

American Society of Mammalogists

Landscape Ecology of Mammals: Relationships between Density and Patch Size

Author(s): Michael A. Bowers and Stephen F. Matter

Source: *Journal of Mammalogy*, Vol. 78, No. 4 (Nov., 1997), pp. 999-1013

Published by: American Society of Mammalogists

Stable URL: <http://www.jstor.org/stable/1383044>

Accessed: 11/11/2008 15:17

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=asm>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact support@jstor.org.



American Society of Mammalogists is collaborating with JSTOR to digitize, preserve and extend access to *Journal of Mammalogy*.

<http://www.jstor.org>

LANDSCAPE ECOLOGY OF MAMMALS: RELATIONSHIPS BETWEEN DENSITY AND PATCH SIZE

MICHAEL A. BOWERS AND STEPHEN F. MATTER

*Department of Environmental Sciences and Blandy Experimental Farm, University of Virginia,
Route 2, Box 210, Boyce, VA 22620*

A much discussed issue in landscape ecology is how processes that operate within spatially subdivided subpopulations scale-up to create a larger, landscape-level dynamic. A first step in answering this question is to ask to what degree subpopulations within a landscape vary in performance. Here we test the null hypothesis that densities of mammalian populations are constant over patches of varied size, i.e., that performance, as estimated via density, does not covary with patch area. Using a composite database from published studies, we found that densities of 20 of 32 species did not vary with patch area, while five showed increasing and seven decreasing density-area relationships. Studies reporting significant density-area relationships tended to include a greater number of patches of a greater range of sizes than those that reported no relationship, suggesting that statistical power may be an issue. Landscapes comprised of smaller, less-isolated patches tended to have negative density-area relationships and landscapes with larger, more isolated patches tended to have positive density-area relationships. Our results suggest that no consistent density-area relationship operates over all systems of patches. Instead, the patterns appear to be scale-dependent: frequent movement of individuals in the process of selecting habitats (patches) over smaller-scaled landscapes produced negative density-area relationships; movement of individuals among more isolated patches appeared to involve larger- and longer-scale population processes involving colonization and extinction and positive density-area relationships. Despite the fact that patches represent a central focus in landscape ecology, they appear to be a construct of human convenience rather than biological entities with a set number and kind of processes.

Key words: landscape ecology, patches

Ecologists have long known that species do not occur uniformly over space, but rather that abundances are patchy. Early attempts to understand such patterns focused on local rates of birth and death. While it was known that animals moved in and out of study areas, immigration was believed to balance emigration, thereby eliminating the need to look at the surrounding habitat matrix. Landscape ecology, by contrast, is a new area of inquiry that identifies spatial heterogeneity as a causal factor affecting biological processes (Levin, 1992; Pickett and Cadenasso, 1995; Turner, 1989; Wiens et al., 1993); it emphasizes models of spatial relationships, the flux of individuals moving over the landscape, collection and

integration of new types of data, and explicit consideration of scaled, hierarchical spatial processes.

The fundamental unit within a landscape is the patch (Hanski and Gilpin, 1991); landscapes, in turn, can be defined in terms of patch mosaics. Kotliar and Wiens (1990: 253) define patches as "... a surface area differing from its surroundings in nature or appearance;" patchiness, in turn, will vary depending on the degree to which patches themselves differ from the surrounding habitat matrix. Operationally, however, patches and patchiness can only be defined relative to the habitat and spatial requirements of individual species and may, depending on the scale, be used by foraging individuals

or by whole populations. Patches come in various sizes, shapes, types, and mixtures and are differentiated by biotic and abiotic gradients, by physical discontinuities, may be the consequence of land-use activities by humans, and may change over time. Some patches are close together and have high connectivity, while others are far apart and are largely isolated, thereby creating landscapes that are markedly different in structure.

Despite the original intent of landscape ecology to be holistic (Forman and Godron, 1986), predictions about landscape-level processes are becoming increasingly specific and mechanistic (Wiens et al., 1993). Two guiding themes underlie much of landscape ecology: that landscapes have emergent properties differing from those operating at the scale of constituent patches (Forman and Godron, 1986; Lidicker, 1995; Turner, 1989), and there are basic, fundamental, and generalizable correlations between ecological parameters and landscape elements. Although no two landscapes are identical (and the same landscape may be perceived differently by different species), general principles are believed to exist that form a common basis for prediction. For example, most landscapes can be described in terms of the degree of subdivision, the connectedness of habitat patches, and their sizes; all features that might represent axes of spatial heterogeneity that are more general than specific (Ims et al., 1993; Wiens et al., 1993).

Nonetheless, most of what is known about responses of populations to subdivision and patchiness of habitats comes from theory that recently has been questioned (Haila et al., 1993) and rarely tested in the field. One problem is that while most theoretical models in landscape ecology treat whole landscapes or regions, field biologists tend to focus on individual landscape elements (patches) or, on occasion, patterns at the so-called meso-scale (a limited subset of patches). Such abstraction in field studies is necessary for the obvious practical and

logistical constraints imposed by studying pattern at large spatial scales. Another problem is that a number of models assume that landscapes are comprised of homogeneous, spatially undefined populations of patches with constant inter-patch distances (Pulliam, 1988), a notion that is not easily transferred to the field.

Small-scale, patch-based studies now need to be linked with regional-scale, landscape ones. One such approach asks how within- and between-patch processes are connected, and how variation in local performance scales-up to influence region-wide dynamics (Bowers and Dooley, 1991; Harrison, 1995). If patches within a landscape support a collection of comparable populations, then a landscape-level analysis that emphasizes transitional states and chance (i.e., that of a metapopulation) may be appropriate. If, however, patches differ in their ability to produce and absorb dispersers, then a more hierarchical treatment that projects variation in local population dynamics to the regional or landscape scale may be required (Hanski and Gilpin, 1991).

