

# Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape

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## Abstract

The ability to make a priori assessments of a species' response to fragmentation, based on its distribution in the landscape, would serve as a valuable conservation and management tool. During 1997–1999, we monitored 717 scent stations to examine seasonal use of forest patches, corridors, and crop fields by coyotes (*Canis latrans*), domestic cats (*Felis catus*), foxes (*Vulpes vulpes* and *Urocyon cinereoargenteus*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), opossums (*Didelphis virginiana*), and long-tailed weasels (*Mustela frenata*). For each species we developed landscape-based ecologically scaled landscape indices (ESLI), and we modeled species spatial distribution across three spatial scales (landscape-level, element-level, and local habitat-level). Our results suggest that these predators view landscape fragmentation at different spatial scales and demonstrate strong interspecific differences in their response to elements of the landscape. All species except coyotes and domestic cats avoided agricultural fields. In general, predator species that were more mobile (i.e. high ESLI for landscape connectivity; coyotes) were characterized by landscape- and element-based logistic models. In contrast, models including local habitat features generally were most appropriate for less mobile or more stenophagous predators (e.g. long-tailed weasels). Our analysis extends the application of the ESLI concept to species assemblages that do not appear to function as metapopulations, and it highlights the importance of examining spatial scale and species-specific responses to habitat fragmentation. We discuss the relevance of these findings for defining ecological landscapes, understanding predator–prey interactions at multiple spatial scales, and conserving predator and prey populations in fragmented landscapes.

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## 1. Introduction

Human land-use practices often result in fragmented patches of remnant vegetation embedded within an agricultural or urban matrix. Typically, habitat fragmentation leads to decreased remnant patch size, higher edge:interior ratios, increased patch isolation, and variation in the degree of connectivity of patches (e.g. Saunders et al. 1991). Such environmental modification can alter the spatial structure of vertebrate populations (Saunders et al., 1991; Noss and Csuti, 1997).

An emerging pattern resulting from the application of landscape indices in habitat modeling has been the recognition that organisms can respond to fragmentation at multiple spatial scales (Donovan et al., 1997). Consideration of multi-scale responses can enhance the effectiveness of conservation strategies. For instance, multi-scale studies of an endangered marsupial, *Gymnobelideus leadbeateri*, revealed important information about the need for large-scale efforts within ash-type eucalypt forests, landscape-scale efforts targeting large reserves and corridors within wood-production areas of ash-type eucalypt forests, and habitat-scale efforts to enhance availability of foraging and denning sites within forest stands (Lindenmayer, 2000). Understanding responses of species at multiple spatial scales should be an important precursor of conservation and

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management activities, especially since interspecific differences in multi-scale responses can occur even in closely related species (Schweiger et al., 2000) and can influence community structure in heterogeneous landscapes (Gabor et al., 2001).

When attempting to predict interspecific differences in responses to fragmentation, ecological and behavioral attributes can play an important role. Wolff (1999) concluded that behavioral attributes, including sociality, territoriality, and sex-biased dispersal may be important determinants of a species' colonization ability in fragmented landscapes. A species' sensitivity to fragmentation often is related to its ability to move through a landscape, and this ability is a function of behavior and morphology (Laurance, 1995; Wolff, 1999; Nupp and Swihart, 2000). Behavioral responses to spatial elements can reflect real or perceived costs of living in a fragmented landscape. For instance, costs of movement (i.e. travel time and predation risk) can vary among individuals and species, depending on the ease with which the potentially hostile matrix surrounding patches can be traversed and the availability of corridors that facilitate movement between foraging patches (Laurance, 1995; Nupp and Swihart, 2000). Larger or more vagile species potentially are better equipped to traverse as well as forage in the matrix with minimal risk of predation. Furthermore, larger species likely have a greater perceptual range (sensu Zollner, 2000), thereby influencing the detection of suitable habitat and the perception of landscape structure (Wiens, 1996). A species which, over its geographic range, is adapted to a diverse array of environments (i.e. a species with a broad geographic niche) may be able to respond better to dramatic changes in a landscape resulting from human disturbance. Thus, characterization of a species' niche breadth over its geographic range should provide a measure of a species' behavioral plasticity to human-induced fragmentation of habitat.

Recently, Vos et al. (2001) proposed ecologically scaled landscape indices (ESLI) to explain interspecific differences in response to fragmentation. Their indices were derived from a consideration of factors influencing metapopulation dynamics, as summarized in the incidence function formulation of Hanski (1994). Empirical tests from a fragmented landscape in The Netherlands demonstrated a positive correlation between ESLI values and the fraction of patches occupied by a variety of taxa, including a small mammal, two species of passeriform birds, two species of amphibians, six species of insects, and two species of plants (Vos et al., 2001).

We quantified the spatial distribution of predators among spatial elements, and we examined the multi-scale responses of individual species in an assemblage of mammalian predators using a modified ESLI approach. Predators in our assemblage included coyotes (*Canis latrans*), foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*),

opossums (*Didelphis virginiana*), striped skunks (*Mephitis mephitis*), domestic cats (*Felis catus*), and long-tailed weasels (*Mustela frenata*).

We hypothesized that habitat fragmentation may affect mammalian predators because it changes the spatial distribution of resources. Accordingly, our objectives were (1) to determine if predator distribution and intensity of use varied among spatial elements and (2) to develop models for relating the presence of mammalian predators to local, element- and landscape-level variables. We predicted that body size and behavioral flexibility would influence the response of predators to fragmentation, and this response would be evidenced in individual use of spatial elements and in the spatial distribution of predators. Specifically, we predicted that larger species would be more equitably distributed among all spatial elements compared to smaller species, because large size would confer an increased ability to traverse the matrix with minimal risk of predation. Similarly, we predicted that species with a broader niche would be more equitably distributed among spatial elements compared to smaller species because broader habitat and diet breadth would allow a species to use the majority of spatial elements and exploit a wider range of resources. Additionally, we predicted that the presence of larger species and species with broader niches would be more closely linked to characteristics of elements and the landscapes surrounding an element, because the combined effects of large size and a broad niche would impose fewer constraints on element and landscape use compared to smaller, more specialized species. By extension, we predicted that the presence of smaller species with narrower niches would be more strongly related to local habitat characteristics within an element.

