Landscape Ecology of Small Mammals

Foreword by Ilkka Hanski

With 51 Illustrations
Habitat Selection in Geographically Complex Landscapes

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Background

The practice of landscape ecology is generally one that attempts to understand how patterns of abundances may interact with the physiognomic and compositional characteristics of landscapes (Dunning et al. 1992, Morris and Brown 1992). However, the goal is to understand why populations, enumerated across large spatial scales, frequently are not equivalent to the sum of the productivities of the component patches of usable habitat across that same region. This discrepancy generally results from the underutilization of available resources (e.g., food, cover, or breeding habitats), which, in turn, may result from the species' inability to find these resources in time to fully exploit them. In this way, fragmented landscapes are thought to pose difficult problems for the persistence of mammalian metapopulations (see Lidicker 1995, and chapters therein for review).

On the other hand, whereas many studies have investigated the effects of landscape composition and physiognomy at the scale of a few tens of hectares or across a small number of patches, few studies have attempted to survey large numbers of fragments and relate the occurrences and abundances of small mammals to the regional distributions of patches of different types of habitats across a range of scales. Even fewer studies (e.g., see Anderson 1995) have done this in temporally dynamic landscapes where patches arise and disappear on a regular basis over short periods of time. The ability to exploit newly created patches quickly should be especially important in affecting the abundances that will be realized in ephemeral patches before the patches senesce. We suspect that the ephemeral quality of suitable habitats will serve to emphasize the degree to which heterogeneity of the landscape affects local within-patch abundances.

Although many authors acknowledge that the spatial scale of a landscape is species specific (e.g., Dunning et al. 1992, Dunning et al. 1995), we are aware of few attempts to assess the spatial scale of landscapes that affect population-level phenomena such as the efficiency with which a species is
able to exploit available habitats. In this sense, the size of a landscape is the spatial extent (or range) over which population abundances or densities are autocorrelated. The rarity of such studies, in part, reflects the difficulties posed by variability in habitat quality across a region. Such variability interferes with our ability to use standard spatial autocorrelation techniques to assess the extent of spatial dependence. For example, the range of the spatial autocorrelation in a species' abundances among patches may reflect the species' ability to colonize and exploit the patches and, thus, the ability of the species to cope with landscape features (sensu Dunning et al. 1992). Alternatively, the autocorrelation may also reflect spatially autocorrelated distributions of habitat quality among patches. The purpose of this chapter is to illustrate an approach to estimating this spatial scale for landscapes that are inhabited by three different species of small mammals that are found in discrete patches of habitat that vary in quality as a function of the degree to which succession has revegetated the patches following timber clearcutting.

The Savannah River Site (SRS) is a good example of a spatially heterogeneous and temporally dynamic region, which may be comprised of any number of independent populations of small mammals. The SRS is spatially a large (~803 km²) region comprised of more than 4400 fragments, the vast majority of which contain monocultures of one of several species of conifer (e.g., long-leaf pine, Pinus palustris, or loblolly pine, P. taeda). These discrete fragments, or patches, are managed by the United States Forest Service as individual forest stands for the purpose of experimental and production silviculture. The SRS is temporally dynamic, especially from the perspective of those species that prefer the relatively open habitats represented primarily by clearcuts. After harvest, these clearcuts are quickly replanted with seedling pines, which grow to a closed canopy in 6 to 8 yr. In this particular forest, the harvest and regrowth rates are such that approximately 11–12% of the stands are between 1 and 8 years old at any given point in time [as calculated from geographic information system (GIS) coverages of the SRS].

The speed of canopy closure (i.e., secondary succession) dictates that species that require open habitat or extensive herbaceous cover must quickly find, colonize, and exploit (i.e., produce new colonists) newly created clearcuts before the patches "degrade" to the point that these species cannot produce offspring and potential colonists for new patches. Thus, to the extent that landscape physiognomy and composition (sensu Dunning et al. 1992) affect the emigration and immigration of individuals, spatial heterogeneity should be especially important in determining the efficiency with which open-habitat species can utilize the suitable habitat that is available at any one time.