Real landscapes are described in terms of the sizes and dispersion of component patches (Fahrig and Merriam, 1985; Verboom et al., 1991; Weddell, 1991). Dispersion affects the ability of individuals to move among patches, and thereby the occupancy of individual patches, and overall regional population dynamics (Hanski and Gilpin, 1991). The effect of patch size, however, is less clear despite the widespread notion that large patches are better than small patches. We know that small patches usually support small populations and theory predicts that small populations should experience chance extinctions more frequently than larger populations (Lefkovich and Fahrig, 1985). What is this patch and population-size threshold? How does it vary among species? When abundance exceeds the threshold, do we still see a monotonic increase in densities with increasing patch size? Geometry dictates that the size and shape of patches also affects the edge:

interior habitat ratio, which has been shown to be important for some species (Bowers et al., 1996a). How general are such edge effects?

A better understanding of how densities covary with patch size is needed to evaluate the importance of individual landscape elements to overall landscape dynamics. While obvious problems exist for directly linking habitat quality with density (Van Horne, 1983), and patch size with quality, these no doubt are connected somehow especially when small patches that have experienced local extirpations (have zero densities) are considered. That fewer larger patches are more desirable from a species management perspective than several small ones underpins what has been called the single-large or several-small (SLOSS) debate (Simberloff, 1988). Much of SLOSS depends on how densities covary with patch (reserve) size. However, those studies that have examined density-area relationships for patches (E. F. Connor, pers. comm.; Kareiva, 1983; Stamps et al., 1987) have produced a diversity of results that should dampen extrapolation and make induction difficult.

Despite the fact that mammals as a group have been touted as model organisms for testing various tenets of landscape ecology (Lidicker, 1995), no study has attempted a comprehensive across-study survey of how mammalian densities vary with patch size. Hence, our understanding about how populations of mammals respond to patchy or fragmented habitats is based more on anecdotal accounts than general analyses. In this paper, we survey the literature and assemble a database that characterizes relationships between densities of mammals and patch size. Specific objectives included a search to determine if general patterns exist or if density-patch size responses were species, system, or study dependent. To aid in making comparisons among studies, we only consider extreme examples of patchiness (i.e., where inhabitable patches are embedded in a largely uninhabitable habitat

matrix); analyzing studies with less-marked habitat differences would, no doubt, add another layer of complexity. Results of our study should be of interest to those with interests in basic or applied landscape ecology.

PREDICTIONS

The simplest system to study patch size-density relationships is where patches are of a similar, relatively uniform habitat type embedded in an inert, uninhabitable matrix. The simplest model for understanding patch size-density relationships within a landscape is that patches contain a sample of individuals in direct proportion to their areas resulting in equal densities across patches of different size (Haila et al., 1993). Deviations from this expectation emerge when the areal extent of patches affects population performance within or the movement of individuals among patches of different size.

A number of scenarios involving between-patch processes have been proposed to account for positive density-area relationships. Specifically, large patches may be easier for dispersing individuals to locate or they may be sufficiently large to accommodate within-patch dispersal, both that can create inequalities where immigration exceeds emigration and relatively high densities. Small patches, by contrast, may be less apparent to dispersers and too confining to residents, producing conditions where emigration exceeds immigration (Kareiva, 1983; Root, 1973). Conditions within or at the level of patches also can affect densities. First, because larger patches have proportionately low amounts of edge, and more areal habitat available, it is more likely that large patches will exceed a critical size threshold of targeted species than smaller patches (Kareiva, 1983). Second, other conceptualizations like the enemies hypothesis (Risch, 1981; Root, 1973) where predation rates are higher on small than large patches, and environmental-demographic stochasticity that would be more

important on small (with lower abundance) than large (with higher abundance) patches may also produce higher densities on larger than smaller patches (Lefkovitch and Fahrig, 1985).

All of the above mechanisms revolve around the interaction between movements of individuals among individual patches and the performance of local populations. Weddell (1991) classified patches according to the ease with which individuals move between patches; from those where movement is frequent enough to affect densities within generations to more-isolated patches where dispersal is rare and persistence (presence/absence) is determined along inter-generational time-lines. The number and behavior of dispersers over the landscape as they affect connectivity (Harrison, 1991) may also be important. In a recent application of percolation theory, Gardner et al. (1987) suggested that the ratio of suitable:unsuitable habitats at the scale of whole landscapes may fundamentally change density-area relationships; from constant densities when the landscape is largely comprised of inhabitable areas and interpatch movements are frequent to positive or negative relationships when the proportion of suitable habitat falls to 10–30% and movements are rare (Andren, 1994). The point is that features of habitat patches and whole landscapes may produce non-random density-area relationships. Whether or not these patterns exist, and whether they occur for certain taxa or in certain situations is one of the central questions in landscape ecology and the focus of this paper.

METHODS

Our working null hypothesis is that population densities are constant over patches of different size; rejection of this hypothesis provides a starting point for making inference about the landscape ecology of mammals. To test this hypothesis we compiled a database from published studies on mammals that either report patch size-density relationships or provide sufficient data to perform such calculations ourselves. We

restricted our analyses to studies where data on the number of individuals per area were provided. Hence, our focus was on population-level responses rather than the usage of patches by foraging individuals, or the analysis of presence-absence data at a biogeographical scale (studies like Lomolino, 1986, were excluded). Using density data as a criteria for inclusion effectively set both a lower and upper bound on the size of habitat patches considered.

We also restricted our analyses to studies that included basic information characterizing the patch landscape. Data on the sizes, number, and degree of isolation of habitat patches and the ratio of suitable:unsuitable habitat over the landscape were either taken from each paper directly or estimated from maps provided. Following Andren (1994), we used the minimum nearest-neighbor distance between patches as a measure of dispersion and isolation of patches.

In categorizing density-patch-size relationships, we followed the authors conclusions. If a significant (level determined by each author) deviation from constant area-density relationship was noted for a species, we scored it according to sign. We did not re-evaluate or reanalyze data except in those cases where patch density-size relationships were not explicitly tested. In such cases, we used simple correlation analyses to test for density-patch-size relationships.