## 2. Methods

### 2.1. Study area

During 1997–1999 we surveyed the spatial distribution of predators in the Indian Pine Study Area (IPSA; 812 km<sup>2</sup>), which encompassed Benton, Tippecanoe, and Warren counties, Indiana, USA. We identified three spatial elements (sensu Forman, 1995) in the IPSA including: (1) woody patches (forest and woodlot); (2) corridors (fencerows, drainage ditches, and railroad rights-of-way); and (3) agricultural matrix (crop fields). Human land use dominated the area, with approximately 12% of the area in human developments and 70% in agricultural production, principally corn and soybeans. Forests, grasslands, and wetlands comprised approximately 10%, 4%, and 1% of the area, respectively. Fencerows and drainage ditches bisected some of the agricultural fields, provided varying levels of connectivity

between forest and grassland patches, and comprised 3% of the area of the IPSA (Gehring, 2000).

## 2.2. Life history data and estimation of niche breadth

We obtained a priori estimates of body mass, population density, and home-range size from published studies. These data were used for calculating ESLIs for each species. We also obtained a priori estimates of niche breadth from the literature for each species. We used three measures for a priori determination of geographic niche breadth; two focused on habitat breadth, whereas the third estimated diet breadth (Table 1). For habitat breadth at the scale of ecoregions, we identified a total of 152 terrestrial ecoregions in North America based on definitions used by Ricketts et al. (1999). We then tallied the number of terrestrial ecoregions contained within each species' geographic range (Table 1). Similarly, across the geographic range of a species, we identified a total of 12 habitat classes including: deciduous forest; coniferous forest; mixed forest; shrubland; wooded savanna; tall grass prairie; short grass prairie; desert; cropland; wooded wetland; marsh; urban. For diet breadth, we identified a total of 15 diet classes including: small mammals (<0.3 kg); medium mammals (0.3–5 kg); large mammals (> 5 kg); wild birds; poultry; amphibians and reptiles; fishes; insects; annelids; crustaceans; hard mast and seeds; soft mast and fruits; cereal grains; vegetation; and carrion. Subsequently, for

each species we determined the number of diet and habitat classes used of the total possible as a measure of diet and habitat breadth, respectively (Table 1). We did not include a class if it comprised <2% of the total.

## 2.3. Predator survey

The spatial distribution of predators was surveyed using scent stations (Roughton and Sweeney, 1982). We selected a simple random sample of spatial elements, without replacement, from the population of patches, corridors, and crop fields in the IPSA, and allocated scent stations similarly among these spatial elements. We randomly located scent stations within spatial elements with the constraint that stations were  $\geq 200$  m apart. Scent-station surveys, using the same station sites, were conducted during the growing season (July), pre-harvest season (September), and fallow season (March–April) to compare differential element use relative to changes in crop fields. Crop fields consisted of relatively short (<1 m) crop vegetation with high ground cover during the growing season. During the pre-harvest season, crop fields were characterized by dense and tall vegetation (1–3 m), with reduced ground cover because of dry soil conditions and crop senescence. Crop fields were nearly barren during the fallow season except for occasional crop residue.

We used scent stations to index spatial variation in predator abundance (Oehler and Litvaitis, 1996) and

Table 1

Interspecific comparison of body mass, three measures of niche breadth, population density, and home-range radius for the suite of mammalian predators detected in a scent-station survey conducted during 1997–1999 in the Indian Pine Study Area, west-central Indiana

Species	Body mass (kg) <sup>a</sup>	Number of ecoregions occupied <sup>b</sup>	Number of diet classes Used <sup>c</sup>	Number of habitat classes used <sup>d</sup>	Mean population density <sup>e</sup>	Mean home-range radius <sup>f</sup>
Domestic Dog	20	–	9	11	–	–
Coyote	12.78	141	11	11	0.7	1829
Fox	4.63	104	10	9	5.9	1112
Raccoon	5.94	111	11	7	44.2	472
Opossum	2.35	74	9	8	26.0	252
Domestic Cat	3.90	–	5	11	22.3	334
Striped Skunk	3.30	80	5	8	3.3	814
Mink	0.88	89	7	3	–	–
Long-tailed Weasel	0.15	95	4	8	14.0	511
Least Weasel	0.04	49	3	5	–	–

Information on ecoregions was obtained from Ricketts et al. (1999). Information on body mass, geographic range, diet composition, habitat use, population density and home-range size was obtained from Baker (1983), Bekoff (1977), Chapman and Feldhamer (1982), Coleman and Temple (1993), Gehring (2000), Hoffmeister (1989), Larivière (1999), Larivière and Pasitschniak-Arts (1996), Liberg (1980), Lotze and Anderson (1979), McManus (1974), Mumford and Whitaker (1982), Nesbitt (1975), Nowak (1991), Seidensticker et al. (1987), Sheffield and Thomas (1997), Svendsen (1982), and Wade-Smith and Verts (1982).

<sup>a</sup> Body mass was calculated as the average mass of males and females.

<sup>b</sup> A total of 152 terrestrial ecoregions were identified in North America based on definitions used by Ricketts et al. (1999).

<sup>c</sup> A total of 15 diet classes were identified including: small mammals (<0.3 kg); medium mammals (0.3–5 kg); large mammals (> 5 kg); wild birds; poultry; amphibians and reptiles; fishes; insects; annelids; crustaceans; hard mast and seeds; soft mast and fruits; cereal grains; vegetation; and carrion. We did not include a class if it comprised <2% of the total.

<sup>d</sup> A total of 12 habitat classes were identified including: deciduous forest; coniferous forest; mixed forest; shrubland; wooded savanna; tall grass prairie; short grass prairie; desert; cropland; wooded wetland; marsh; urban. We did not include a class if it comprised <2% of the total.

<sup>e</sup> Density expressed as individuals/km<sup>2</sup>.

<sup>f</sup> Radius of home ranges was calculated as the average distance (m) for males and females.

relative intensity of use of spatial elements (Heske, 1995). Heske (1995) and Oehler and Litvaitis (1996) used soot-covered track plates (70 × 70 cm aluminum panel) to examine mammalian predators in fragmented landscapes. Both studies suggested that some predators (e.g. coyotes and weasels) might have been under-sampled due to their behavioral avoidance of track plates. We used sand stations to provide a more natural tracking medium and to minimize the bias of under-sampling wary predator species. A primary use of scent stations in this study was to index predator use within the immediate vicinity of the spatial element in which the station was located.

