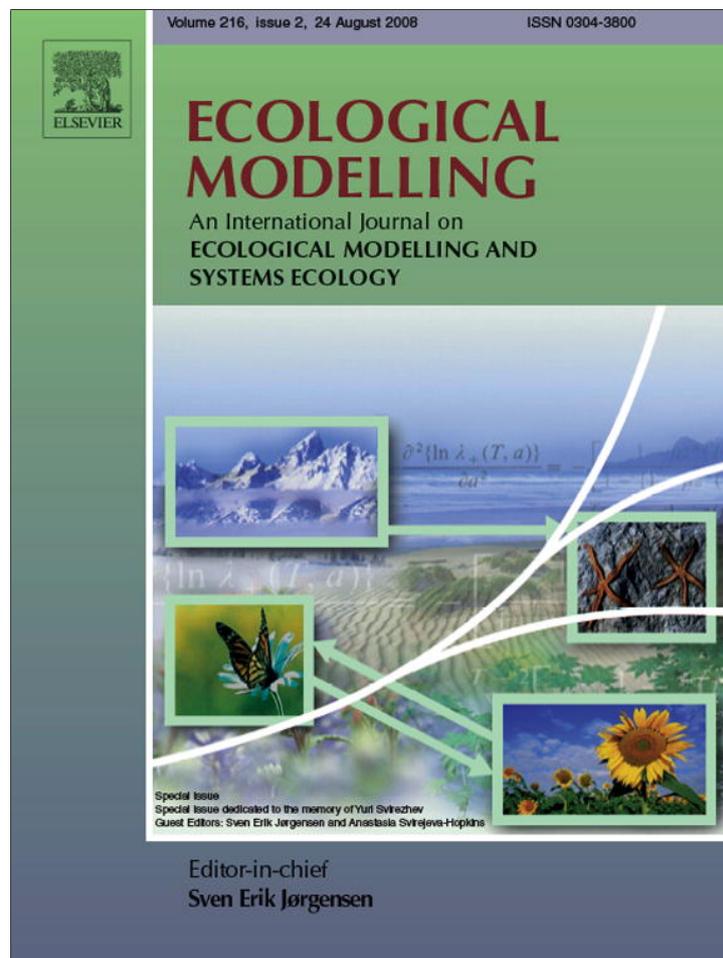


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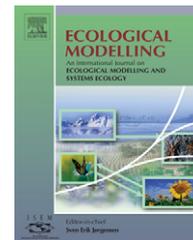
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Short communication

Estimated home ranges can misrepresent habitat relationships on patchy landscapes

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ABSTRACT

Home ranges of animals are generally structured by the selective use of resource-bearing patches that comprise habitat. Based on this concept, home ranges of animals estimated from location data are commonly used to infer habitat relationships. Because home ranges estimated from animal locations are largely continuous in space, the resource-bearing patches selected by an animal from a fragmented distribution of patches would be difficult to discern; unselected patches included in the home range estimate would bias an understanding of important habitat relationships. To evaluate potential for this bias, we generated simulated home ranges based on optimal selection of resource-bearing patches across a series of simulated resource distributions that varied in the spatial continuity of resources. For simulated home ranges where selected patches were spatially disjunct, we included interstitial, unselected cells most likely to be traveled by an animal moving among selected patches. We compared characteristics of the simulated home ranges with and without interstitial patches to evaluate how insights derived from field estimates can differ from actual characteristics of home ranges, depending on patchiness of landscapes. Our results showed that contiguous home range estimates could lead to misleading insights on the quality, size, resource content, and efficiency of home ranges, proportional to the spatial discontinuity of resource-bearing patches. We conclude the potential bias of including unselected, largely irrelevant patches in the field estimates of home ranges of animals can be high, particularly for home range estimators that assume uniform use of space within home range boundaries. Thus, inferences about the habitat relationships that ultimately define an animal's home range can be misleading where animals occupy landscapes with patchily distributed resources.