We were interested in variables that may actually reflect differences in landscape-level responses of species (patch size and dispersion, and the proportion of the landscape mosaic comprised of suitable habitat), and variables that may affect the statistical power to detect such relationships (number of patches; range in patch sizes). We used Kruskal-Wallis one-way analysis of variance to test for differences in patch or landscape among species in three groups; those showing a negative, neutral, or positive patch-size-density relationship. Finally, those studies reporting a positive patch density-size relationship were further analyzed following Loman (1991) to see if the trend was due to small patches having zero densities or to a more graded response operating over a range of patch areas. Accordingly, regression analysis was used to estimate the slope in the regression of density with $\log(\text{area in hectares})$ separately for all patches, and then for just those patches that were inhabited. A large decrease in slope when patches with zero density were omitted was used to infer

TABLE 1.—Features of landscapes and studies for species showing neutral, negative, and positive density-area relationships.

Relationship	Neutral (n = 20)	Negative (n = 7)	Positive (n = 5)
	($\bar{X} \pm 1 SD$)	($\bar{X} \pm 1 SD$)	($\bar{X} \pm 1SD$)
Number of patches examined	10.5 \pm 5.7	30.7 \pm 27.7	20.4 \pm 22.1
Size of range patch (ha)	186 \pm 210	40 \pm 106	250 \pm 310
Minimum size of patch (ha)	1.09 \pm 0.96	0.02 \pm 0.03	1.04 \pm 1.01
Maximum size of patch (ha)	187.12 \pm 210.50	40.32 \pm 105.69	251.13 \pm 310.81
Minimum distance to nearest neighbor (km)	0.13 \pm 0.09	0.02 \pm 0.01	0.13 \pm 0.10
Maximum distance to nearest neighbor (km)	1.27 \pm 0.81	0.07 \pm 0.05	1.14 \pm 0.84
Portion of landscape with suitable habitat (%)	15.7 \pm 12.9	18.0 \pm 16.4	14.8 \pm 12.4

the degree to which empty small patches were responsible for the pattern.

Our analyses identified species within studies as the unit of observation. Although multiple species often were included in the same study, many studies have shown that each species is scaled-to and may respond to the same landscape differently (Bowers et al., 1996b; Diffendorfer et al., 1995a, 1995b, 1995c; Dooley and Bowers, 1996). Hence, there is some basis for treating responses of species, even in the same study and same landscape, as if they were independent. A similar argument can be made regarding the inclusion of the same species inhabiting different landscapes. Such an approach assumes that within a study, species respond to the habitat template of patches independently of one another (i.e., interspecific interactions do not affect distributions or patch-dependent performance). Although this assumption is probably simplistic in some cases (Diffendorfer et al., 1995a), understanding single-species responses first, and multi-species responses second, is a standard reductionist approach that we follow here.

RESULTS

Survey of the mammalian literature produced only 12 studies of 32 species where relationships between density and size of patches could be scored relative to sign (Appendix I). The database included a wide range of mammals and patch systems; Neotropical primates (Bernstein et al., 1976), arboreal marsupial folivores (Laurance 1990; Pahl et al., 1988), and various European and

North American rodents in isolated forest fragments and woodlots (Geuse et al., 1985; Gottfried, 1979; Henderson et al., 1985; Loman, 1991; Telleria et al., 1991) pikas (*Ochotona princeps*) on talus outcroppings (Smith, 1974), rodents inhabiting everglade hammocks (Smith and Vrieze, 1979), and rodents in experimental, mowed landscapes (Dooley and Bowers, 1996; Foster and Gaines, 1991).

The density of 20 of 32 species (ca. 63%) did not covary with increasing size of patches, whereas density of five species increased and seven decreased with size of patch (Appendix I). Studies with species showing density-patch-size relationships tended to include more patches than those showing no significant relationship (Table 1; $\chi^2 = 2.24$, $P < 0.31$; $d.f. = 2$ unless specified otherwise). This suggests that statistical power may be an issue in these analyses. Although some of the studies fell above and some below the 10–30% suitable-habitat threshold of Andren (1994), patch-size-density relationships did not appear to be related to the proportion of the landscape comprised of suitable habitat (Table 1; $\chi^2 = 0.001$, $P > 0.99$).

Patch landscapes scoring negative area-density relationships had significantly smaller minimum and maximum patch areas ($\chi^2 = 10.42$ and 8.00, respectively; both $P < 0.02$), and smaller minimum and max-

imum distances to nearest neighbor ($\chi^2 = 7.65$ and 9.32 , respectively; both $P < 0.02$) than those showing nonsignificant or positive area-density relationships (Fig. 1; Table 1). The range of patch sizes within a study was much larger for studies reporting neutral or positive relationships than for negative area-density relationships (Table 1; $\chi^2 = 7.28$, $P < 0.03$). Among studies, the area of patches was scaled to interpatch distances, i.e., minimum distances to nearest neighbor tended to be positively correlated with the smallest patch area ($r = 0.58$, $d.f. = 21$, $0.05 < P < 0.10$). Hence, studies of landscapes with relatively small patch sizes also had small distances to nearest neighbor; larger patches were, as a rule, more isolated.

The proportion of patches with zero density also varied according to area-density pattern. Studies reporting negative relationships had all patches occupied, while $24\%(\pm 17\%)$ of species with positive and $34\%(\pm 32\%)$ of those with no density pattern included patches with zero density. Using regression analysis to relate the logarithm of area to densities showed that the positive area-density relationship for *Pseudoechirus herbertensis* reported by Pahl et al. (1988) and *Sorex araneus* reported by Loman (1991) was due partly to the inclusion of zero densities in small patches (density = $Y + B[\log(\text{area})]$), with $B = 2.10$ and 3.62 , respectively, for all patches and 1.06 and 2.56 for just-occupied patches).

