Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries

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Abstract. An ability to predict species' sensitivities to habitat loss and fragmentation has important conservation implications, and numerous hypotheses have been proposed to explain interspecific differences observed in human-dominated landscapes. We used occupancy data collected on 32 species of vertebrates (16 mammals and 16 amphibians) in an agricultural landscape of Indiana, USA, to compare hypotheses that focus on different causal mechanisms underlying interspecific variation in responses to habitat alteration: (1) body size; (2) morphology and development; (3) behaviour; (4) niche breadth; (5) proximity to range boundary; and multiple-process models combining main effects and interactions of hypotheses (1)–(2) and (4)–(5). The majority of habitat alteration occurred over a century ago and coincided with extinction of several species; thus, our study dealt only with variation in responses of extant species that often are considered 'resistant' to human modifications of native habitat. Corrected Akaike scores and Akaike weights provided strongest support for models incorporating niche breadth and proximity to range boundary. Measures of dietary and habitat breadth obtained from the literature were negatively correlated with sensitivity to habitat alteration. Additionally, greater sensitivity was observed for species occurring at the periphery of their geographical ranges, especially at northern or western margins. Body size, morphological, developmental and behavioural traits were inferior predictors of tolerance to fragmentation for the species and landscape we examined. Our findings reinforce the importance of niche breadth as a predictor of species' responses to habitat alteration. They also highlight the importance of viewing the effects of habitat loss and fragmentation in a landscape within a biogeographical context that considers a species' level of adaptation to local environmental conditions.

Key words. Agricultural landscape, Akaike weights, amphibians, geographical range boundary, habitat loss and fragmentation, mammals, niche breadth, vertebrates.

INTRODUCTION

Differential responses of vertebrate species to habitat loss and fragmentation (*sensu* Mönkkönen & Reunanen, 1999) are well documented (e.g. Andrén, 1994; Laurance, 1995; Bender *et al.*, 1998; Gibbs, 1998; Knutson *et al.*, 1999). A species' sensitivity to habitat fragmentation generally is related to its ability to persist in local patches and to recolonize patches by moving across a landscape (Etienne & Heesterbeek, 2001; Hanski, 1998; Vos *et al.*, 2001). Therefore, morphological,

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ecological and behavioural attributes are expected to interact with abiotic landscape attributes to determine viability of metapopulations (Hanski & Ovaskainen, 2000; Vos *et al.*, 2001). Here, we provide an overview of hypotheses that propose links between species' attributes and their sensitivities to habitat alteration. We then assess the relative adequacy of the hypotheses using data on the distributions of 32 species of mammals and amphibians inhabiting an agricultural landscape in Indiana, USA. The hypotheses that we have tested are not intended to be exhaustive; rather, they were chosen based on prior theoretical and empirical work suggesting their importance (Anderson *et al.*, 2000).

Hypothesis 1: Effect of body size

Within a taxon or guild, larger species often are more vagile, have greater perceptual ability and are less susceptible to predation (Swihart *et al.*, 1988; Kelt & Van Vuren, 1999; Zollner 2000), all of which suggest that they should be able to move more easily through less suitable (often man-made) habitat such as crop fields. In agricultural regions, crop fields represent a major barrier to recolonization of patches by some species. Recolonization of unoccupied patches is an important determinant of a species' persistence in fragmented habitats, and larger body size may confer upon species an ability to respond to landscape structure at larger spatial scales (Wiens, 1996; Zollner, 2000). The body-size hypothesis thus predicts that larger size should reduce the negative consequences of fragmentation, leading to reduced effects of human disturbance on patch occupancy and species distribution across a landscape. An important assumption in the preceding argument is that either individual patches are sufficiently large to support viable local populations or individuals are sufficiently mobile to incorporate several patches into their home ranges. We focused on the role of patch isolation in developing our prediction because of the highly fragmented nature of the landscape in which our work was conducted. In relatively well-connected landscapes, a dominant effect of patch area (rather than isolation) would yield the prediction that larger body size should exacerbate effects associated with habitat loss. Likewise, intermediate levels of connectivity and patch size should lead

to maximal negative effects on vertebrates of medium size (Lunney *et al.*, 1997).