We created scent stations by clearing a 1-m<sup>2</sup> area of debris and sifting masonry sand over the area (Rough-ton and Sweeney, 1982). We misted the scent station with water to create a suitable medium for track impressions. A microcentrifuge tube containing 1.0 ml of domestic rabbit urine was placed in the center of each station as a mild attractant. We used rabbit urine, a mild attractant, rather than powerful attractants such as fatty acid or fermented egg tablets (Linhart and Knowlton, 1975) to avoid attracting predators from great distances and thus misrepresenting their use of spatial elements. We checked scent stations daily for 2 days. Equal numbers of stations within the three spatial elements were sampled during each 2-day period to avoid differences among spatial elements due to temporal variation in mammalian activity (Heske, 1995; Oehler and Litvaitis, 1996). We identified tracks at scent stations using shape characteristics and track dimensions (Halfpenny, 1987) and recorded a visitation event as a present or absent for each predator species for each 2-day period. Frequency of visitation to scent stations within a spatial element was treated as an index of the intensity of use.

The presence or absence of small prey (<150 g; principally *Blarina brevicauda*, *Peromyscus* spp., *Microtus* spp., and *Tamias striatus*) and medium prey (150–2000 g; principally *Sciurus* spp., *Tamiasciurus hudsonicus*, *Spermophilus* spp., and *Sylvilagus floridanus*) was assessed at each station using soot-covered track plates (0.5 × 0.25 m) to record tracks. A single, unbaited track plate was placed 10 m from each scent station when it was established. We arbitrarily chose to place track plates north or east from the station, depending on the direction of the long axis of the spatial element. Track plates were checked concurrently with scent stations.

#### 2.4. Habitat analysis

We measured local habitat attributes, including percent ground cover, vertical structure, and percent canopy cover for each sampling period, within a 10-m radius plot centered on the scent station. Percent ground cover (GC) and percent canopy cover (CC) were

estimated at the scent station and 10 m from the station in the four cardinal directions using a 1-m<sup>2</sup> quadrat and ocular tube, respectively (James and Shugart, 1970). We averaged GC and CC estimates for each site. Vertical structure (VS) of woody and herbaceous vegetation was measured with a density board (De Vos and Mosby, 1969) subdivided into four height intervals (VS1 = 0–0.3 m; VS2 = 0.3–1 m; VS3 = 1–2 m; VS4 = 2–3 m; Robbins et al., 1989). Vertical structure was the mean of four density board estimates (i.e. average of the proportion of each height interval that was at least 50% obstructed by vegetation) taken 10 m from the scent station in the four cardinal directions for each height interval.

#### 2.5. Element and landscape analysis

We digitized all habitat types in the IPSA from 1998 digital ortho quadrangles using ArcView (ESRI, Redlands, California) and converted these data into an ARC/INFO (ESRI, Redlands, California) coverage with 1-m resolution. We identified seven habitat types in the IPSA: herbaceous corridor, wooded corridor, forest, wetland, grassland, agricultural field, and human dwelling. Subsequently, we measured element-level and landscape-level attributes using ArcView and FRAGSTATS\*ARC (Berry et al., 1998; Pacific Meridian Resources, Fort Collins, Colorado).

We chose three element-level metrics, including area, fractal dimension, and distance to nearest edge. Fractal dimension was calculated as 2 times the natural logarithm of element perimeter (m) divided by the natural logarithm of element area (m<sup>2</sup>) and was used as an index of element shape complexity; larger values of fractal dimension denote elements with more complex shapes (Forman, 1995). Distance to nearest edge was measured in ArcView as the straight-line distance (m) from the scent station to the nearest boundary with a dissimilar habitat type.

Three landscape-level metrics were calculated within a 1-km (3 km<sup>2</sup>) and 3-km (28 km<sup>2</sup>) radius buffer region centered on individual scent stations. We selected a 1-km and 3-km radius measure to approximate the average radius of long-tailed weasel and raccoon home ranges, respectively (e.g. Baker, 1983; Gehring, 2000). Mean nearest-neighbor distances were computed as the average of the straight-line distances (m) from a scent station to herbaceous corridors, wooded corridors, grasslands, forest, and wetlands. A corresponding standard deviation of nearest-neighbor distances also was computed for each scent station. Landscape composition, indexed as the proportion of the buffer area consisting of each of the seven habitat types, was measured for 3- and 28-km<sup>2</sup> scales. We used the Shannon-Wiener Index as a diversity measure of habitat types within the 3 km<sup>2</sup> and 28 km<sup>2</sup> buffers. We used an arcsine transformation on proportions to achieve normal distributions (Zar, 1996).

## 2.6. Ecologically scaled landscape indices

Vos et al. (2001) introduced ESLIs as an alternative approach for modeling the distribution of species in landscapes. They developed two ESLIs (average patch carrying capacity and average patch connectivity) based on landscape- and species-specific characteristics to account for the two primary consequences of fragmentation (i.e. decreased habitat area and increased patch isolation; Vos et al., 2001). The ESLI for average patch carrying capacity incorporated the average patch size and species-specific area requirements (e.g. territory size), whereas the ESLI for average patch connectivity incorporated distances between patches weighted by species-specific dispersal abilities (Vos et al., 2001).

The ESLIs of Vos et al. (2001) were patch-based, reflecting an emphasis on metapopulation dynamics occurring among distinct subpopulations within a landscape. The mammalian predators we studied do not fit neatly into a metapopulation framework, because these species typically have home ranges comprised of multiple habitat patches and multiple patch types in agricultural landscapes (Gehring, 2000). Thus, we opted to compute landscape-based ESLIs. Specifically, we developed an index of landscape carrying capacity,  $ESLI_{K_i}$ , as a landscape analog to ESLI average patch carrying capacity:

$$ESLI_{K_i} = p_i \log(A) D_i,$$

where  $p_i$  represents the fraction of all diet classes used by species  $i$  (range from 0 to 1, based on 15 diet classes);  $A$  is the area of usable habitat (corridors, grassland, forest land, and wetland patches) within the IPSA landscape; and  $D_i$  is the average density (number of individuals per km<sup>2</sup>) for species  $i$ . The index combines a landscape index (area of usable habitat) and species-specific attributes (diet breadth and population density). For a given landscape, a species with greater breadth of diet and population density yields a higher  $ESLI_{K_i}$ . We predicted that species with high values of  $ESLI_{K_i}$  should be more abundant in available habitat, as reflected in the fraction of scent stations in non-matrix habitat that were visited.