DISCUSSION

General overview.—One goal of landscape ecology is to better understand the causes and consequences of spatial pattern; to map spatially explicit processes onto the spatial template (Kareiva and Wennergren, 1995; Pickett and Candenasso, 1995). A primary challenge in linking pattern with process is to determine whether a given phenomena operates over a narrow or broad range of scales (Levin, 1992). Despite the fact that most features of landscapes (including patches) are not explicitly or im-

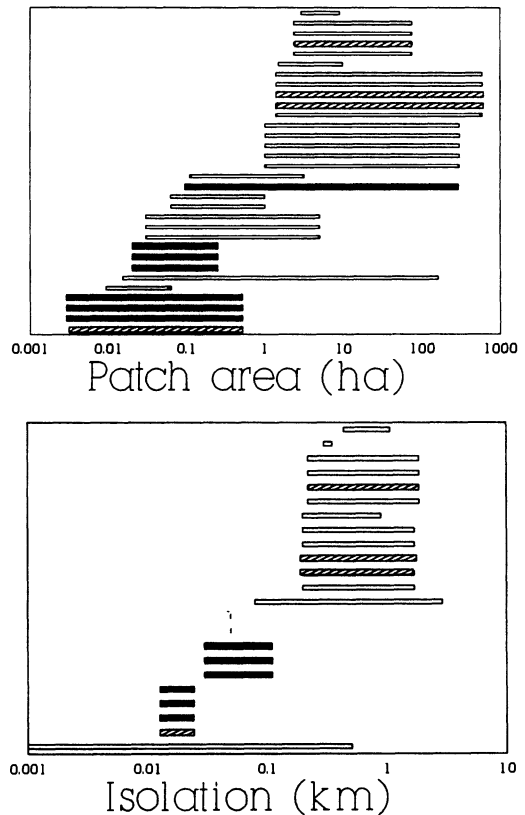


FIG. 1.—Range in areas of patches (top) and distances to nearest neighbor (bottom) for those species showing nonsignificant (clear bars), positive (shaded bars), and negative (solid bars) patch area-density relationships.

plicitly tied to a particular scale (Kotliar and Wiens, 1990), our study suggests that scale can be vital in understanding organismal responses to patch mosaics. Specifically, we found that in systems where patch areas and interpatch distances were small (< 1 ha), six of nine species occurred at higher densities in smaller than larger patches. By contrast, species that inhabited more isolated patch systems either showed no density-area relationship or occurred at higher densities in larger than smaller patches.

Earlier studies of insects, birds, and mammals reported a diversity of relationships between patch size and density. Kareiva (1983) reported positive patch-area-

density relationships for nine species of phytophagous insect, no relationship for eight and a negative relationship for two species. Stamps et al. (1987) reported positive patch-area-density relationships for 18 of 27 avian species. E. F. Connor (pers. comm.) found taxonomic differences with insects and birds showing positive and mammals negative or neutral density-area relationships. Our study, with seven negative, five positive, and 20 neutral relationships, is comparably diverse. Hence, surveys of existing data argue against a general theory of density-area relationships that applies to all species and systems (see Predictions section).

Given that all patch systems may not be comparable, it is possible that an explicit consideration of scale may help account for some of the diversity in patterns. Specifically, small-close systems of patches tend to show a different density-area pattern than large-isolated systems. We suggest two possible explanations for these patterns. First, those species that tend to be studied at smaller absolute scales may be ecologically distinct from those studied at larger scales. Murphy et al. (1990:43) noted that a majority of field studies on patches have focused on "small-bodied, short-lived species with high reproductive rates and high habitat specificity." Such species might be expected to be opportunistic, to have high dispersabilities, to be relatively common, and generally be adapted to exploit perturbed or transient habitats. As one example, Getz (1985) argued that the ecology of *Microtus*, a favored species in mammalian patch studies, predisposes it to exploit small, isolated, and ephemeral habitat patches. That the majority of studies in our review treated highly distinct patches embedded in highly disturbed landscapes, and that especially strong density responses occurred within the smallest patches within the most-fragmented landscapes, is consistent with this notion. The suggestion then is that studies focusing on large, rare mammals with poor abilities for dispersal may

show a different set of responses than small, vagile ones. E. F. Connor (pers. comm.) suggested that common species of mammals may have density-area relationships that are qualitatively different (less positive, more negative) than rarer species.

A second, but not exclusive, explanation is that responses to habitat heterogeneity change qualitatively along a patch size and isolation continuum, from responses involving movement patterns of individuals on short temporal and spatial scales to larger-scale and longer-term patterns of colonization and survival of populations (Weddell, 1991). At the small patches-as-habitats scale, individuals encounter and choose among adjacent patches, and it is the collective response of many individuals that determines local density. The response to small-scale heterogeneity would be largely behavioral, and may follow models of coarse-grained habitat selection (Rosenzweig, 1991). At a larger scale, patches are larger and more isolated, meaning that interpatch movements would be infrequent. Responses to habitat heterogeneity at this scale would reflect longer-term processes of colonization and extinction of populations, i.e., the classic patches-as-islands as discussed in Hanski and Gilpin (1991:8). We suggest that more detailed analyses of the types of species included in a study or scale-sensitive studies that distinguish between individual and population responses would provide a more mechanistic accounting of patch-density-area relationships than has been offered in the past.

Responses at the patches-as-habitat scale.—The net flux of individuals over the landscape at the small scale may vary with a number of factors that are largely patch and landscape specific. First, there is the nature of the patches themselves, or the patch system considered collectively. Lovejoy et al. (1986) noted for Amazonian birds that when habitat is destroyed and the landscape fragmented, birds became concentrated in remnant fragments. They noted that the influx of individuals from impacted areas to

remaining fragments will result in greater proportional and absolute increases in density in smaller than larger fragments. Smith and Vrieze (1979) also noted some similarities in that temporal changes in the quality of interpatch habitat caused individuals to recruit disproportionately to smaller patches. Specifically, they found for *Peromyscus*, *Sigmodon*, and *Oryzomys*, that the displacement of individuals from lower prairie habitat in wet seasons and their concentration on higher hammock patches contributed to negative patch-density-area relationships during wet, but not during dry, periods. Telleria et al. (1991) documented a similar pattern of higher densities of *Apodemus* on smaller than on larger forest fragments in central Spain, where mice living in agriculture fields during the growing season migrated to woodlot refugia in winter.