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1. Introduction

Researchers studying home ranges of animals assume selective use of resources distributed spatially among habitats

structures how their study subjects use space, and that time spent in habitat is proportional to its resource value (Ebersole, 1980; Schoener, 1981; Powell, 2000; Mitchell and Powell, 2004). Thus, home ranges estimated from location data are often

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used to derive habitat relationships by comparing use of habitat within home ranges to habitat available within or around them (Johnson, 1980; Manly and McDonald, 2002; Morrison et al., 2006). Generally implicit in this approach is the assumption that habitat as defined by researchers is a surrogate for the resources contributing to the fitness of their study subjects; few researchers define such resources explicitly for their analyses (Blackwell, 2007; Mitchell and Powell, 2002).

Field estimates (e.g., adaptive and fixed kernels, convex-hull, minimum convex polygon [MCP]; Getz and Wilmers, 2004; Powell, 2000) of home ranges for animals based on location data generally depict home ranges as contiguous in space, by definition for MCP estimates and dependent on the magnitude of the smoothing parameter, h , for kernel estimates (Seaman and Powell, 1996). A depiction of home ranges as contiguous in space can be problematic for discerning habitat relationships where resource-bearing habitat patches have a fragmented distribution on a scale smaller than an animal's home range. Such landscapes have the potential to strongly influence habitat selection of animals (e.g., Kotliar and Wiens, 1990). Mitchell and Powell (2004) hypothesized that animals inhabiting landscapes with patchily distributed resources will have home ranges comprising selected resource-bearing patches embedded in a matrix of unimportant patches used primarily for travel. Presuming that travel resources are not limiting (and thus not resources themselves to be selected), use-availability analyses based on contiguous home range estimates could misrepresent how animals use a patchy landscape because all patches within a home range are classified as "used," irrespective of whether they contained resources structuring animal movements or were simply areas through which animals traveled. This begs the question of what a home range truly is, the sum of all places an animal goes or the portions of the landscape it chooses to use (Powell, 2000). We prefer the latter definition because we think it important to discern causes of animal behaviors rather than simply describe them.

Along these lines, we have presented mechanistic home range models based on optimal selection of patches from a landscape, depending on the value of resources in each patch and the average cost of traveling to it (Mitchell and Powell, 2004). We have used these models to predict accurately the content, size, and spatial configuration of home ranges of real animals (Mitchell and Powell, 2007). The models do not portray the movements of animals within their home ranges but rather the reasons for those movements, i.e., the resource-bearing patches the animals use and move between. We showed that contiguity of patches selected for home ranges should be, in part, a function of the continuity of resource values among patches; in our simulations, home ranges were more fragmented on landscapes with overdispersed or random distributions of resource values than on those where resource values were clumped (Mitchell and Powell, 2004). Importantly, our simulations also showed that selective use of highly patchy landscapes can result in home ranges comparable in quality and efficiency to those on landscapes with highly clumped resources; for selective animals, fragmentation of resource-bearing patches need not result in poorer home ranges than those found on more contiguous distributions, even when travel costs are considered (Mitchell and Powell, 2004). If optimal patch selection underlies move-

ments of animals within their home ranges, then our models suggest that the potential for continuous home range estimates to misrepresent habitat relationships in use-availability analyses increases with the spatial discontinuity of resource-bearing patches on a landscape.

To evaluate the potential for this bias, we generated home ranges based on optimal patch selection (Mitchell and Powell, 2004) across 5 simulated landscapes differing only in the spatial contiguity of resource-bearing patches. Where selected patches within home ranges were non-contiguous, we added interstitial patches most likely to be used for travel between selected patches. To evaluate how inferences on home range size, resource content (summed resource value), quality (mean resource value), efficiency (the extent to which mean resource content exceeds mean availability within the "neighborhood" of the home range), and fragmentation might differ, we compared the home ranges based solely on optimal patch selection to those where unselected interstitial patches were included. If our hypothesis that patch selection underlies the movements of animals within their home ranges is valid, then the contrast between the 2 types of home ranges should shed light on what animals do (patch selection) versus what we observe (home ranges estimated from location data), and thus how our home range estimates might misrepresent behavior of animals inhabiting patchy landscapes.