On the SRS, an excellent example of an open-habitat species is the old-field mouse, Peromyscus polionotus, (Golley 1962, Golley et al. 1965). To a slightly lesser extent, the hispid cotton rat, Sigmodon hispidus, is an open-habitat specialist (Golley 1962, Golley et al. 1965), but the species is also found in small numbers along logging roads and grassy Carolina bays.
(Anderson 1995, Anderson and Danielson in review), both of which are common on the SRS. The third abundant open-habitat small mammal on the SRS is the cotton mouse, *P. gossypinus*. This species is found in clearcuts, edges (Golley et al. 1965), and anywhere that downed woody material is abundant (S. Loeb, pers. comm.). This includes fallen logs and slash in clearcuts as well as fallen timber in older stands.

Thus, these three species occupy a gradient in the degree to which they are open-habitat specialists. We might predict that the landscape will appear much more fragmented to the most specialized, *P. polionotus*, and least fragmented to most generalist species, *P. gossypinus*. On the other hand, the three species also represent a gradient in body sizes from the cotton rat (approximately 130–150 g) to the cotton mouse (25–30 g), to the old-field mouse (11–13 g) that spans at least an order of magnitude (Silva and Downing 1995). To the degree that body size is related to dispersal distance (J.H. Brown, pers. comm.), and home range size (Kelt and Van Vuren 1999). The relative abilities of these species to exploit complex landscapes may reflect this gradient.

### Sampling Methods

To test our hypothesis, we systematically sampled a total of 196 forest stands during two 11-week intervals in the summers of 1993 and 1994. These stands were clearcuts ranging from 1 to 8 years of age at the time they were trapped for small mammals. In 1993, we sampled 102 forest stands in the northwest and southeast quadrants of the SRS. In 1994, we sampled 94 different stands in the northeast and southwest quadrants (Fig. 5.1). Each sample was comprised of a 15-station trapline with two traps at each station and stations separated by 15 m. Traps were baited and locked open for 2 days prior to sampling. After this prebaiting interval, we marked and released all individuals captured during 5 consecutive days (sampling procedures are described in greater detail in Anderson 1995). The distances between sampled stands (patches) were determined by analyses with a GIS database maintained by the United States Forest Service’s Savannah River Institute.

### Abundances versus Habitat Preferences

Because clearcut vegetation changes so rapidly during the first few years of secondary succession, we first assessed the relationship between patch age and the relative abundances of each species of small mammal. In general, the two most specialized species, *S. hispidus* and *P. polionotus*, showed declining abundances with increasing stand age (Fig. 5.2A–C); however, regressing abundances against stand age results in a significant relationship for only *P. polionotus* (Table 5.1). Although statistically significant at the *P* < 0.05 level, this regression explained only about 11% of the variation in abundances.
Figure 5.1. One hundred two stands on the Savannah River Site that were censused for small mammals in 1993 (open polygons) and 94 stands censused in 1994 (black polygons). The region encompassed by the entire set of polygons is approximately 803 km². All censused stands were clearcut 1–8 yr prior to sampling. Solid lines indicate powerline and pipeline rights-of-way permanently maintained as open-field habitat that potentially could be used by small mammals as additional suitable habitat or dispersal corridors.

Visual inspection of these distributions, nevertheless, showed clear patterns in the form of upper bounds to the abundances of *S. hispidus* and *P. polionotus* that are not revealed by simple regression techniques. This type of relationship has been discussed in detail and termed a "factor-ceiling distribution" by Thomson et al. (1996). Factorceilings result when the independent variable limits the extreme value that the dependent variable can attain, but other factors, perhaps unmeasured, sometimes regulate the dependent variable to levels below the extreme. Thomson et al. point out that the very nature of the ecological theory of limiting factors suggests that such ceilings should often be expected in nature, and that conventional correlation analyses are inappropriate and likely to miss such relationships.
Figure 5.2. Relationship of the age of the stand (time since clearcutting) and the abundance of three species of small mammals. Plots A–C show abundances for all 196 stands. Each panel shows the regression line for that data set. Only the regression for *P. polionotus* (B) is significant. Plots D–F show factor-ceiling regressions on the same data set. For each species, the maximum abundance for each stand age class is regressed against age of the stand. Stands of age 2–8 yr were used for the factor-ceiling regression for *S. hispidus* and *P. polionotus*. Stands of age 3–8 yr were used for the factor-ceiling regression for *P. gossypinus*. Regressions are highly significant for *P. polionotus* and *S. hispidus*.