Hypothesis 2: Effect of morphology and ontogeny

A species' morphology or ontogeny may impose constraints on habitat use or mobility that affect persistence in fragmented landscapes. For instance, morphological constraints on locomotion (e.g. quadrupedal, glissant, volant) or substrate use (e.g. aquatic, semiaquatic, terrestrial) may influence species' responses to fragmentation by affecting a species' mobility (Lynam & Billick, 1999; Nupp & Swihart, 2000). Developmental factors may play a similar role by restricting the response of a species to habitat disturbance. For instance, species exhibiting life stages with multiple habitat or substrate requirements are likely to be more susceptible to disturbances caused by alteration than species with developmental stages that require only one type of habitat (e.g. Dodd & Cade, 1998; Semlitsch, 1998; Richter *et al.*, 2001). The morphology-development hypothesis predicts, then, that species with morphological or developmental constraints should respond negatively to habitat alteration, leading to reduced distributions and levels of patch occupancy.

Hypothesis 3: Effects of social and territorial behaviour

Sociality or gregariousness may impose limits on colonization rates or on the size of a patch that can support a viable population, because social groups rather than solitary individuals are instrumental to population growth (Courchamp *et al.*, 1999; Smith & Peacock, 1990; Ray *et al.*, 1991; Tyutyunov *et al.*, 1996; Minchinton, 1997; Lawes *et al.*, 2000). Similarly, territorial species are likely to be more sensitive to fragmentation because of the need for exclusive use of space. Wolff (1999) hypothesized that behavioural attributes, including sociality, territoriality and sex-biased dispersal may be important determinants of a species' colonization ability in fragmented landscapes. Wolff (1999) included these traits, along with trophic level, when considering behavioural model systems that use species with comparable behavioural traits as surrogates to predict responses to habitat fragmentation. Species of

higher trophic levels were considered more likely to be sensitive to fragmentation because of the wider dispersion and lower overall density of their food base. The behavioural hypothesis thus predicts that highly territorial and highly social species, especially carnivores, should be negatively affected by habitat fragmentation, due principally to area effects that limit the carrying capacity of the landscape.

Hypothesis 4: Effect of niche breadth

Individuals of widespread species should have broader tolerances for environmental conditions than individuals of restricted species (Brown, 1995). In one sense this may seem obvious, because widespread species encounter a broader array of environmental conditions across their ranges. However, a species' niche breadth may reflect geographical differences among populations, with relatively little variation in niche breadth evident within populations. Thus, it is important to assess the degree to which niche breadth, measured across a species' geographical range, corresponds to a single population's ability to cope with habitat alteration.

Field studies have shown that species capable of using a wide variety of habitats are more likely to find human-altered portions of a landscape usable (Laurance, 1991; Andrén, 1994). This should be especially true of species that use early successional habitats, as evolution in these habitats should favour species with larger dispersal rates or dispersal ranges (Comins *et al.*, 1980; Hanski, 1999). Most human disturbances result in reversion of portions of the landscape to earlier successional stages. In contrast to a specialist, a generalist is probably capable of using the human-created matrix as an alternative habitat and extracting some resources from it (Laurance, 1995; Sarre *et al.*, 1995; Gascon *et al.*, 1999; Bentley *et al.*, 2000; but see MacNally *et al.*, 2000). In addition, species that are dietary generalists should be less negatively affected by fragmentation, because they will be less susceptible to increased variation in the availability of native food resulting from habitat loss (Swihart & Nupp, 1998; Swihart *et al.*, 2001). The niche-breadth hypothesis thus predicts that a species with the ability to use a broad array of habitats and food types, as determined from studies across its

geographical range, should be less adversely affected by fragmentation of native habitat than a more stenotypic species.

Hypothesis 5: Effect of geographic range boundaries

A species' abundance tends to decline spatially from the core to the periphery of its range (Brown *et al.*, 1995). Presumably this pattern arises because core areas of a range tend to contain more suitable habitat in terms of niche requirements and more suitable abiotic conditions for the species' survival, resulting in lower rates of local extinction and colonization (Enquist *et al.*, 1995; Pulliam, 2000). The range-boundary hypothesis thus predicts that the effects of fragmentation will be more severe for species near the edge of their geographical ranges. Species occupying a landscape near a geographical range boundary should experience greater variation in local dynamics, all else being equal.

Multiple-process hypotheses

Responses to habitat loss and fragmentation may be based on additive or interactive effects of > 1 underlying process. Consequently, we also considered three multiple-process hypotheses. The specific hypotheses were chosen because of logical relationships and suspected interactions between explanatory variables.