Similarly, we propose an index of landscape connectivity,  $ESLI_{M_i}$ , as an analog to ESLI average patch connectivity (sensu Vos et al., 2001):

$$ESLI_{M_i} = \frac{q_i DR_i}{\log(C)},$$

where  $q_i$  is the fraction of all habitat classes used by species  $i$  (ranging from 0 to 1 based on 12 habitat classes);  $C$  is a connectivity index for the IPSA landscape, expressed as a product of mean nearest-neighbor distances and standard deviation of nearest-neighbor distances; and  $DR_i$  is a measure of movement rates within a home

range.  $DR_i$  was comprised of a time-to-independence measure (TTI, Swihart et al., 1988) scaled by the mean radius of the home range (MHRR<sub>*i*</sub>):  $DR_i = \frac{MHRR_i}{TTI_i}$ . We used a predictive allometric relationship for mammalian noncentral-place foragers to estimate TTI (i.e.  $TTI = 354M^{0.22}$ , where  $M$  = body mass in kg; Swihart et al., 1988).  $ESLI_{M_i}$  thus combines a landscape index (connectivity = mean distance and dispersion of usable habitat) and species-specific attributes (habitat breadth and rate of movement within a home range). For a given landscape, a species with greater breadth of habitat and greater rate of movement yields a greater value for  $ESLI_{M_i}$ . We predicted that movements of species with large values for  $ESLI_{M_i}$  should be affected less by agriculturally induced fragmentation of native habitat, due to their greater mobility and habitat breadth. That is, these species should be more matrix tolerant, as reflected in the fraction of scent stations visited in the crop fields. Although body size and niche breadth were positively correlated for our assemblage, we avoided potential confounding effects by incorporating body size (dispersal ability and density) and niche breadth (available habitat area) into ESLIs.

## 2.7. Statistical analysis

Laurance (1995) concluded that matrix intolerance (i.e. the inability or reluctance of a species to use the agricultural matrix) was the most important predictor of extinction proneness in Australian mammals subjected to habitat fragmentation. Accordingly, we used an index of matrix tolerance to indicate a species' ability to cope with human-induced fragmentation of native habitat (i.e. a species' ability to use crop fields and tolerance to agriculturally induced fragmentation). For each species we computed the fraction of observations occurring in crop fields as a relative measure of matrix tolerance. For example, 21 of 71 coyote visits were to crop fields, yielding a matrix tolerance measure of 0.30 (Table 2). Additionally, we computed the fraction of observations in corridors and forest patches as a measure of use of suitable habitat. We then computed product-moment correlations and conducted one-tailed tests of significance between matrix tolerance and  $z$ -scores for body size and each of the three measures of niche breadth, as well as a composite  $z$ -score representing the average of the four variables (Table 1). We also tested our ESLI predictions by computing product-moment correlations and conducting one-tailed tests of significance between use of suitable habitat and  $ESLI_{K_i}$  and between matrix tolerance and  $ESLI_{M_i}$ .

We used the chi-square goodness-of-fit statistic (Zar, 1996) to test for differential use of spatial elements by each species within each season. The Bonferroni procedure for multiple comparisons (Manly et al., 1993) was used to identify selection or avoidance of spatial elements. As a

Table 2

Number of scent-station visits recorded for individual mesopredator species in the three landscape elements surveyed during 1997–1999, Indian Pine Study Area, west-central Indiana

Species	Number of visits		
	Forest patch ( $n=249$ )	Corridor ( $n=261$ )	Crop field ( $n=207$ )
Raccoon	195	166	51
Opossum	55	56	24
Long-tailed weasel	42	38	7
Coyote	14	36	21
Striped skunk	28	17	9
Domestic Cat	18	22	8
Fox	25	20	8
Domestic Dog	4	3	4
Mink	3	3	1
Least weasel	1	3	0

Numbers in parentheses after each element type refer to the number of scent stations established.

precursor to constructing our predictive models, we examined pairwise correlations via Pearson correlation analysis (SAS Institute, 1994) to identify highly correlated pairs of variables. Subsequently, we found high correlations among all local habitat variables and conducted a principal components analysis (PCA) on these variables (Gehring, 2000). We used factors from PCA as substitutes for the original habitat variables.

We used logistic regression (Hosmer and Lemeshow, 1989) and a multiscale approach (Bergin et al., 2000) to develop predictive relationships between predator occurrence and season, type of spatial element, presence of prey, local habitat attributes, element-level characteristics, and landscape-level features. Season and type of spatial element were incorporated into the analysis as indicator variables (Neter et al., 1996). We developed three sets of models for each predator species: (1) a general model built using all variables for a scent station located within a 3-km<sup>2</sup> landscape; (2) a general model based on all variables measured within a 28-km<sup>2</sup> landscape surrounding the scent station; and (3) a spatially explicit model based on variables categorized as landscape, element, or local habitat. The two general logistic models (3- and 28-km<sup>2</sup> landscapes) were virtually identical for all species; thus, only results for the 3-km<sup>2</sup> landscape are reported. We examined explicitly how spatial scale was related to the ability to predict species-specific distributions. We used a spatially hierarchical modeling approach by building models incorporating progressively greater spatial resolution: (1) landscape model; (2) landscape-element model; and (3) landscape-element-habitat model (i.e. “full” model).

We selected the logistic models with the lowest Akaike’s Information Criterion (AIC; Burnham and Anderson, 1998) as the best model. As we modeled predator distributions from the landscape-level to the element-level to the habitat-level, we forced the variables from the previous spatial scale into the current

model. For example, after building the best landscape model, we forced the selected landscape-level variables into the landscape-element model in addition to the subset of element-level variables that built the best model at this spatial scale. We rescaled AIC values relative to the best model (i.e. model with the minimum AIC) which received an AIC value of 0. We calculated the difference between AIC values among models ( $\Delta_i$ ) and ranked models in ascending order relative to the  $\Delta_i$  values. We then calculated Akaike weights ( $w_i$ ) to aid in the determination of which spatial scale yielded the best model;  $w_i$  values approximate the probability that a model is the best Kullback-Leibler model (Burnham and Anderson, 1998). Subsequently, we determined the relative likelihood that one model was better than another as  $w_i/w_j$  (Burnham and Anderson, 1998).

### 3. Results

#### 3.1. Visitation and matrix tolerance

We recorded visitation by 10 predator species during 1103 of 1434 station-nights (77% visitation, Table 2). This community of predators also facilitated a comparison of differential responses to fragmentation based on interspecific differences in life history and ecology (Table 1). The seven species with the highest visitation rates were analyzed (Table 2).