There are several methods that can be used to define a factor-ceiling (Kaiser et al. 1994, Thomson et al. 1996, Scharf et al. 1998). In short, they involve regressing the extreme values of the dependent variable for discrete intervals within the range of the independent variable against the ranked interval of the independent variable. Our eight discrete age classes lend themselves well
Table 5.1. Results of linear regressions and factor-ceiling analyses of abundances as a function of stand age for three species of small mammals.

<table>
<thead>
<tr>
<th>Species</th>
<th>Linear regression</th>
<th>Factor-ceiling analysis</th>
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<tbody>
<tr>
<td></td>
<td>Slope</td>
<td>$r^2$</td>
</tr>
<tr>
<td><em>S. hispidus</em></td>
<td>-0.14</td>
<td>0.005</td>
</tr>
<tr>
<td><em>P. polionotus</em></td>
<td>-0.54</td>
<td>0.111</td>
</tr>
<tr>
<td><em>P. gossypinus</em></td>
<td>-0.02</td>
<td>0.000</td>
</tr>
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</table>

The complete sample of 196 stands was used in each linear regression. Factor-ceiling analyses regress only the maximal abundances in each stand age class for stands of ages 2–8 yr for *S. hispidus* and *P. polionotus* and stands of ages 3–8 yr. for *P. gossypinus* (see text for details).

to this analysis. Stands of age 1 for *S. hispidus* and *P. polionotus* and ages 1 and 2 for *P. gossypinus*, however, have decidedly fewer animals than stands just one year older. This could reflect lower carrying capacities for these small mammals species in these stands. Thus, because we wish to know if there are spatial signals to the scatter below the ceiling, we excluded these age classes (recognizing, of course, that conclusions reached about the cause of the scatter in the age-class abundances analyzed may not be relevant to these younger stands that we have excluded). We then used simple linear regression on the maximum abundances in each of the remaining age classes to define the factor ceiling for each species.

For *S. hispidus* and *P. polionotus*, the “ceiling” clearly declines with age for stands of age 2 years and older (Fig. 5.2d,e). Factor-ceiling regressions for these species are highly significant and have high correlation coefficients (Table 5.1). The relationship for *P. gossypinus*, however, is less clear (Fig. 5.2f), and a factor-ceiling regression of the stands greater than 2-years-old is not significant for this species ($P = 0.10$). The linear relationship, however, does explain more than half of the variation in maxima for these age classes (Table 5.1).

Where such a ceiling to abundances exists, we interpret it as an estimate of the potential carrying capacity for stands in each age class. If this interpretation is correct, then the scatter in abundances below the ceilings for species in each age class of clearcuts represents the degree to which the species are not efficiently exploiting the available habitat. These inefficiencies may reflect the spatial heterogeneity in the landscapes that surround each sampled forest stand. Alternatively, they may reflect other ecological factors, such as predators or competitors, that limit each species to abundances below the age-specific potential represented by the ceiling. In any case, we simply wish to determine the scale at which the available habitat is well exploited, or underexploited, as the case may be. For each species, spatial autocorrelation of the deviations from the factor ceiling will provide an estimate of the spatial scale of the population’s dynamics (i.e., an estimate of the true species-specific landscape over which local, within-stand abundances are related to the abundances of surrounding patches). Beyond this scale, populations are independent in their dynamics.
Local Scales of Abundances and Habitat Selection

We attempted to block for local spatial variation in the landscape immediately adjacent to stands (landscape patches) that were sampled by comparing the abundances of small mammals in the stands to a single type of habitat that is immediately adjacent to the target stand. On the SRS, a candidate for such a “standard” habitat type is the powerline and gas pipeline rights-of-way (ROWs). These ROWs are maintained by periodic mowing. They are, therefore, fairly similar throughout the site. All three species are frequently found in ROWs, although ROWs tend to have less woody vegetation and downed timber. Thus, the ROWs could serve as sources of colonists for the newly created clearcut patches. Because they run throughout the SRS (Fig. 5.1), the ROWs also have the potential to serve as dispersal corridors between clearcuts, which would further ensure that newly created clearcuts are quickly colonized. Thus, the ROWs should minimize the degree to which local patch isolation might affect each species’ ability to reach its intrinsic carrying capacity. For these reasons, we utilized ROWs as a standard measure of habitat quality against which stands of different ages might be compared.