1.1. Home range models

We used the modeling approach presented by Mitchell and Powell (2004). We defined patches as equal-sized cells on a grid. We modeled the benefit of including a patch in a home range as its resource value, V , ranging from 0 (low value) to 1 (excellent value). For each simulated home range, we discounted the value of resources in a patch for the average cost of traveling to that patch as:

$$V' = \frac{V}{D}$$

where V' is discounted resource value, and D is distance of the patch from home range core. We set D equal to 1/2 of the patch width for the center patch. For each simulated home range, we identified patches available for selection as those within a circular area containing 95% of the V' distribution.

For each simulated home range, we modeled patch selection by establishing a center point on a distribution of V , using that center point to calculate V' , and selecting patches sequentially from highest to lowest V' using our resource-maximizing model M_R (although our area-maximizing model, M_A , would have served equally well; Mitchell and Powell, 2004). For each model home range (designated the "true" home range) comprising spatially disjunct patches, we added interstitial patches likely to be used by an animal moving among selected patches (designated the "estimated" home range because it resembles what a researcher will estimate using conventional home range estimators and location data). This approach assumes that animals do not consider patches used only for travel to add resource value to their home ranges.

2. Methods

We simulated 5 landscapes on a 109×131 matrix of patches. Means and standard deviations of V for the 5 landscapes were approximately equal (Mitchell, 1997; Mitchell and Powell, 2004). We designed the simulated landscapes to range from over-dispersed resources (Landscape OD, Moran's $I = -0.80$; Cliff and Ord, 1981; Mitchell and Powell, 2004), through randomly distributed resources (Landscape R; Moran's $I = 0.00$), to slightly, moderately, and highly clumped resources (Landscapes SC [Moran's $I = 0.35$], MC [Moran's $I = 0.71$], and HC [Moran's $I = 0.89$], respectively).

We generated 100 true home ranges for each simulated landscape. Each true home range had a randomly selected starting point for patch selection; all starting points were separated from the edges of the landscape by a buffer of 12 patches. We calculated the estimated home range for each of the 500 true home ranges. To identify interstitial patches for estimated home ranges, we used a kernel estimator (KERNELHR fixed kernel option; Seaman et al., 1998) to “smooth” over patches selected as the true home range (Isaaks and Srivastava, 1989), generating a distribution of kernel values across selected and interstitial patches for each true home range. These kernel distributions were not valid utility distributions (Powell, 2000). We added interstitial patches within the 80th percentile of the kernel distribution to each true home range because they filled the most interstitial space in fragmented home ranges while increasing the area of contiguous home ranges least (Fig. 1; Mitchell, 1997). For each true and estimated home range, we summed V as a measure of resource content, and we calculated mean V to assess quality, representing what might be inferred for home ranges based on field observations. We used the difference between mean resource value of the home range and that of the neighborhood (Mitchell and Powell, 2004) as an estimate of efficiency. We also evaluated the spatial contiguity of home ranges using a fragmentation index, F (ranging from 0, indicating low fragmentation, to 1, indicating high fragmentation; Mitchell and Powell, 2004). We graphically assessed mean values of these home range metrics calculated for each simulated landscape to infer how variation in spatial continuity of resource distributions influenced differences between true and estimated home ranges. We excluded from analysis home ranges for which the iterations of patch selection were arbitrarily truncated by computing constraints and home ranges exceeding 1000 patches (Mitchell and Powell, 2004).

3. Results

We discarded 20 of the 500 true home ranges because they exceeded our size or iteration limits; the number of home ranges discarded did not vary consistently across simulated landscapes (Mitchell, 1997). Predictably, the addition of interstitial patches affected simulated home ranges most on landscapes where resources were least clumped and home ranges were thus most fragmented (Fig. 2B). As spatial continuity of resources increased across landscapes, all parameters for estimated home ranges converged with

those for true home ranges. Particularly where resources were over-dispersed (Landscape OD) or randomly distributed (Landscape R), the addition of a large number of interstitial patches resulted in estimated home ranges that were larger (Fig. 2A) and appeared to be of lower quality (mean V ; Fig. 2C) and efficiency (Fig. 2D) than their underlying true home ranges. Accumulated resources were much higher for estimated than true home ranges on these landscapes (Fig. 2E).