Second, the crowding of individuals into a limited number of small patches may be limited by dominant, resident individuals via despotic habitat selection. For example, M. A. Bowers and J. L. Dooley (in litt.) found that when an experimental landscape was mowed the movement of displaced *Peromyscus* and *Microtus* into unmowed patches involved juveniles and subdominants rather than adults. Foster and Gaines (1991) also noted that densities of *Microtus* and *Peromyscus* occurred at higher-than-expected densities on small habitat fragments, that animals often visited small patches without staying, and that territories were established preferentially on larger patches. Smith and Vrieze (1979) also noted that their largest patch (hammock) had fewer vagrant *Peromyscus* compared to smaller patches suggesting not only that densities may be higher on smaller than on larger patches, but the turnover of individuals may also be higher.

Finally, small patches also have a higher proportion of boundary areas with surrounding habitats than larger patches, and the selection-avoidance of edge (or ecotonal) habitats may also affect density-area relationships. For example, Bowers et al.

(1996a) reported that female *Microtus pennsylvanicus* with home ranges on fragment edges were of larger body size, they reproduced more frequently and had longer residence times than those in more continuous habitats, all suggesting that edge habitats may be of higher quality than non-edges. A corollary is that landscapes with high proportions of edge would contain more high-quality habitats, and therefore, could support higher densities of rodents; a prediction confirmed in subsequent analyses (J. L. Dooley and M. A. Bowers, in litt.). However, in an earlier study, Bowers and Dooley (1993) found that another inhabitant of the same system (*Peromyscus leucopus*) appeared to avoid edge habitats, especially during illuminated nights when predatory risk would have been greatest, suggesting that edge effects are highly species-specific. Responses of species to edges will vary with the type of surrounding habitat and the nature of patch boundaries, which are phenomena of both patches and the landscape within which they are embedded (Stamps et al., 1987).

Responses at the patches-as-islands scale.—As the landscape is expanded in scale or interpatch areas become more inhospitable, interpatch movements become rarer, connectivity decreases, and patch densities appear to reflect processes that affect survival and persistence of populations. These more-isolated patches appear to be closer to being true islands in the sense of MacArthur and Wilson (1967), with small, isolated populations believed to be particularly vulnerable to extinction (Fahrig and Merriam, 1985; Lefkovitch and Fahrig, 1985). For example, the highly arboreal Herbert River ringtail (*P. herbertensis*) was absent from the two smallest patches in Pahl et al. (1988), the smallest patch in Laurance (1990), and rarely was found in any fragment <20 ha. The absence of these marsupials in small patches and their presence in larger patches suggests that chance extinctions vary with size of local populations and that recolonization events are rare.

The observation that these animals never have been observed on the ground supports the notion that forest fragments are truly insular. Hence, the positive patch area-density reported in both Pahl et al. (1988) and Laurance (1990) for this species of ringtail appears to be due to its absence in smaller patches. Another case of a positive relationship between area and density involved the shrew, *S. areneus*, inhabiting uncropped patches in an agriculture matrix. In this study, only 36 of 66 patches were occupied, and Loman (1991) suggested that poor dispersal abilities and low patch connectivity, in combination with the increased sensitivity of small populations to chance events (Lefkovich and Fahrig, 1985) produced the pattern.

General discussion.—The degree to which patterns of abundance of species vary spatially will depend on spatial usage and dispersal abilities of species relative to axes of habitat heterogeneity (Addicot et al., 1987; Noss, 1991). Matching spatial usage patterns of species to appropriately scaled landscapes is a prerequisite for successful management plans for species (Harrison, 1995; Kareiva and Wennergren, 1995; Wiens, 1994). However, the appropriate ecological scale demarcating what is and is not a patch can be hard to identify, and will vary with the organism considered and the question asked. Our study suggests that entities that ecologists call habitat patches, fragments, and islands often vary markedly in scale, meaning that the whole notion of labeling landscape features is vague, relative, and prone to confusion (Kotliar and Wiens, 1990). Habitat patches usually characterize axes of habitat heterogeneity at an intermediate scale, somewhat below the level of whole landscapes and somewhat above that used by foraging individuals. Even in our own studies we have documented responses of small mammals to axes of habitat heterogeneity within (Bowers and Dooley, 1993; Dooley and Bowers, 1996), at the level of (Bowers et al., 1996a), and at the above-patch, landscape

scale (Bowers et al., 1996b). Distinguishing patch-level from landscape-level responses is problematic because neither has been adequately defined in the literature (Kotliar and Wiens, 1990), and because whatever processes operate within patches are sensitive to those operating over the landscape. The point is that ecologists have tended to view patches and landscapes as entities with set processes rather than a spatial template over which different processes operate at different scales. Responses to patches, however, appear to be highly species and scale-dependent; patches at one end of the scale continuum may involve a fundamentally different set of processes (and, perhaps, a different set of species) than those at the other end.

It is the confounding of processes, such as habitat selection and colonization, that has made it difficult to advance landscape ecology to a more mechanistically based and predictive science. Wiens et al. (1993: 370) noted that “There has been little appreciation of the rich texture of explicit spatial patterns and their potential effects, which is the focus of landscape ecology.” Our review supports this conclusion. Part of the problem is that it is difficult to view landscapes at scales other than that of human perception and convenience. Another problem is that in order to treat large-scale phenomena, we average-out small-scale variability to focus on landscape patterns of populations, community, and ecosystems. By doing so, we have largely taken individual responses out the domain of landscape ecology, but it is the individual that chooses habitats and patches (Lomnicki, 1988), and it is the rarer individual that disperses over the landscape and finds empty patches within which to live. An emphasis on individual behavior, as it is constrained, and modified by landscape elements, would do much to advance our understanding of spatial processes and spatial patterning. Such an approach follows the standard paradigm for landscape ecology; to examine ecological phenomena over a hierarchy of

spatial scales and look to higher scales for significance but to lower scales for mechanism (Levin, 1992; O'Neill et al., 1986).