Matrix tolerance (i.e. fraction of observations occurring in crop fields) was correlated positively with body size ( $r=0.895$ ,  $P<0.001$ ), ecoregion breadth ( $r=0.636$ ,  $P=0.048$ ), diet breadth ( $r=0.585$ ,  $P=0.076$ ), and habitat breadth ( $r=0.616$ ,  $P=0.058$ ). Matrix tolerance also was correlated positively with a composite measure of body size and niche breadth, represented by the average of the  $z$ -scores of individual variables ( $r=0.877$ ,  $P=0.001$ ).

### 3.2. Reduction of explanatory variables

Significant correlations existed between local habitat variables. A PCA of these variables resulted in two principal components that explained 78% of the variation in the six original variables. We interpreted the principal components as: PC1 = increasing scores with increased vertical structure; and PC2 = increasing scores with greater ground cover and lower canopy cover. Linear combinations of the principal components were: PC1 = 0.20(GC) + 0.45(VS1) + 0.50(VS2) + 0.48(VS3) + 0.47(VS4) + 0.23(CC); and PC2 = 0.70(GC) + 0.29(VS1) + 0.16(VS2) – 0.19(VS3) – 0.30(VS4) – 0.52(CC) (Gehring, 2000). The remaining explanatory variables were used to fit species-specific logistic models (Table 3).

### 3.3. Seasonal use of spatial elements and predator occurrence

Coyotes demonstrated differential use of spatial elements during the growing season ( $\chi^2_{\text{grow}} = 7.57$ , 2 df,  $P = 0.02$ ), but not during the other seasons ( $\chi^2_{\text{pre-harvest}} = 3.50$ , 2 df,  $P = 0.17$ ;  $\chi^2_{\text{fallow}} = 1.90$ , 2 df,  $P = 0.39$ ). During the growing season, coyotes avoided forest patches, selected corridors and used fields in proportion to their availability. Logistic regression indicated that coyote presence was correlated with the growing and fallow seasons, absence of forest patches, and closer proximity to edges (Table 4).

Foxes exhibited strong differential use of spatial elements during the pre-harvest season ( $\chi^2_{\text{pre-harvest}} = 12.78$ , 2 df,  $P = 0.002$ ), but weaker discrimination during the other seasons ( $\chi^2_{\text{grow}} = 5.80$ , 2 df,  $P = 0.06$ ;  $\chi^2_{\text{fallow}} = 5.67$ , 2 df,  $P = 0.06$ ). During the pre-harvest season, foxes selected forest patches, avoided fields, and used corridors in proportion to their availability. Logistic regression indicated that the presence of foxes covaried with the pre-harvest season, presence of small and medium mammal prey, greater vertical structure, and greater proportion of wetlands within 1 km of scent stations (Table 4).

Raccoons exhibited differential use of spatial elements during all sampling seasons ( $\chi^2_{\text{grow}} = 28.80$ , 2 df,  $P < 0.001$ ;  $\chi^2_{\text{pre-harvest}} = 23.87$ , 2 df,  $P < 0.001$ ;  $\chi^2_{\text{fallow}} = 38.02$ , 2 df,  $P < 0.001$ ). During the growing season, raccoons used forest patches in proportion to their availability, whereas corridors were selected and fields were avoided. The use of spatial elements shifted during the pre-harvest and fallow seasons when raccoons selected forest patches, used corridors in proportion to their availability, and avoided fields. Raccoon visitation at scent stations was correlated with the pre-harvest and fallow seasons, presence of patches and corridors, greater vertical structure, lower ground cover and higher canopy cover, and shorter distances between habitat patches (Table 4).

Opossums used spatial elements differentially in the pre-harvest ( $\chi^2_{\text{pre-harvest}} = 10.26$ , 2 df,  $P = 0.006$ ) and fallow ( $\chi^2_{\text{fallow}} = 9.25$ , 2 df,  $P = 0.010$ ) seasons, but not during the

Table 3

Abbreviations for explanatory variables included in logistic models for predicting predator presence in the Indian Pine Study Area, west-central Indiana, 1997–1999

Variable	Definition
GRO	Growing season (July)
PRH	Pre-harvest season (September)
PAT	Forest patch
COR	Corridor
<i>Local scale</i>	
PC1	Local habitat principal component incorporating higher levels of foliage density
PC2	Local habitat principal component for higher ground cover and lower canopy closure
SMP	Small-mammal prey (< 150 g)
MMP	Medium-mammal prey (150–2000 g)
<i>Element scale</i>	
AREA	Area of spatial element
FD	Fractal dimension of spatial element
DNE	Distance to nearest edge
<i>Landscape Scale</i>	
MNN	Mean distance to nearest neighboring habitat (herbaceous corridor, wooded corridor, forest, grassland, wetland)
PW	Proportion of wetland habitat within 3-km <sup>2</sup> landscapes
PWC	Proportion of wooded corridor habitat within 3-km <sup>2</sup> landscapes
PH	Proportion of human homestead within 3-km <sup>2</sup> landscapes
PG	Proportion of grassland habitat within a 3-km <sup>2</sup> landscape
PFD	Proportion of crop field within a 3-km <sup>2</sup> landscape
SD	Shannon-Weiner Diversity Index of habitats within a 3-km <sup>2</sup> landscape

Table 4

Summary of general logistic models selected as the best Kullback-Leibler models for predicting the presence of mesopredator species at scent stations using a 3-km<sup>2</sup> buffer around scent stations in the Indian Pine Study Area, west-central Indiana, 1997–1999

Species	Logistic model
Coyote	−1.72 - 0.36 (PRH) - 0.74 (PAT) - 0.01 (DNE)
Fox	−4.17 + 0.59 (PRH) + 0.67 (SMP) + 0.47 (MMP) + 0.01 (PC1) + 2.89 (PW)
Raccoon	−0.39 - 0.59 (GRO) + 1.13 (PAT) + 1.38 (COR) + 0.02 (PC1) - 0.01 (PC2) - 0.001 (MNN)
Opossum	−2.95 + 1.02 (GRO) + 0.89 (PRH) + 0.52 (MMP) + 0.01 (PC1) - 0.01 (PC2) + 6.19 (PWC)
Striped Skunk	−9.05 + 0.95 (PAT) + 1.70 (FD) + 4.18 (PG) + 2.19 (PFD) + 2.75 (PH)
Domestic Cat	−2.67 + 0.64 (COR) - 0.02 (PC2) - 0.01 (AREA) + 2.37 (PH) - 0.53 (SD)
Long-tailed Weasel	−4.59 + 1.81 (PAT) + 1.48 (COR) + 1.17 (SMP) + 0.66 (MMP) + 0.01 (PC2)

Explanatory variables (Table 3) included in this model were measured at three spatial scales (i.e. local habitat, element-level, and landscape-level). We selected the best models based on the lowest Akaike Information Criterion values and Akaike weights using procedures outlined in Burnham and Anderson (1998).