Single-process models 1 and 2 overlap in terms of their morphological focus. More importantly, body size can constrain morphologically based lifestyles. For instance, the structural integrity of burrows limits the feasible maximum size for fossorial mammals (Eisenberg, 1981), and aerodynamic considerations may constrain the size of volant and glissant vertebrates (Gill, 1995). Joint consideration of body size and morphology–ontogeny (model 6) results in the prediction that large species with modes of locomotion conducive to vagility or with ontogenies that permit flexible responses to disturbance should be least affected by fragmentation, and that interactions between size and modes of locomotion should enhance the overall effect of these variables.

Geographic range size implicitly unites single-process models 4 and 5. For any given study locality, species with larger geographical ranges

are less likely to occur in proximity to their range boundary. Species with broad niches tend to be characterized by larger geographical ranges (e.g. Thompson *et al.*, 1998, 1999; Pyron, 1999; Gaston & Spicer, 2001; but see MacNally, 1995), resulting in negative collinearity between niche breadth and proximity to a geographical range boundary. Thus, an additive model of niche breadth and range boundary (model 7) was considered.

The mechanisms producing a range boundary also may influence the nature of the relationship between niche breadth and sensitivity to habitat alteration at the boundary. A common pattern among terrestrial taxa is the predominant import-ance of physical stressors in setting range limits with increasing latitude, elevation, or aridity. In contrast, limitations at the opposite margin of the geographical range commonly are imposed by biotic interactions (Brown *et al.*, 1996). We hypothesized that if a range boundary were formed due to interspecific interactions, a generalist would be less affected by habitat loss or fragmentation than a specialist because alteration of preferred habitat would leave a specialist with fewer options for maintaining its competitive superiority, escaping predation, etc. In contrast, if a species' range boundary were formed in response to abiotic stressors, niche breadth should be less important in deter-mining the occupancy pattern exhibited by the species near its boundary, corresponding to an increase in the importance of physiological toler-ances. Thus, joint consideration of range boundaries and niche breadth required recognition of the mechanism creating the boundary (model 8).

Patch occupancy and population viability

Our objective was to compare the empirical support for each of the hypotheses, using data on 32 species of vertebrates collected as part of a long-term research project examining consequences of agriculturally induced fragmentation of habitat on population and community ecology. An information–theoretical approach was used to evaluate the candidate models (Burnham & Anderson, 1998). Our general metrics for quan-tifying sensitivity to habitat alteration were patch occupancy and occurrence in the matrix (see Methods). Ideally, patch-specific demographic data would be used (e.g. Pulliam, 2000). Unfor-tunately, these data are seldom feasible to collect

on a large scale, nor are they meaningful for species that incorporate > 1 patch into individual home ranges. We assessed occurrence during the breeding season, presumably before population growth and dispersal could mask local extinction events. Although it is possible that sink patches or the matrix could be used during this period, we are reasonably confident that occupancy was not an artefact of density-dependent habitat selection. Occurrence data should thus serve as a useful surrogate of a population's viability and tolerance to fragmentation (Hanski, 1994; Laurance, 1995; Vos *et al.*, 2001).

STUDY AREA

Field sampling was conducted in an 812-km^2 portion of the Middle Wabash–Little Vermillion watershed of west-central Indiana, USA. The watershed is flat to gently rolling, with fertile soils. Historically, the area was characterized by a confluence of ecoregions, including the savannah transition zone from hardwood forest to tall-grass prairie, the south-western extent of the northern hardwoods (dominated by *Acer* and *Fagus grandifolia*), and the northern edge of the central hardwoods (dominated by *Quercus* and *Carya*) (Petty & Jackson, 1966; Ricketts *et al.*, 1999). A substantial portion of the watershed (*c*. 20%) originally consisted of wetlands and swales (Ulrich, 1966). Today, human land use dominates the watershed, with approximately 12% of the area in human developments and 70% in agricultural production, principally corn and soybeans. Considerable clearing of forests and draining of wetlands have occurred over the past 150 years, and native grasses have largely been replaced by cool-season exotics. Currently, forests, grasslands and wetlands comprise approximately 10%, 4%, and 1% of the area, respectively. Fencerows and drainage ditches bisect some of the agricultural fields, providing varying levels of connectivity between forest and grassland patches and com-prising 3% of the area (Gehring, 2000).