4. Discussion

Home ranges estimated from field locations are commonly used to identify “used” habitat for use–availability analyses of habitat selection (Johnson, 1980; Manly and McDonald, 2002; Morrison et al., 2006). Such analyses reveal habitat relationships based on the assumptions that (1) habitat as defined represents the resources contributing to the fitness of animals (Blackwell, 2007; Mitchell and Powell, 2002) and, (2) the spatial distribution of habitat structures the home ranges of animals (Ebersole, 1980; Schoener, 1981; Powell, 2000; Mitchell and Powell, 2004). Mitchell and Powell (2004) hypothesized that animals inhabiting landscapes where habitat is patchily distributed on fine spatial scales, home ranges are likely to comprise resource-bearing patches important to an animal's fitness embedded in a matrix of unimportant patches. We evaluated the potential for erroneous inferences based on using contiguous home range estimates for animals inhabiting patchy landscapes by comparing simulated, optimal home ranges (“true” home ranges) to the same home ranges with interstitial space between selected patches added to the home range (“estimated” home range). Our estimated home ranges, though still based on optimal patch selection, were comparable to what a field researcher might estimate for wild animals. On landscapes with resources evenly or randomly distributed, estimated home ranges appeared to be of low quality, whereas the quality of the true home ranges on which they were based was actually quite high, suggesting a fundamental disconnection between what an observer might conclude and what an animal perceives. The inclusion of interstitial patches that have no benefits (i.e., their resource values were too low to be selected) beyond travel, and are thus irrelevant to the animal's perception of where it chooses to live, biases inferences on home range quality proportional to the fine-scale patchiness of resources on the landscape. Our models indicate that optimal home ranges on highly diffuse resources can be of comparable quality and efficiency to those on clumped resources (Fig. 2C and D; Mitchell and Powell, 2004). Nonetheless, an observer using a contiguous home range estimator could be misled to conclude that those home ranges were inefficient and resource-poor compared to those observed on more clumped resources.

An inverse relationship between home range area and quality of resources is commonly accepted by researchers. Estimated home ranges followed this pattern whereas true home ranges did not (Fig. 2A and D). Our results suggest that home ranges of real animals consisting of optimally selected resource-bearing patches (equivalent to our “true” home ranges) will be comparable in quality and number of