Table 5

Results from spatially hierarchical models for species detected using scent stations during 1997–1999, Indian Pine Study Area, west-central Indiana

Species	Model	AIC	$\Delta_i$	$w_i$	Relative likelihood ( $w_i/w_j$ )
Coyote	Land	452.11	2.48	0.224	–
	Land + Element	449.63	0.00	0.776	3.5
	Land + Element + Habitat	– <sup>a</sup>	–	–	–
Fox	Land	376.94	4.70	0.067	–
	Land + Element	374.51	2.27	0.227	3.4
	Land + Element + Habitat	372.24	0.00	0.706	3.1
Opossum	Land	682.38	29.07	<0.001	–
	Land + Element	671.91	18.60	<0.001	–
	Land + Element + Habitat	653.31	0.00	>0.999	999
Striped Skunk	Land	372.41	1.82	0.287	–
	Land + Element	370.59	0.00	0.713	2.5
	Land + Element + Habitat	– <sup>a</sup>	–	–	–
Raccoon	Land	910.87	130.95	<0.001	–
	Land + Element	818.57	38.65	<0.001	–
	Land + Element + Habitat	779.92	0.00	>0.999	999
Domestic Cat	Land	343.04	7.56	0.020	–
	Land + Element	339.74	4.26	0.104	5.2
	Land + Element + Habitat	335.48	0.00	0.876	8.4
Long-Tailed Weasel	Land	538.91	34.81	<0.001	–
	Land + Element	518.31	14.21	<0.001	–
	Land + Element + Habitat	504.10	0.00	>0.999	999

Full models include landscape, element, and local habitat variables, the subsequent model omits local habitat variables, and the most restrictive model contains only landscape-level variables. AIC = Akaike's Information Criterion,  $\Delta_i = AIC_i - AIC_{\text{minimum}}$ ,  $w_i = \frac{\exp(-1/2\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$ .

<sup>a</sup> Addition of local habitat variables did not result in an AIC value lower than the landscape-element model.

growing season ( $\chi^2_{\text{grow}} = 1.12$ , 2 df,  $P = 0.572$ ). During the pre-harvest and fallow seasons, opossums avoided fields, but used patches and corridors in proportion to their availability. Logistic regression indicated that opossum presence covaried with the growing and pre-harvest seasons, presence of medium-sized mammalian prey, greater vertical structure, lower ground cover and higher canopy cover, and greater proportion of wooded corridors (Table 4).

Striped skunks exhibited differential use of spatial elements during the pre-harvest ( $\chi^2_{\text{pre-harvest}} = 7.00$ , 2 df,

$P = 0.030$ ) and fallow ( $\chi^2_{\text{fallow}} = 13.25$ , 2 df,  $P = 0.001$ ) seasons, but not during the growing season ( $\chi^2_{\text{grow}} = 2.33$ , 2 df,  $P = 0.310$ ). During the pre-harvest and fallow seasons, skunks selected forest patches and used corridors in proportion to their availability. Agricultural fields were avoided during the fallow season. Logistic regression indicated that striped skunk presence was correlated with the presence of forest patches, greater shape complexity of elements, greater proportion of grasslands, greater proportion of cropland, and greater proportion of human dwellings (Table 4).



Domestic cats did not demonstrate differential use of spatial elements during any season ( $\chi^2_{\text{grow}} = 6.00$ , 2 df,  $P = 0.05$ ;  $\chi^2_{\text{pre-harvest}} = 2.17$ , 2 df,  $P = 0.34$ ;  $\chi^2_{\text{fallow}} = 2.57$ , 2 df,  $P = 0.28$ ). During the growing season, use of spatial elements by cats was nonsignificant, but patterns of use suggested greater use of corridors and reduced use of fields. Logistic regression predicted that cat presence was correlated with corridor presence, lower ground cover and higher canopy cover, smaller element area, greater human development, and lower diversity of habitat (Table 4).

Long-tailed weasels used spatial elements differentially during all seasons ( $\chi^2_{\text{grow}} = 7.22$ , 2 df,  $P = 0.03$ ;  $\chi^2_{\text{pre-harvest}} = 12.69$ , 2 df,  $P = 0.002$ ;  $\chi^2_{\text{fallow}} = 14.25$ , 2 df,  $P = 0.001$ ). During the growing season, long-tailed weasels avoided fields, but they used patches and corridors in proportion to their availability. During the pre-harvest season, long-tailed weasels used patches in proportion to their availability, selected corridors, and avoided fields. During the fallow season, long-tailed weasels selected patches, used corridors in proportion to their availability, and avoided fields. Logistic regression indicated that long-tailed weasel presence was correlated with the presence of patches and corridors, the presence of small and medium mammal prey, and greater ground cover and lower canopy cover (Table 4).

### 3.4. Ecological scaling of responses

Models incorporating all three spatial scales (i.e. “full” models) provided the best fit to the data for all predator species except coyotes and striped skunks (Table 5). The landscape-element model was only 3.5 and 2.5 times more likely to be superior than the landscape model for coyotes and skunks, respectively. For foxes, the full model was 3.1 times more likely to be the best model than the landscape-element model (Table 5). Inclusion of local habitat variables resulted in vastly superior models for detecting the presence of opossums, raccoons, long-tailed weasels, and to a lesser degree domestic cats (Table 5).

Values of  $ESLI_K$  and  $ESLI_M$  ranged from 1 to 52 and 0.07 to 0.50, respectively (Fig. 1a). Species exhibited a tradeoff in terms of their ability to respond to fragmentation. Species with well-developed mobility or habitat breadth (e.g. coyotes) also had large area requirements leading to low carrying capacities, whereas species with large carrying capacities (e.g. raccoons) were constrained to a greater degree by the matrix (Fig. 1a,  $r = -0.66$ ,  $P = 0.10$ ). As predicted,  $ESLI_K$  was correlated with a species’ overall use of habitat in the landscape (Fig. 1b,  $r = 0.95$ ,  $P = 0.0005$ ). Similarly,  $ESLI_M$  was marginally correlated with a species willingness to venture into the agricultural matrix (Fig. 1c,  $r = 0.57$ ,  $P = 0.09$ ).