MATERIALS AND METHODS

Field sampling

Granivorous forest rodents were sampled via live-trapping in forest patches. Thirty-five woodlots

(0.1–150 ha) and two sites representative of more extensive wooded areas (~1500 ha) were selected to span a range of patch sizes and levels of isolation, subject to the constraint that they consisted of relatively mature, deciduous woody vegetation (Nupp & Swihart, 2000). Patch occupancy was determined during spring of 1992–96 by live-trapping. Sherman™ live-traps ($7.5 \times 9.0 \times 30$ cm) were placed at 15-m intervals and Tomahawk™ live-traps ($15 \times 15 \times 60$ cm) at 30-m intervals on sampling grids established at each study site. All traps were pre-baited for 2 days and followed by 5 days of trapping. Sherman traps were baited with a mixture of rolled oats, sunflower seeds and peanut butter and Tomahawk traps were baited with English walnuts. Additional details of trapping are provided in Nupp & Swihart (2000).

Amphibians were sampled during spring and summer 1996–97 in 30 forest patches. Twenty-six woodlots (0.6–143 ha) and four sites representative of more extensive wooded areas (> 1400 ha) were sampled using a stratified design intended to encompass the range of patch size, isolation and forest wetland types occurring in the watershed (Kolozsvary & Swihart, 1999). To document patch occupancy, we sampled for amphibians using multiple methods. We installed drift fences leading to pitfall traps around breeding areas and in forested uplands. In addition, we surveyed for calling anurans, sampled amphibian larvae and placed boards on the ground for amphibians to seek refuge under throughout the upland area of forest patches (Kolozsvary & Swihart, 1999).

The majority of habitat patches in the watershed were of insufficient size to support viable populations of medium-sized mammalian predators (mesopredators), instead being used by predators on a temporary basis for foraging (Rosenblatt *et al.*, 1999). Consequently, during 1997–99 we estimated the distribution of mammalian predators among habitats and agricultural fields across the landscape using scent stations (Gehring & Swihart, 2002). We selected a simple random sample of spatial elements, without replacement, from the population of habitat patches, corridors and crop fields in the area, and allocated scent stations similarly among these spatial elements. We modified our random sample to ensure that we adequately sampled patches, corridors and fields from the entire study area. To reduce pseudoreplication (Hurlbert, 1984), we located scent stations randomly within spatial elements with the constraint that stations were $\geq$ 200 m apart. Scent-station surveys were conducted during the growing season (July), pre-harvest season (September) and fallow season (March–April), thereby spanning the range of protective cover afforded by fields. At 717 selected sites, we created scent stations by clearing a 1-m^2 area of debris and sifting masonry sand over the area (Roughton & 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 centre of each station as a mild attractant. 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 & Litvaitis, 1996). We identified tracks at scent stations and recorded a visitation event over the 2-day period as a binary response variable (present or absent) for each predator species.

Derivation of explanatory variables

We used published reports to derive values for explanatory variables of all species, except as noted below. Body size (models 1 and 6) was estimated for mammals using mass (Tables 1 and 2) and for amphibians using snout–vent length (Table 3).

Mammals were classified morphologically by their mode of locomotion (Tables 1 and 2). A binary indicator variable was used to identify modes of locomotion most likely to be affected by human alteration of native habitat (i.e. arboreal, glissant, semi-aquatic). Because the latter classification is somewhat arbitrary, we also conducted the analysis by omitting arboreal species from the locomotion-sensitive category. The outcome did not differ noticeably; thus, we present only the results of the analysis categorizing arboreal species as locomotion-sensitive (models 2 and 6). Amphibians were classified developmentally in terms of the number of substrates required to complete development (Table 3). A binary indicator variable was used to differentiate species that relied on more than one substrate to complete development (i.e. developmentally sensitive) from species that relied only on one substrate (models 2 and 6).

Table 1 Morphological, behavioural, and ecological attributes of forest rodents occurring in the Middle Wabash–Little Vermillion watershed of Indiana, USA, as determined from the literature. Scientific names follow Wilson & Reeder (1993). Sources of data are given in Nupp & Swihart (2000), with exceptions noted in the text

| Species | Body mass | | Mode of locomotion | Behaviour[1] | | | Niche breadth | | | | Range edge[2] |
	kg	Z-score		T	G	Trophic	Seeds	Other foods	Habitat	Z-score	
Peromyscus leucopus	0.023	−0.81	terrestrial	0	1	O	0.952	5.0	5.0	1.53	0
Tamias striatus	0.096	−0.60	terrestrial	1	0	O	0.650	3.5	3.5	0.26	0
Sciurus niger	0.900	1.73	semi-arboreal	0	1	G	0.404	3.5	4.0	0.20	0
Sciurus carolinensis	0.533	0.66	arboreal	0	1	G	0.270	3.0	2.0	−0.81	0
Tamiasciurus hudsonicus	0.200	−0.30	arboreal	1	0	O	0.245	4.0	4.0	0.18	1B
Glaucomys volans	0.070	−0.68	glissant	0	1	O	0.363	2.0	1.0	−1.36	0