Of the 196 forest stands that we live trapped, 54 were immediately adjacent to ROWs. Using two trapline transects, we simultaneously trapped each stand and the sections of the adjacent ROWs where the ROWs passed along side the stand. Identical trapping techniques were used in each stand and ROW. To make comparisons between stand and ROW abundances, we utilize isodars (Morris 1988) as a tool. Because the two habitats (clearcut and ROW) are immediately adjacent to each other in each of these 54 paired samples, local landscape effects should be minimized. For each species of small mammal and each stand age class, we quantify habitat preference by comparing the slopes and intercepts of a regression of abundance against ROW abundance. Even when controlling for forest stand age and isolation in this fashion, however, variability is very high and age-specific regressions are not significant, thus preventing us from ranking habitat preference in this fashion. In fact, regressing all 54 stand abundances against the abundances in their accompanying ROWs (Fig. 5.3) is significant for only P. polionotus, and even then, very little of the variation was explained ($P = 0.025, r^2 = 0.09$). Thus, if landscape factors are responsible for the variation in the abundances of small mammals within each stand age-class, then these factors must be doing so at larger spatial scales than that of the immediate patch (clearcut) and neighboring adjacent patches.

Regional Scales of Abundances and Habitat Selection

The presence of spatial autocorrelation can be detected with the use of semivariogram analysis. Semivariograms quantify the degree to which pairs of observations are spatially independent as a function of the distance between the
Figure 5.3. Isodar regressions for 54 stands versus 54 adjacent stretches of utility rights-of-way. Age classes are combined for these plots, and only the regression for *P. polionotus* is significant.

observations (see Deutsch and Journel 1992). A semivariogram specifically quantifies the average squared difference between pairs of sampled points separated by a distance $h$. This distance is often referred to as the lag distance. We initially estimated the semivariograms for each species of small mammal directly from the observed abundance data using the distance between the geographic centers of two sampled stands as the distance between the two samples. If there is spatial structure to the observations (i.e., if they are spatially autocorrelated), then pairs of observations that are close together should be similar and the semivariogram should be small. As $h$ increases, pairs of observations should become statistically more independent and the semivariogram should increase until, at some lag distance, pairs of observations are sufficiently far apart as to
represent truly independent samples. At this point, the semivariogram will equal the total variance in the data set. All plots of the semivariograms are standardized by dividing the semivariogram, as calculated for each lag, by the variance of the entire sample. Thus, a lag distance that produces a standardized semivariogram value of 1 indicates that pairs of observations that are separated by at least this distance are spatially independent of one another.

In practical application when using data that are continuously distributed in space (as opposed to spaced on a regular grid or lattice), it is necessary to specify the lag as a band interval, and the semivariance is computed for all pairs of points that fall within that interval. In this instance, we use a band width of 300 m and calculate semivariograms for 20 different lags (0–300 m, 300–600 m, 600–900 m, ..., and 5700–6000 m). The 300-m increment is a reasonable compromise between very narrow bands that encompass only a few pairs of observations and, thus, produce poor estimates of the semivariogram, and wider bands that could potentially obscure the entire range of spatial dependence.

Because we sampled different regions of the SRS in each year (1993 and 1994), we divided our data into six sets representing all species–year combinations. For each data set, we plotted an omnidirectional semivariogram, and two directional semivariograms that are sensitive to anisotropy within the data sets (i.e., directional bias in the degree of spatial dependence) in a north–south and an east–west direction. In all cases, the directional semivariograms were functionally similar to the omnidirectional semivariograms. Therefore, only the omnidirectional results are presented and discussed in this chapter.

In general, the semivariogram plot for abundances of *S. hispidus* showed strong spatial dependence for distances of about 1–2 km in both years (Fig. 5.4A). At distances of greater than 2 km, abundances are not correlated. *P. polionotus* and *P. gossypinus*, however, demonstrate little or no spatial autocorrelation (Fig. 5.4B,C), although it should be noted that this analysis cannot assess spatial autocorrelation at distances shorter than that of the lag interval—300 m in this instance. Thus, a first approximation suggests that functionally independent populations of *S. hispidus* are on the order of 1–2 km in radius in this landscape, whereas functionally independent populations of *P. polionotus* and *P. gossypinus* may be less than 300 m in radius.