It also simplistic to focus on individuals to the exclusion of populations. For example, our review suggests that using results of one study to predict the behavior of others is prone to failure, especially if the scales are different. For example, a highly touted method for understanding detailed responses of organisms to large-scale heterogeneity of habitats is through the use of experimental-model systems (EMS—Ims and Stenseth, 1989; Ims et al., 1993; Wiens et al., 1993). This approach assumes that pattern-process relationships are easier to understand when landscapes can be experimentally created, patches defined as replicated experimental units, and individual responses to such microlandscapes studied in detail. Out of methodological necessity, such systems tend to fall toward the small-scale end of the patch-scale continuum. Nonetheless, it usually is assumed that insights gained from such studies can be projected to account for pattern-process relationships at larger scales. Those using this approach often have used rodents as models because of their small size and short generation times (Bowers and Dooley, 1993; Bowers et al. 1996a, 1996b; Diffendorfer et al., 1995a, 1995b, 1995c; Dooley and Bowers, 1996; Foster and Gaines, 1991; Harper et al., 1993; Ims et al., 1993; Lidicker, 1995). The value of the EMS approach to landscape ecology ultimately rests with how findings at a small scale can be extrapolated to account for patterns at larger scales. Specifically, how do the responses of individuals to small-scale patch mosaics relate to responses of populations to more isolated, larger-scaled ones? Our results suggest that moving up from the scale of individuals to that of populations involves strongly non-linear changes in the way patch systems operate. This is an example of transmutation (O'Neill, 1989; O'Neill et al., 1986), where patterns change qualitatively as one changes the scale.

There is a danger in extrapolating results from studies conducted at one scale to predict that at another different scale. Consider, for example, habitat fragmentation (a process that by definition creates habitat patchiness and spatial subdivision of populations) has been called the principle threat to most species in the temperate zone (Wilcove et al., 1986) and the single greatest threat to biological diversity (Noss, 1991). Most attempts to understand the mechanisms by which fragmentation affects populations have called for a hierarchical analysis of how the landscape affects small-scale, local (within-patch) demographic processes as well as larger-scale patterns of movement of individuals among patches (Bowers et al., 1996a; Wiens et al., 1993). Extrapolating the results presented here (without the caveats) may indicate that highly fragmented landscapes comprised of small patches may be preferable for some species than less-fragmented ones with larger patches (after all, small patches tended to have higher densities in EMS types of studies). While this result may hold only for opportunistic species over a limited range of the patch size-isolation continuum, larger and rarer species that, by definition, are more susceptible to extirpation may operate quite differently (Haila et al., 1993; Saunders et al., 1991).

That is not to say that small-scale processes involving individuals show no similarities with larger-scale responses of populations. Several models that treat the occupancy of individual territories, and the colonization of these by individuals, predict responses to patches that, when scaled-up, and are allowed to run over many generations are comparable to that predicted by metapopulation analyses (Lande, 1988; Verboom et al., 1991). It is unlikely, however, that larger scale patterns can be understood through detailed studies of individual behavior without integrating these into models of population dynamics. A conceptual framework that

links long-distance dispersal movements with shorter distance ones involving habitat selection, and patch usage based on quality with population persistence may provide keys in understanding why the behavior of patch systems changes so dramatically between small and larger scales (Stenseth and Hansson, 1981). We believe, in fact, that individual-level responses as studied in EMS types of studies, and the incorporation of these in population-level models holds much promise, and represents the most logical way of understanding the spatial ecology of mammals.

ACKNOWLEDGMENTS

The manuscript benefited greatly from reviews of a previous version by E. F. Connor, J. L. Dooley, R. D. Holt, D. W. Kaufman, and E. W. Schweiger. This research was supported by National Science Foundation grants DEB-9420195 and DEB-9623127.