[1] T = territorial (1 = yes), G = gregariousness (1 = yes), trophic (O = omnivore, G = granivore). [2] A = abiotically induced range margin, B = biotically induced.

Table 2 Morphological, behavioural, and ecological attributes of mammalian mesopredators occurring in the Middle Wabash–Little Vermillion watershed of Indiana, USA, as determined from the literature. Scientific names follow Wilson & Reeder (1993). Data are from Baker (1983), Bekoff (1977), Chapman & Feldhamer (1982), Coleman & Temple (1993), Fagerstone (1987), Gehring (2000), Gier (1975), Hoffmeister (1989), King (1989), Larivière (1999), Larivière & Pasitschniak-Arts (1996), Liberg (1980), Lotze & Anderson (1979), McManus (1974), Mumford & Whitaker (1982), Nesbitt (1975), Nowak (1991), Seidensticker *et al.* (1987), Sheffield & Thomas (1997), Svendsen (1982), and Wade-Smith & Verts (1982)

| Species | Body mass | | Mode of locomotion | Behaviour[1] | | | Niche breadth | | | Range edge[4] |
	kg	Z-score		T	G	Trophic	Food[2]	Habitat[2]	Z-score	
Canis latrans	14.50	1.35	terrestrial	1	1	O	0.73	0.92	1.23	0
Vulpes vulpes[3]	5.20	−0.06	terrestrial	1	1	O	0.67	0.75	0.71	0
Canis familiaris	20.00	2.18	terrestrial	1	1	O	0.60	0.92	0.90	0
Procyon lotor	5.72	0.02	terrestrial	0	0	O	0.73	0.58	0.52	0
Didelphis virginiana	3.75	−0.28	terrestrial	0	0	O	0.60	0.67	0.36	0
Mephitis mephitis	3.90	−0.60	terrestrial	0	1	O	0.33	0.67	−0.30	0
Mustela frenata	0.20	−0.81	terrestrial	1	0	C	0.27	0.67	−0.46	0
Mustela vison	0.79	−0.72	semi-aquatic	1	0	C	0.47	0.25	−0.86	0
Mustela nivalis	0.04	−0.84	terrestrial	1	0	C	0.20	0.42	−1.17	1B
Felis catus	3.90	−0.25	terrestrial	1	0	C	0.33	0.92	0.24	0

[1] T = territorial (1 = yes), G = gregariousness (1 = yes), trophic (O = omnivore, C = carnivore). [2] Proportion of diet classes and habitat types used, out of 15 and 12, respectively. See text for details. [3] A second species of fox, *Urocyon cinereoargenteus*, was uncommon in the watershed. [4] A = abiotically induced range margin, B = biotically induced.

Three behavioural variables were derived for adults of each species (model 3). Species were categorized as territorial and gregarious using binary indicator variables. Published accounts of territoriality were unavailable for four species of amphibians (Table 3); classification for these species was based on personal experience. We also categorized species by trophic status. For each functional group, the trophic class with the most restricted food availability was categorized as

Table 3 Morphological, behavioural, and ecological attributes of amphibians occurring in the Middle Wabash–Little Vermillion watershed of Indiana, USA, as determined from the literature. Scientific names follow Conant & Collins (1991). Data are from Conant & Collins (1991), Cunjak (1986), Dickerson (1969), Klemens (1993), Marvin (1996), Minton (1972), Nagel (1977), Petranka (1998), Petranka & Sih (1987), Pfingsten & Downs (1989), Pough *et al.* (1998), Sayler (1996), Shirose & Brooks (1995), Stebbins & Cohen (1995), Tyning (1990) and Wright & Wright (1949)