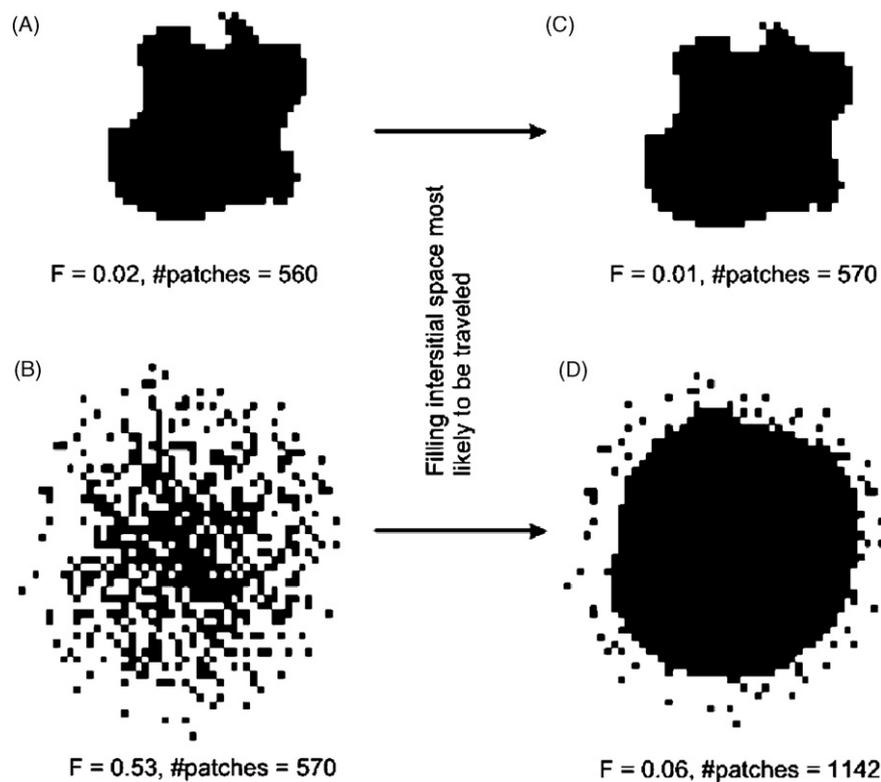


Fig. 1 – Effects of adding interstitial patches to simulated home ranges consisting of selected resource-bearing patches created on even and clumped distributions of resources. (A) Patches from a home range created on a clumped distribution of resource values. (B) Patches from a home range created on an over-dispersed distribution of resource values. (C and D) The effects of adding interstitial patches from within the 80th percentile of values in a smoothed kernel distribution generated from the patches in (A) and (B). F is an index of home range fragmentation ranging from 0 (no fragmentation) to 1 (high fragmentation).

selected patches across a variety of landscapes. Thus, the size of a home range estimated from location data may not allow accurate estimation of the actual mean quality and density of resources available to an animal. For example, animal A living on a landscape with over-dispersed patches of very high quality habitat (Fig. 1B), and who does not consider the low quality, interstitial areas to be part of its home range, has a home range of high quality and relatively small size. Travel costs to cross interstitial, non-home range areas are small. In contrast, animal B living on a landscape with highly clumped patches of mediocre quality, must have a large home range of contiguous patches of similar breadth to that of animal A but having a mean low quality and a relatively large size (this would be a home range as shown in Fig. 1A but of the size shown in Fig. 1D). Conventional home range estimators would estimate both animals to have home ranges of similar size and quality whereas the true home range of animal A is of high quality and its foraging behavior, reproductive success and survival would reflect its high quality home range. Though having an apparently similar home range, animal B's foraging behavior, reproductive success and survival would reflect the poorer quality of its home range. Most habitat studies, however, do not evaluate these important indicators of fitness (Garshelis, 2000), instead inferring fitness indirectly from home range characteristics, thus the critical distinctions

between the home ranges of animals A and B would go undetected and a researcher would erroneously conclude they are similar.

Our models suggest that optimal patch selection can create true home ranges comparable in quality and size across a variety of resource distributions but these similarities are unlikely to be observed by estimating home ranges using present estimators and location data. The potential for erroneous conclusions about how habitat relationships structure the behavior of animals within their home ranges increases with the spatial dispersion of limiting resources. Without evaluating how such resources are distributed, a priori, no means exist for controlling the potential bias from including unselected, largely irrelevant patches in the estimates of home ranges of wild animals inhabiting patchy landscapes. When irrelevant patches are identified as “used” in use-availability analyses, observers can be misled about the fundamental relationships between animals and the resources that ultimately define their home ranges.

Not all home range estimators are equally vulnerable to this bias. MCP estimates (Powell, 2000) are the most vulnerable because relative use of habitats within the home range boundary is undifferentiated; all “used” habitat is weighted equally and thus the potential for bias is directly proportional to the amount of irrelevant, unselected habitat included in the home