Because the body size of *S. hispidus* is five to 10 times greater than either *P. gossypinus* or *P. polionotus*, it seems reasonable that the range of spatial autocorrelation should be much greater for the larger species; however, because we know that stand age affects abundances of these species, and because stands are created by forest management activities, rather than by biotic interactions with these small rodents, we cannot be sure that these spatial distributions truly reflect the spatial properties and dispersal behaviors of the rodents rather than the spatial distributions of the stand age classes. Furthermore, as we discussed earlier, it is really the efficiency with which each species exploits available habitat, not raw abundances, that should be most sensitive to the effects of landscape complexity.
Figure 5.4. Separate standardized semivariograms for each species in 1993 and 1994. Each semivariogram is standardized by its total sample variance such that values of 1.0 indicate no spatial autocorrelation. Calculations of semivariograms (A–C) used abundance data for small mammals from all stands that were censused in each year. Plots D–F are semivariograms calculated with each stand’s proportional deviation from the factor-ceiling prediction. Stands of age 2–8 yr were used for *S. hispidus* and *P. polionotus*. Stands of age 3–8 yr were used for *P. gossypinus*.

Regional Scales of Efficiency in Habitat Exploitation

If spatial properties of the landscape mosaic do, in fact, result in many stands failing to reach a maximal carrying capacity, then we should be able to use semivariogram analysis to find a spatial signal in the scatter of the variation below the ceiling. To do this, we subtracted the observed abundance in each stand from the estimated factor-ceiling regression for stands of the appropriate age. Although the factor-ceiling regression for *P. gossypinus* is not significant, the regression does explain more than 50% of the variation in abundance maxima for age classes 3 to 8 years (Table
5.1). In lieu of a better estimator of potential abundances of this mammal, we, therefore, elect to use the regressions for all three species in estimating the deviation between realized and potential stand abundances. If the ceilings are analogous to carrying capacities for these species, then these deviations from the ceilings represent the degrees to which the species are failing to fully exploit the landscape.

To assess the spatial pattern of efficiency, as defined here, the deviations from the factor ceilings for stands of different ages must be made comparable. We do this by dividing each deviation by the factor-ceiling value for the stand. In this way, all deviations from the factor ceiling are scaled relative to the potential of the stand to support a local population of a specific species of small mammal, and we can compare the efficiency by which a species exploits a 2-year-old clearcut to the efficiency with which the same species exploits an 8-year-old clearcut.

We then calculate semivariograms for each of the three species using these proportional deviations and the lag distances as we describe for the analyses using actual abundances of small mammals. These variograms are standardized to the sample variance, and the resulting standardized semivariograms are plotted in Figure 5.4D–F. In general, these semivariograms do not differ strongly from those produced from the abundance data (Fig. 5.4A–C), which suggests that spatial autocorrelation in stand management practices has not strongly influenced the spatial autocorrelation of each species’ abundance. Where the two types of semivariograms do differ, however, the proportional deviations from the factor-ceilings appear to show slightly longer ranges than do the raw abundances.

Discussion

It was initially surprising that we could not successfully block for spatial autocorrelation effects by comparing stand abundances to adjacent ROW habitat. We had originally hoped that the effects of corridors and interpatch connectivity would overwhelm other spatial influences on local abundance. Indeed, many studies of corridors suggest that such linear strips of habitat are strongly influential to small mammals (e.g., Wegner and Merriam 1979, 1990, Fahrig and Merriam 1985, Lorenz and Barrett 1990, Zhang and Usher 1991, LaPolla and Barrett 1993, Bennett et al. 1994). We intended to capitalize on this and, by using isodars, construct a “standard curve” for the relationship between stand age and habitat quality. As concluded by Peles et al. (Chapter 3), however, the small spatial scale encompassed by our stand-ROW paired observations is probably a trivial spatial distance for small mammals such as S. hispidus.

The two semivariogram analyses suggest that there is little spatial autocorrelation in the distribution of habitat quality in our particular data set, or, at least, that habitat distribution has relatively little effect on the efficiency or habitat exploitation. Nonetheless, the spatial analyses of the
factor-ceiling deviations provide the best insights into the effects of spatial scale in explaining species abundances. Factor-ceiling regression happens to work nicely in this instance, in part, because we have reasonably large sample sizes in each age class that provide high probabilities of observing at least a few occasions where abundances are at or near their maxima (i.e., when the ceiling is well defined). There may, however, be other ways of achieving similar results. For example, good habitat-specific demographic data, collected from large regions of relatively homogeneous habitat, might well be used to calculate per capita rates of growth and potential carrying capacities. Such data, however, are often hard to obtain, particularly for vertebrates (Pulliam 1996).