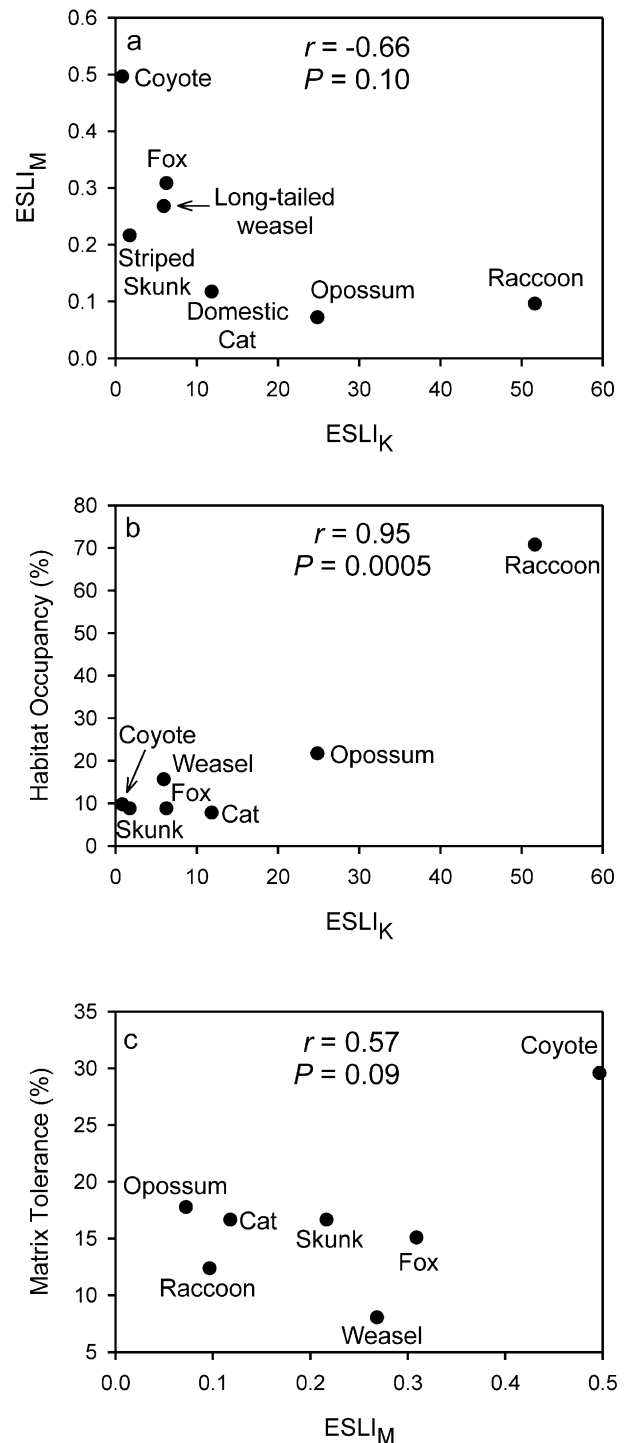


Fig. 1. Ecologically scaled landscape indices (ESLI) for mammalian mesopredators occupying an agricultural landscape in west-central Indiana, USA. Panel (a) depicts the position of each species in an ecologically scaled landscape context that accounts for vagility ( $ESLI_M$ ) and abundance ( $ESLI_K$ ). Note that no species occupy the upper right quadrant, an area reserved for species with the greatest freedom from effects of fragmentation. Panel (b) illustrates the positive relation between the logarithm of  $ESLI_K$  and the percentage of sites in suitable habitat that were visited by each species; panel (c) illustrates the relation between  $ESLI_M$  and matrix tolerance, expressed as the percentage of scent stations in the agricultural matrix that were visited by each species.

## 4. Discussion

### 4.1. Predator use of spatial elements

Numerous studies have documented differential responses of mammalian species to habitat fragmentation (e.g. Andr n, 1994; Laurance, 1995; Nupp and Swihart, 1998, 2000; Rosenblatt et al., 1999). Generalist species often are regarded as benefiting from agriculturally induced habitat fragmentation (e.g. Matthiae and Stearns, 1981) because they often are highly mobile, able to use diverse habitats or food items, or exploit edge habitats (Saunders et al., 1991; Noss and Csuti, 1997). Of the seven mammalian predators that we studied, all can be classified as generalist species in their ability to use a variety of habitat types, including edge habitat. Nonetheless, they differ considerably in their ecology and life history, and these differences are borne out in their differential responses to habitat fragmentation. All species, except domestic cats, exhibited non-random use of spatial elements in this fragmented landscape. Tolerance to croplands, measured in terms of the relative frequency of use, was positively related to body size and niche breadth. Based on Table 1 and the correlations with our index of crop-field tolerance, we expected species to exhibit the following ranking in terms of increasing sensitivity to fragmentation, as reflected in empirical models of occurrence: coyote < (fox = opossum = domestic cat = striped skunk)  $\leq$  raccoon < long-tailed weasel.

The mesopredator responses to fragmentation were consistent with a priori predictions based on a consideration of ecological characteristics of the individual species. For a given amount of available habitat, species with generalized diets potentially can avail themselves of a broader array of resources. In a heterogeneous landscape, then, energy can be extracted from a greater fraction of nonmatrix habitat by species with broader diets. Likewise, species characterized by high local densities by definition are more abundant within a given area, which may be reflected in greater overall use of available habitat. In our study, raccoons and opossums were notable for their large values of  $ESLI_K$ , and these species also exhibited the greatest visitation rates at scent stations in nonmatrix habitat (Fig. 1b). Similarly, for a given level of connectivity, species with generalist habitat requirements presumably can make more complete use of nonmatrix habitat when moving through a fragmented landscape, or may even view the matrix as habitat. Likewise, species characterized by greater mobility (as measured with TTI and MHRR) can move more readily between habitats. Coyotes were notable for their large  $ESLI_M$  value among the mesopredators studied, and they also displayed the greatest matrix tolerance (Fig. 1c). The overall correlation between  $ESLI_M$  and matrix tolerance was reduced considerably by the

lower-than-predicted use of the matrix by long-tailed weasels.  $ESLI_M$  does not take into account predation risk, and we suspect that weasels, because of their small size, are more prone to predation than the other species we considered (Palomares and Caro, 1999). Removal of long-tailed weasels from the analysis improved the correlation between  $ESLI_M$  and matrix tolerance to 0.79 ( $P=0.03$ ).