Species	Body length			Behaviour[1]			Niche breadth					
	mm	Z-score	Ontogeny	T	G	Trophic	Aquatic habitat	Terrestrial habitat	Timing		Z-score	Range edge[3]
									D[2]	B[2]		
Bufo americanus	68.0	0.22	semi-aquatic	0	1	I	5.0	3.5	5	4	1.14	0
Bufo woodhousii fowleri	60.2	−0.10	semi-aquatic	0	1	I	3.0	1.0	5	4	0.21	1A
Hyla versicolor	48.1	−0.59	semi-aquatic	1	1	I	5.0	3.0	5	3	0.74	0
Pseudacris triseriata	29.0	−1.36	semi-aquatic	1	1	I	3.0	5.0	5	4	1.01	0
Pseudacris crucifer crucifer	26.3	−1.47	semi-aquatic	1	1	I	4.5	2.5	5	4	0.74	0
Rana clamitans melanota	66.8	0.17	aquatic	1	1	O	3.0	1.5	1	2	−1.52	0
Rana palustris	55.5	−0.29	aquatic	0	1	I	3.0	3.0	3	4	−0.06	1A
Rana pipiens	57.1	−0.22	aquatic	0	1	I	3.0	3.0	3	4	−0.06	1B
Rana catesbeiana	107.5	1.82	aquatic	1	1	O	1.5	1.0	1	2	−2.05	0
Rana sylvatica	50.0	−0.51	semi-aquatic	0	1	I	5.0	1.5	3	5	0.34	1A
Ambystoma tigrinum	105.0	1.71	semi-aquatic	0	1	I	3.0	5.0	3	5	0.74	0
Ambystoma texanum	85.0	0.90	semi-aquatic	0	1	I	3.5	4.5	3	5	0.74	0
Ambystoma laterale-jeffersonianum	77.8	0.61	semi-aquatic	0	1	I	2.0	—	3	5	−0.16	1A
Ambystoma maculatum	86.4	0.96	semi-aquatic	0	1	I	3.0	1.5	3	5	−0.19	1A
Plethodon cinereus	44.0	−0.75	terrestrial	1	0	I	—	2.0	—	—	−0.44	1A
Eurycea cirrigera	35.0	−1.12	semiaquatic	0	0	I	1.0	1.0	1	4	−1.65	1A

[1] T = territorial (1 = yes), G = gregariousness (1 = yes), trophic (O = omnivore, I = insectivore). [2] D = score for development time (5 = fast, 1 = slow); B = score for breeding phenology (5 = early spring, 1 = late summer). [3] A = abiotically induced range margin, B = biotically induced.

'sensitive' to fragmentation using a binary indicator variable.

Niche breadth (models 4, 7 and 8) for mammals was derived from published accounts of food habits and habitat use (Tables 1 and 2). Although comparison of resource use with resource availability is desirable when assessing niche breadth (e.g. Manly *et al*., 1993), data on availability seldom are reported. Thus, we relied solely on resource use for our calculations. For rodents, dietary breadth was determined in two ways. Because the species within this functional group are principally granivorous, we computed a measure of seed diet breadth from stomach contents (for *Tamias striatus*; Mumford & Whitaker, 1982; Snyder, 1982) and from cafeteria-style feeding trials (all other species; Ivan & Swihart, 2000). Because all species occasionally feed on other types of food, we also rated species on a scale of 1–5 in terms of their use of other food types (e.g. insects, fungi, vegetation), with 1 indicating restricted use and 5 indicating frequent use of food types other than seeds (Table 1). Habitat breadth of rodents also was rated on a scale of 1–5, with 5 representing the greatest variety of habitat use. For mammalian mesopredators, dietary breadth was determined by tallying the number of diet classes, from a total of 15, that comprised at least 2% of the diet (Table 2). Diet classes included 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. Habitat breadth was determined using an identical procedure with a total of 12 habitat classes, including deciduous forest, coniferous forest, mixed forest, shrubland, wooded savannah, tall grass prairie, short grass prairie, desert, cropland, wooded wetland, marsh and urban. Niche breadth for amphibians was estimated from four variables (Table 3). Habitat breadth was based on the variety of wetland habitats used for breeding and the variety of upland habitat types used during the nonbreeding season. Both parameters were scored on a scale from 1 to 5, with 5 indicating a species capable of using a wide array of habitat types, including disturbed sites. Because all but one species of amphibian relied on wetlands for breeding, we considered breeding phenology and length of development (egg to terrestrial stage) as potentially important indicators of each species' sensitivity to hydroperiod. Species with rapid developmental rates such as *Bufo americanus*, or early spring breeders such as *Rana sylvatica*, are able to use temporary wetlands for breeding sites, in contrast to species with slow developmental rates or later breeding dates, such as *Rana catesbeiana* (Snodgrass *et al*., 2000). Both developmental rate and breeding phenology were weighted equally on a scale of 1–5, with 5 indicating rapid development or early spring breeding (Table 3).