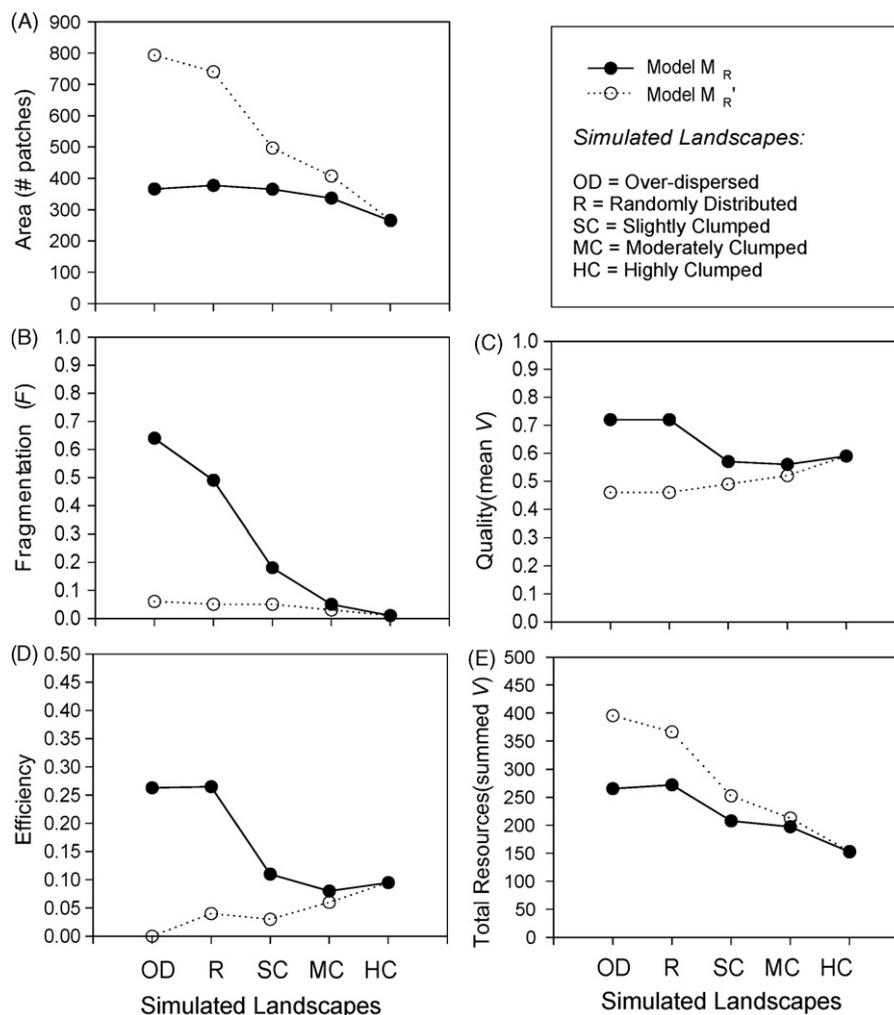


Fig. 2 – Relationships of simulated home ranges created using optimal patch selection with the simulated landscapes on which they were generated. Landscapes consisted of distributions of resource values, V , that varied only in the spatial continuity of V . On each of the 5 landscapes 100 simulated home ranges were created under a resource-maximization model (M_R), simulating the “true” home ranges of animals. Where patches of M_R home ranges were spatially disjunct, interstitial patches were added to account for non-selected patches likely to be traveled by animals and designated M'_R , simulating the “estimated” home ranges generated using spatially contiguous home range estimators. (A) Mean area of home ranges (number of patches of equal size), (B) mean fragmentation of home ranges (fragmentation index F , ranging from 0, no fragmentation to 1, high fragmentation), (C) quality of home ranges (mean V), (D) mean efficiency of home ranges (the difference between mean resource content of home ranges and mean availability), and (E) mean total resources contained in the home ranges (summed V).

range estimate. The use of MCP home range estimates has been widely criticized (Powell, 2000; Börger et al., 2006; Laver and Kelly, 2008) and our findings further support concerns that MCP estimates are unlikely to contribute to insightful and robust analysis of habitat relationships. Kernel (Powell, 2000) and convex-hull (Getz and Wilmers, 2004) home range estimates are vulnerable to the biases we observed proportional to the extent that the h and k parameters are large enough to result in unselected habitat being included within estimated home ranges; large values of h and k increase the likelihood of this bias, small values reduce it. Use-availability studies that weight “used” habitat for kernel values within estimated home ranges (as opposed to weighting all use within a 95% home

range equally; Millspaugh et al., 2006) reduce the prospects for bias further because unselected habitat included within home ranges due to smoothing will have relatively low utility values. The h and k parameters, however, are limited by telemetry location error and using values too small when location error is large introduces a different bias.

Our modeling was based on explicit consideration of resource quality among patches available for optimal selection for a home range. Few researchers, however, consider resources explicitly in their analyses of habitat selection, instead assuming that their habitat definitions encompass accurately the resources contributing to the fitness of their study subjects (Blackwell, 2007; Mitchell and Powell, 2002).

Where this often untested assumption is unjustified, analyses based on arbitrary habitat definitions can yield misleading assessments of effects of patchy resource distributions on habitat selection.

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