patch selection and from random use would decrease proportionately, and the size of the home range at which the difference between the two rates is maximized will not change

(Fig. 2A). In contrast, uniform decrease in resource quality across a landscape will have an inverse relationship with area of area-minimizing home ranges; e.g., decreasing resource productivity or availability will result in larger home ranges as the rate of resource accumulation per unit area decreases while the resource threshold remains the same (Fig. 2B). Second, area-minimizing home ranges should contain consistently comparable levels of total resources within a population, whereas those for resource-maximizing home ranges should not. Third, whereas area-minimizing home ranges should be nearly identical to resource-maximizing home ranges at low resource thresholds, at other thresholds area and resource content of resource-maximizing home ranges will exceed what would be expected under a resource-maximizing strategy (Figs. 1B, 4 and 5). Finally, because the resource-maximizing model incorporates no biological parameters, predicting only the optimal use of a resource distribution, it can represent a null model for evaluating hypothesized spatial behaviors incorporating biological parameters.

The relationship between an animal and its limiting resources changes over time, corresponding to seasonal changes in behavior and resource needs (e.g., breeding season, rearing young), to seasonal and annual variation in the productivity of important foods, to increases in density as a population approaches carrying capacity, and to deaths of higher ranking individuals within the population. One could reasonably hypothesize that the home range strategies of an individual might also vary, where an animal maximizes use of a landscape during one phase of its spatial behavior, and satisfies resource thresholds during another. If the causes are known for changes in use of space, a home range model combining the two strategies can be developed. For example, an animal might pursue an area-minimizing strategy prior to breeding and a resource-maximizing strategy thereafter, if doing so yields more resources. Alternatively, an animal might have a resource-maximizing home range except when food productivity is insufficient for survival or reproduction, at which time it will adopt an area-minimizing strategy and increase the size of its home range to meet the threshold requirement.

Our models that did not incorporate resource depression assumed that animals construct home ranges

independently of each other and that resources are fixed in time in space. In reality, interactions among animals and changes they impose on the resources they use are likely to strongly affect characteristics and spatial distribution of home ranges within a population. Our results suggest that at low population densities, home ranges of animals that consume or protect resources should be similar to those of animals that do not, but more evenly dispersed on the landscape. For higher population densities, the proximity and overlap of home ranges should be dependent on the distribution and quality of resources and on the number of animals living in the area. As population density increases, the home ranges of resource-maximizing animals should stay roughly the same size and decline in total resource content, but those of area-minimizing animals should increase in size and accumulate more resources. An area-minimizing strategy including resource depression should result in home ranges distributed on a landscape roughly according to an ideal free distribution Fretwell (1972). Each animal in a population would have a home range that meets its threshold requirement as efficiently as possible, but resource depression would set a limit to the number of home ranges any landscape can support. At some point, resources should be so depleted that meeting a resource threshold is impossible, and no further viable home ranges can be added. As the number of area-minimizing home ranges approaches this limit, home ranges should increase geometrically in size and their quality will converge with the landscape average; the last home range landscape can hold should be nearly indistinguishable from an area traversed during random wandering. Because minimum resource thresholds and the consumption or protection of resources are, to varying degrees, biological realities for all animals, an accurate model of these effects for a species should predict carrying capacity for any landscape with a known distribution of resource quality.

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