Indicator variables were used to differentiate species for which the study area occurred near the edge of their geographical ranges (models 5 and 7). A species was classified as near the edge of its range if the study area occurred in the outer 10% of the range, based on visual assessment of range maps (Hall, 1981; Conant & Collins, 1991). The 10% cut-off was arbitrary and intended to differentiate populations for which stressors could be important. We categorized range boundaries as abiotically induced if at the northern or western margin of a species' range, corresponding to temperature and precipitation gradients, respectively, in the central United States. Range boundaries were classified as biotically induced if at the southern or eastern margin. Thus, three codes were possible for the two indicator variables: 00 = not near a range boundary; 10 = near an abiotically induced range boundary; 01 = near a biotically induced range boundary (model 8).

Our primary interest was to test hypotheses regarding sensitivity to habitat fragmentation across functional groups (i.e. forest rodents, mammalian mesopredators, and amphibians). However, functional groups varied widely in terms of measures for body size and niche breadth, because input variables and rating procedures varied among groups. Thus, we transformed our variables within each group to a common scale (zero mean, unit variance). To enable comparisons of body size across functional groups, we computed a standardized *Z*-score of size for each species within a functional group, where the *i*th species' score was defined as $z_i = (x_i - \bar{x})/s_x$. Standardized *Z*-scores also were computed for each measure of niche breadth used for a functional group. For each rodent species, a separate *Z*-score was computed for seed diet breadth and for the rating of non-seed diet breadth. These *Z*-scores were then averaged to yield a diet breadth *Z*-score, which was averaged

with the habitat *Z*-score to yield a niche breadth score (Table 1). For mammalian mesopredators, standardized *Z*-scores of diet and habitat breadth were averaged for each species to produce a niche breadth score (Table 2). For amphibians, standardized *Z*-scores were computed for habitat breadth and hydroperiod breadth. We transformed averaged values into *Z*-scores with zero mean and unit variance for analysis (Table 3). *Plethodon cinereus* does not require aquatic sites for breeding, thus we used only the terrestrial habitat *Z*-score for this species.

Quantifying species' distributions

Populations of rodents and amphibians occupied well-defined patches within the study area. For these functional groups, we used the proportion of patches occupied as a measure of a species' current occupancy rates. For mammalian mesopredators, we used the fraction of all observations for a species that occurred in fields as a measure of the species' tolerance to human-induced alteration of the landscape, because willingness to use or travel through the matrix separating native patches of habitat is critical to a species' success (Gascon *et al.*, 1999; Laurance, 1991, 1995). To facilitate comparison across functional groups, standardized *Z*-scores were computed for each species within a functional group using the raw measures of sensitivity to fragmentation.

Model selection and inference

Kullback–Leibler distance (or discrepancy) is a measure of the information lost when an approximating model, *g*, is used in place of full reality, *f* (Burnham & Anderson, 1998). The Kullback–Leibler distance between *g* and *f* is defined for continuous functions as $I(f,g) = \int f(x) \log_e \left(\dfrac{f(x)}{g(x|\theta)} \right) dx$, where θ is a vector of parameters to be estimated from data (*x*). Viewed from the context of probability distributions, $I(f,g)$ is a measure of the inefficiency associated with assuming a distribution *g* when the true model is *f* (Cover & Thomas, 1991). Selection from among a set of candidate models thus involves minimizing $I(f,g)$. Akaike demonstrated in a series of papers that model selection does not depend on the specific exist-