LITERATURE CITED

- ADDICOTT, J. F., J. M. AHO, M. F. ANTOLIN, D. K. PADILLA, J. S. RICHARDSON, AND D. A. SOLUK. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos*, 49:340–346.
- ANDREN, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*, 71:355–366.
- BERNSTEIN, I. S., ET AL. 1976. Differential effects of forest degradation on primate populations. *Primates*, 17:401–411.
- BOWERS, M. A., AND J. L. DOOLEY, JR. 1991. Role of habitat mosaics on the outcome of two-species competition. *Oikos*, 60:180–186.
- . 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. *Oecologia*, 94:247–254.
- BOWERS, M. A., K. GREGARIO, C. J. BRAME, S. F. MATTER, AND J. L. DOOLEY, JR. 1996a. Use of space and habitats by meadow voles at the home range, patch and landscape scales. *Oecologia*, 105:107–115.
- BOWERS, M. A., S. F. MATTER, J. L. DOOLEY, JR., J. L. DAUTEN, AND J. A. SIMKINS. 1996b. Controlled experiments of habitat fragmentation: a simple computer simulation and a test using small mammals. *Oecologia*, 108:182–191.
- DIFFENDORFER, J. E., M. S. GAINES, AND R. D. HOLT. 1995a. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). *Ecology*, 76:827–839.
- DIFFENDORFER, J. E., N. A. SLADE, M. S. GAINES, AND R. D. HOLT. 1995b. Population dynamics of small mammals in fragmented and continuous old field habitat. Pp. 175–199, in *Landscape approaches in mammalian ecology and conservation* (W. Z. Lidicker, Jr., ed.). University of Minnesota Press, Minneapolis, 215 pp.
- DIFFENDORFER, J. E., R. D. HOLT, N. A. SLADE, AND M. S. GAINES. 1995c. Small mammal community patterns in old fields. Pp. 421–465, in *Long-term studies of vertebrate communities* (M. L. Cody and J. A. Smallwood, eds.). Academic Press, Orlando, Florida, 521 pp.
- DOOLEY, J. L., JR., AND M. A. BOWERS. 1996. Influences of patch size and microhabitat on the demography of two old-field rodents. *Oikos*, 75:543–562.
- FAHRIG, L., AND G. MERRIAM. 1985. Habitat patchy connectivity and population survival. *Ecology*, 66:1762–1768.
- FORMAN, R. T. T., AND M. GODRON. 1986. *Landscape ecology*. John Wiley & Sons, New York, 619 pp.
- FOSTER, J., AND M. S. GAINES. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology*, 72:1358–1373.
- GARDNER, R. H., B. T. MILNE, M. G. TURNER, AND R. V. O'NEILL. 1987. Neutral models for analysis of broad-scale landscape pattern. *Landscape Ecology*, 1:19–28.
- GETZ, L. L. 1985. Habitats. Pp. 286–309, in *Biology of New World *Microtus** (R. H. Tamarin, ed.). Special Publication, The American Society of Mammalogists, 8:1–309.
- GEUSE, P., V. BAUCHAU, AND E. LE BOULENGE. 1985. Distribution and population dynamics of bank voles and wood mice in patchy woodland habitat in central Belgium. *Acta Zoologica Fennica*, 173:65–68.
- GOTTFRIED, B. M. 1979. Small mammal populations in woodlot islands. *The American Midland Naturalist*, 102:105–112.
- HAILA, Y., I. K. HANSKI, AND S. RAIVIO. 1993. Turnover of breeding birds in small forest fragments: the “sampling” colonization hypothesis corroborated. *Ecology*, 74:714–725.
- HANSKI, I., AND M. GILPIN. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, 42:3–16.
- HARPER, S. J., E. K. BOLLINGER, AND G. W. BARRETT. 1993. Effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). *Journal of Mammalogy*, 74:1045–1055.
- HARRISON, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biological Journal of the Linnean Society*, 42:73–88.
- . 1995. Metapopulations and conservation. Pp. 111–128, in *Large-scale ecology and conservation biology* (P. J. Edwards, R. M. May, and N. R. Webb, eds.). Blackwell Publishers, Cambridge, Massachusetts, 375 pp.
- HENDERSON, M. T., G. MERRIAM, AND J. WEGNER. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. *Biological Conservation*, 31:95–105.
- IMS, R. A., AND N. C. STENSETH. 1989. Divided the fruitflies fall. *Nature*, 342:21–22.
- IMS, R. A., J. ROLSTAD, AND P. WEGGE. 1993. Pre-

- dicting space use responses to habitat fragmentation: can voles (*Microtus oeconomus*) serve as an experimental model system (EMS) for capercaillie grouse, *Tetrao unrogallus*, in boreal forests? *Conservation Biology*, 63:261–268.
- KAREIVA, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pp. 259–289, in *Variable plants and herbivores in natural and managed systems* (R. F. Denno and M. S. McClure, eds.). Academic Press, New York, 367 pp.
- KAREIVA, P., AND U. WENNERGREN. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature*, 373:299–320.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, 59:253–260.
- LANDE, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia*, 75:601–607.
- LAURANCE, W. F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *Journal of Mammalogy*, 71:641–653.
- LEFKOVITCH, L. P., AND L. FAHRIG. 1985. Spatial characteristics of habitat patches and population survival. *Ecological Monographs*, 30:297–308.
- LEVIN, S. A. 1992. The problem of pattern and scale in ecology. *Ecology*, 73:1943–1967.
- LIDICKER, W. Z., JR. 1995. *Landscape approaches in mammalian ecology*. University of Minnesota Press, Minneapolis, 215 pp.
- LOMAN, J. 1991. Small mammal and raptor densities in habitat islands: area effects in a South Swedish agricultural landscape. *Landscape Ecology*, 5:183–189.
- LOMNICKI, A. 1988. *Population ecology of individuals*. Princeton University Press, Princeton, New Jersey, 223 pp.
- LOMOLINO, M. V. 1986. Mammalian community structure on islands: the importance of immigration, extinction, and interactive effects. *Biological Journal of the Linnean Society*, 28:1–21.
- LOVEJOY, T. E., ET AL. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285, in *Conservation biology: the science of scarcity and diversity* (M. E. Soule, ed.). Sinauer Associates, Inc. Sunderland, Massachusetts, 584 pp.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, 203 pp.
- MURPHY, D. D., K. E. FREAS, AND S. B. WEISS. 1990. An environment-metapopulation approach to the conservation of an endangered invertebrate. *Conservation Biology*, 4:41–51.
- NOSS, R. F. 1991. Landscape connectivity: different functions at different scales. Pp. 27–39, in *Landscape linkages and biodiversity* (W. E. Hudson, ed.). Island Press, Washington, D.C., 194 pp.
- O'NEILL, R. V. 1989. Perspectives in hierarchy and scale. Pp. 140–156, in *Perspectives in ecological theory* (J. Roughgarden, R. M. May, and S. A. Levin, eds.). Princeton University Press, Princeton, New Jersey, 394 pp.
- O'NEILL, R. V., D. L. DEANGELIS, J. B. WAIDE, AND T. A. ALLEN. 1986. *A hierarchical concept of ecosystems*. Princeton University Press, Princeton, New Jersey, 325 pp.
- PAHL, L. I., J. W. WINTER, AND G. HEINSOHN. 1988. Variation in responses of arboreal marsupials to fragmentation of tropical rainforest in north eastern Australia. *Biological Conservation*, 46:71–82.
- PICKETT, S. T. A., AND M. L. CADENASSO. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science*, 269:331–334.
- PULLIAM, H. R. 1988. Sources, sinks and population regulation. *The American Naturalist*, 137:S50–S66.
- RISCH, S. J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology*, 62:1325–1340.
- RONSENZWEIG, M. L. 1991. Habitat selection and population interactions: the search for mechanism. *The American Naturalist*, 137:S5–S28.
- ROOT, R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. *Ecological Monographs*, 43:95–194.
- SAUNDERS, D. A., R. J. HOBBS, AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5:18–29.
- SIMBERLOFF, D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics*, 19:473–511.
- SMITH, A. T. 1974. The distribution and dispersal of pikas: consequences of insular population structure. *Ecology*, 55:1112–1119.
- SMITH, A. T., AND J. M. VRIEZE. 1979. Population structure of everglade rodents: responses to a patchy environment. *Journal of Mammalogy*, 60:778–794.
- STAMPS, J. A., M. BUECHNER, AND V. V. KRISHNAN. 1987. The effects of edge geometry on territorial defense costs: intruder pressure in bounded habitats. *American Zoologist*, 27:307–325.
- STENSETH, N. C., AND L. HANSSON. 1981. The importance of population dynamics in heterogeneous landscapes: management of vertebrate pests and some other animals. *Agro-Ecosystems*, 7:187–211.
- TELLERIA, J. L., T. SANTOS, AND M. ALCANTARA. 1991. Abundance and food-searching intensity of wood mice (*Apodemus sylvaticus*) in fragmented forests. *Journal of Mammalogy*, 72:183–187.
- TURNER, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics*, 20:171–197.
- VAN HORNE, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, 47:893–901.
- VERBOOM, J. A., A. SCHOTMAN, P. OPDAM, AND J. A. J. METZ. 1991. European nuthatch populations in a fragmented agricultural landscape. *Oikos*, 61:149–156.
- WEDDELL, B. J. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands. *Journal of Biogeography*, 18:385–394.