In another study, using this same data set, a qualitatively similar conclusion was reached regarding the relative unimportance of corridors as landscape elements in affecting the presence or absence of these three species (Anderson 1995, and Danielson, in review). This study used logistic regression to assess the degree to which successively larger buffers (0–250 m, 0–500 m, and 0–750 m) around sampled stands could be used as predictors of species occurrence. This analysis was compared with a similar analysis that used only local, within-stand, habitat features. The within-stand analysis was moderately successful at predicting the presence of *P. polionotus* and *S. hispidus*, the two most open-habitat specialized species. The within-stand variables that significantly predicted the presence and absence of *P. polionotus* and *S. hispidus* were stand age and the amount of herbaceous ground cover, respectively; however, none of the landscape buffers consistently predicted species occurrences. Thus, it appears that there is stronger spatial autocorrelation in the distributions of abundances than in the distributions of species’ occurrences. The precise implications of this result, however, are unclear.

The differences in the range of spatial autocorrelation among these three species of small mammals provides us with objective estimates of the spatial extent of a species-specific landscape. We expected that the effective landscape size (i.e., the range of spatial autocorrelation) should be positively related to body size in some allometric fashion, much like home-range area scales to body size (Calder 1984, Kelt and Van Vuren 1999). Our results support the idea that factors such as body size might be better indicators of the relative sizes of species-specific landscapes than natural-history characteristics such as the degree of habitat specialization. The body-size hypothesis predicts that *S. hispidus* should have the largest range of spatial autocorrelation, followed by *P. gossypinus*, and then *P. polionotus*. The habitat-specialization hypothesis predicts that *P. gossypinus* should have the largest range of spatial autocorrelation followed by *S. hispidus* and then *P. polionotus*. In fact, we observed that the longest range of spatial autocorrelation was clearly that for *S. hispidus*, and the shortest range that of *P. polionotus*, thus suggesting that general movement or dispersal capabilities (as related to body size) are more important than habitat specialization in determining the spatial extent of a species’ landscape. Such a relationship
should be an extremely useful tool in assessing the true spatial extent of a landscape for populations of small mammals, for designing experiments, and for developing species management plans. Of course, with only three species, ranked order differences between species cannot be statistically tested. Furthermore, it is also probable that both body size and habitat specificity will influence effective landscape sizes to some degree, but many more similar analyses of other species are needed to ascertain this.

Like any exploratory statistical technique, the factor-ceiling and semivariogram analyses do not provide clear explanations of the mechanisms that cause variation such as that of the species’ abundances below their factor ceilings (Fig. 5.2). Nonetheless, this approach may prove useful in selecting candidate factors such as interspecific competition, predation, or some combination of ecological factors, for further assessment, and we are currently pursuing these possibilities. In addition, distinct spatial patterns, such as those observed here, may also prove to be valuable fingerprint-like indicators useful in the comparative testing of models of dispersal and colonization, habitat selection, and recruitment. Finally, in testing metapopulation theory, the selection of landscapes at spatial scales appropriately defined by the organism of interest, should provide much greater analytical power, and hence, much greater abilities to discriminate among competing models of metapopulation dynamics.

Applications for Management at the Landscape Scale

The most useful application suggested by this study may be to attempt to derive means of estimating effective landscape dimensions. In particular, development of allometric predictors of effective landscape size would be especially useful for the conservation of rare or endangered species with largely unknown ecologies and for which little time or resources exist to develop better species-specific studies. This study provides only the barest of beginnings with respect to this goal, however, so much work remains to be done.

Where the goal of a management plan is the maintenance or restoration of ecologically functional populations, estimates of ecologically defined landscapes will almost certainly be superior to anthropocentrically defined landscapes. We argue that the spatial distributions of the efficiencies of habitat exploitation, as measured by departures from a factor ceiling, provide objective measures of such ecologically defined landscapes that comprise the spatial extent of a metapopulation. At a minimum, the metapopulations for the species such as Sigmodon hispidus appear to occupy areas as large as several square kilometers. Also, with such estimates, we may also much better assess the degree to which habitat fragmentation is impacting a species’ regional or local abundance, and, perhaps, better partition the effects of landscape fragmentation from other environmental or ecological influences. This type of analysis, when performed on species of conservation concern may be useful in assessing the minimum size of management units or preserves.
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Literature Cited