The responses to fragmentation noted in our ecological scaling of landscape indices should also be reflected in the multi-scale hierarchical models. In general, species characterized by large  $ESLI_M$  values responded to features of the landscape or patch more strongly than they responded to local habitat features (Table 5). Data for coyotes, foxes, and skunks resulted in best models that were either exclusively or substantially dependent upon larger-scale features of the environment. These species also exhibited the largest home ranges of the mesopredators we studied (Table 1). In contrast, models including local habitat features were most appropriate for raccoons, opossums, and long-tailed weasels. Raccoons and opossums exhibit relatively restricted home ranges, in concordance with our predictions. Long-tailed weasels, however, are more mobile. The dependence of weasels on local habitat features stems from their more carnivorous diet, perhaps in conjunction with constraints imposed by predation risk. Prey abundance and ground cover were significant predictors of weasel occurrence (Table 4).

### 4.2. Perception of landscape structure by predators

Species-specific responses to fragmentation are related to interspecific differences in the perception of landscape structure and the scale of fragmentation (Lord and Norton, 1990; Vos et al., 2001). Highly vagile species likely perceive landscape heterogeneity on a different scale than less mobile species (Kolasa and Rollo, 1991). For a given level of fragmentation, a species' response to landscape structure is influenced by its perceptual range (Lima and Zollner, 1996; Zollner and Lima, 1997). Lidicker and Koenig (1996) suggested that landscape perception by mammals is dependent on body size, with large-bodied mammals perceiving landscapes as more homogenous than smaller species. Relative to smaller, less vagile mammals, larger mammals appear to view the matrix less as a barrier to movement, and patches within landscapes as less isolated and largely undivided (Addicott et al., 1987). Our results tend to support this hypothesis. Species in this predator assemblage view landscape fragmentation at different spatial scales, as evidenced by the differential importance of local habitat characteristics, element-level attributes, and landscape-level attributes in predicting predator occurrence. In accordance with our a priori predictions, large species with broad niches exhibited relatively little differentiation

in resource selection as a function of multiple spatial scales, whereas smaller species with narrower niches apparently were more constrained spatially in their resource selection.

Zollner (2000) demonstrated that sciurids differed in their perceptual range, and that these differences were related to body size. Coyotes and foxes, because of their greater mobility, are characterized by larger ecological neighborhoods (*sensu* Addicott et al., 1987) than raccoons, opossums, striped skunks, or long-tailed weasels. All species demonstrate similar levels of plasticity relative to habitat use (Table 1), yet we observed strong interspecific differences in their responses to spatial elements. For example, coyotes and foxes appear capable of assessing all components of the landscape and moving relatively freely among elements, whereas long-tailed weasels are confined to linear elements and forest patches in close proximity to wetlands (Gehring, 2000). Thus, landscape connectivity, the degree to which the landscape facilitates movements among resource patches (Taylor et al., 1993), appears to be much greater for coyotes and foxes in the IPSA than it is for raccoons, opossums, striped skunks, or long-tailed weasels.

Our results reinforce the idea that a species' behavioral attributes are important in defining ecological landscapes (With, 1994; Zollner and Lima, 1997). Our results also highlight the need to consider a range of spatial scales in order to understand complex responses of individual species and predator–prey interactions (Brown and Litvaitis, 1995). This is especially true for the suite of predators that we examined. We believe that further modeling within a hierarchical framework would refine our ability to address differential species sensitivities to fragmentation of habitat. Additional studies are needed to test whether our multi-scale model is translatable to other species assemblages and other landscapes. Such tests may be particularly useful in conjunction with field manipulations designed to assess the role of predators in structuring vertebrate communities (e.g. Henke and Bryant, 1999).

#### 4.3. Conservation implications

From a conservation perspective, our multi-scale modeling approach highlights the importance of spatial scale in determining a species' response to habitat fragmentation (e.g. Lindenmayer, 2000; Lindenmayer et al., 2000; Orrock et al., 2000; Wu and Smeins, 2000). For the species that we examined, this was particularly relevant for long-tailed weasels. Attributes of the landscape, spatial element, and local habitat were important predictors of the presence of long-tailed weasels, and, in a separate radio-telemetry study, we found that the use of habitat features by long-tailed weasels was dependent on scale (Gehring, 2000). Without an understanding of the scale-dependent responses of long-tailed weasels to

habitat fragmentation, management actions implemented to ameliorate the negative effects of fragmentation, such as habitat-based prescriptions for reducing nest predation, might be less effective or fail (Gehring, 2000; Lindenmayer, 2000; Orrock et al., 2000).

The disproportionate use of forest patches and corridors by predators such as raccoons and long-tailed weasels indicates the potential for increased predation on avian and mammalian prey species restricted to these habitats (Barbour and Litvaitis, 1993; Paton, 1994). In particular, ground-nesting birds in fencerows may be negatively impacted by mammalian predators actively foraging for nests and/or incidental nest predation while the predator species forages for other resources abundant in fencerows (e.g. soft mast or small mammals; Vickery et al., 1992; Gehring, 2000). Thus, it is likely that the differential responses of generalist predators to the spatial elements of a landscape can have important ramifications in altering the composition, structure, and distribution patterns of prey communities in fragmented landscapes, consistent with predictions from theoretical models (Swihart et al., 2001).

Our results also highlight the importance of maintaining landscape configuration, such as the juxtaposition of spatial elements, and landscape connectivity for species conservation (Kareiva and Wennergren, 1995; Gehring, 2000). Although conservation of species should begin with habitat protection and restoration (e.g. Danielson, 1994; Fahrig, 1997), the arrangement of spatial elements can strongly affect the ability of species to move among and between elements (Gehring, 2000). Our study area was a high-production agricultural region that has been dominated by humans for nearly a century (Warner, 1994). Restoration of most habitats that have been destroyed via conversion to row crops will not occur in the foreseeable future, making considerations of landscape configuration critical to management efforts.

In situations where habitat restoration or acquisition is possible, the ESLI concept could be used as a planning tool for targeting sites in fragmented landscapes (Vos et al., 2001). In particular, land managers could relatively easily apply a multi-scale and ESLI approach to large areas using current GIS technology (Orrock et al., 2000). Our analysis extends the work of Vos et al. (2001) by demonstrating the utility of landscape-based ESLIs for species occupying fragmented landscapes but not necessarily occurring as metapopulations. By increasing the number and taxonomic scope of species studied, our findings provide additional support for the general applicability of ESLIs in a conservation context.

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