- WIENS, J. A. 1994. Habitat fragmentation: island v landscape perspectives on bird conservation. *The Ibis*, 137:s97–s104.
- WIENS, J. A., N. C. STENSETH, B. VAN HORNE, AND R. A. IMS. 1993. Ecological mechanisms and landscape ecology. *Oikos*, 66:369–380.
- WILCOVE, D. S., C. H. MCLELLAN, AND A. P. DOBSON. 1986. Habitat fragmentation in the temperate zone. Pp. 237–256, *in Conservation biology: science of scarcity and diversity* (M. E. Soulé, ed.). Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts, 584 pp.

APPENDIX I

Description of studies of mammals including general nature of patches and landscapes, number and sizes of patches, distances to nearest neighbor, and qualitative description of area-density relationships of patches. Correlation coefficients are given for those studies where we analyzed density-area relationships.

Description (source)	Percentage of area covered by habitat (number of patches; landscape area)	Density-area relationship (by species)	Size of patch (range-ha)	Isolation of patch (range-km)
Unmowed patches in mowed pasture (Dooley and Bow- ers, 1996)	39 (12; 13.5 ha)	<i>Peromyscus leucopus</i> none <i>Microtus pennsylvanicus</i> none	(1.0–0.0625)	(0.05)
Rainforest fragments (Bernstein et al., 1976)	? (5; ?)	<i>Saguinus leucopis</i> none ($r = -0.42$) <i>Ateles belzebuth</i> none ($r = -0.387$) <i>Alouatta seniculus</i> none ($r = -0.613$) <i>Cebus albifrons</i> none ($r = -0.608$) <i>Lagothrix lagothricha</i> none ($r = -0.371$)	(300–1)	?
Successional plants in mowed matrix (Foster and Gaines, 1991)	33 (60; 6 ha)	<i>Reithrodontomys megalotis</i> negative <i>Microtus ochrogaster</i> negative <i>Peromyscus maniculatus</i> negative <i>Sigmodon hispidus</i> positive	(0.5–0.0032)	(0.024–0.013)
Woodlots in farmland (Geuse et al., 1985)	? (25; ?)	<i>Clethrionomys gareolus</i> none ($r = 0.008$)	(160.0–0.02)	(0.70–0.00)
Woodlots surrounded by cornfields (Gottfried, 1979)	? (10; ?)	<i>Peromyscus leucopus</i> none	(0.064–0.009)	(2.88–0.08)
Woodlots in farmland (Henderson et al., 1985)	2.25 (5; 1,332 ha)	<i>Tamias striatus</i> none	(8.9–2.9)	(0.9–0.2)
Rainforest fragments (Laurance, 1990)	~8 (10; ~10,000)	<i>Trichosurus vulpecula</i> none <i>Hemibeldeus lemuroides</i> none <i>Pseudocheirus herbertensis</i> positive <i>Dendrolagus lumholtzi</i> positive <i>Pseudocheirus archeri</i> none	(590–1.4)	(1.7–0.2)
Uncultivated area in agricultural landscape (Loman, 1991)	~3 (11; ~1,200 ha)	<i>Clethrionomys glareolus</i> none <i>Microtus agrestis</i> none <i>Sorex araneus</i> none	(5.00–0.03)	(0.46–0.03)

APPENDIX I

Continued.

Description (source)	Percentage of area covered by habitat (number of patches; landscape area)	Density-area relationship (by species)	Size of patch (range-ha)	Isolation of patch (range-km)
Rainforest fragments in clearcut (Pahl et al., 1988)	~22 (11; ca. 4,800)	<i>Trichosurus vulpecula</i> none ($r = 0.389$) <i>Pseudocheirus archeri</i> none ($r = 0.128$) <i>Hemibelideus lemroides</i> none ($r = 0.103$) <i>Dendrolagus lumholtzi</i> none ($r = 0.353$) <i>Pseudocheirus herbertensis</i> positive ($r = 0.841$)	(74.49–2.36)	(1.85–0.22)
Mine-tailing in sage- brush (Smith, 1974)	6.0 (25; 508 ha)	<i>Ochotona princeps</i> none	(3.19–0.11)	(1.07–0.04)
Hardwood hammocks in everglade prairie (Smith and Vrieze, 1979)	3 (6; 15 ha)	<i>Peromyscus gossypinus</i> negative <i>Sigmodon hispidus</i> negative <i>Oryzomys palustris</i> negative	(0.25–0.02)	(0.11–0.03)
Woodlots in grain fields (Talleria et al., 1991)	? (17; ?)	<i>Apodemus sylvaticus</i> negative	(280–0.1)	(?)