ence of *f* (Burnham & Anderson, 1998; Anderson *et al.*, 2000). Akaike's Information Criterion (AIC) links $I(f,g)$ to the maximized log-likelihood function; i.e. $\text{AIC} = -2\log_e(L(\hat{\phi}|data)) + 2K$, where *K* = the number of parameters estimated. Because the objective is to minimize the loss of information due to using an approximating model, for a set of candidate models, this is equivalent to minimizing AIC. We used least squares regression to estimate parameters for our candidate models, rather than the method of maximum likelihood. For the method of least squares, $\text{AIC} = n\log_e(\hat{\sigma}^2) + 2K$, where $\hat{\sigma}^2 = (\text{SS}_{error}/n)$ and *n* represents the number of observations (Anderson *et al.*, 2000). If $n/K < 40$, a corrected form of AIC, called AIC_c, is recommended (Burnham & Anderson, 1998):
$\text{AIC}_c = -2\log_e(L(\hat{\theta}|data)) + 2K + \dfrac{2K(K+1)}{(n-K-1)}$. We computed AIC_c to assess the competing models. To assess evidence easily for the alternative models, we rescaled the AIC_c values by subtracting from each the minimum AIC_c. The resulting values, Δ_i, were scaled such that $\Delta_i = 0$ for the model with minimum AIC_c. Rules of thumb provided by Burnham & Anderson (1998: 123) suggest that models with $\Delta_i \le 7$ will probably contain the actual best model from a candidate set in 95% of all samples. For models with $\Delta_i > 10$, this is strong evidence that the model is not competitive as the Kullback–Leibler best model. Finally, the likelihood of a model, given the data, $\exp\left(-\dfrac{1}{2}\Delta_i\right)$, was computed and normalized so that the values summed to 1 for all *R* models, yielding the Akaike weights used in model averaging:

$$w_i = \dfrac{\exp\left(-\dfrac{1}{2}\Delta_i\right)}{\displaystyle\sum_{r=1}^{R}\exp\left(-\dfrac{1}{2}\Delta_r\right)}.$$

Our goal was to compare the ability of process-based hypotheses to explain variation in sensitivity to habitat loss and fragmentation. Because we were less interested in prediction than in model comparison, we restricted inference to a subset of all possible models as suggested by Anderson *et al.* (2000). After the models with greatest support had been selected using AIC_c, we used least-squares regression to derive parameter estimates and sampling variances.

Table 4 Responses to habitat loss and fragmentation recorded for 32 species of vertebrates in an agricultural landscape in Indiana, USA. Effects on forest rodents and amphibians were estimated using total patch occupancy, i.e. the fraction of patches sampled at which the species occurred. Effects for mammalian mesopredators were estimated using the fraction of all visits to scent stations for a species that were in agricultural fields. Standardized *Z*-scores were calculated for each species within a functional group (forest rodents, mammalian mesopredators, amphibians)

Functional group species	Effect		Functional group species	Effect	
	Fraction	*Z*-score		Fraction	*Z*-score
Forest rodents			Amphibians		
Peromyscus leucopus	1.00	1.19	*Bufo americanus*	1.00	1.86
Tamias striatus	0.86	0.82	*Hyla versicolor*	1.00	1.86
Sciurus niger	0.86	0.82	*Pseudacris triseriata*	0.67	0.84
Tamiasciurus hudsonicus	0.30	−0.70	*Pseudacris crucifer*	0.60	0.63
Sciurus carolinensis	0.19	−0.99	*Rana clamitans*	0.60	0.63
Glaucomys volans	0.14	−1.14	*Ambystoma tigrinum*	0.50	0.33
Mesopredators			*Ambystoma texanum*	0.50	0.33
Canis familiaris	0.36	1.93			
Canis latrans	0.30	1.26	*Rana palustris*	0.37	−0.08
Didelphis virginiana	0.18	0.11	*Rana pipiens*	0.33	−0.18
Mephitis mephitis	0.17	0.00	*Plethodon cinereus*	0.33	−0.18
Felis catus	0.17	0.00	*Rana catesbeiana*	0.20	−0.59
Vulpes vulpes	0.15	−0.16	*Eurycea cirrigera*	0.10	−0.90
Mustela vison	0.14	−0.24	*Bufo woodhousii*	0.07	−1.00
Procyon lotor	0.12	−0.42	*Ambystoma laterale-jeffersonianum*	0.03	−1.10
Mustela frenata	0.08	−0.85	*Rana sylvatica*	0.00	−1.21
Mustela nivalis	0.00	−1.64	*Ambystoma maculatum*	0.00	−1.21

RESULTS

Collectively, the 32 species exhibited a wide range of ecological, behavioural and morphological traits (Tables 1–3), which suggests that they also should differ in their responses to habitat alteration induced by agriculture. Our sampling data bore this out. Distributional data were tabulated from 33 790 trap nights, 13 031 pitfall nights, and 1434 scent-station nights of effort for forest rodents, amphibians, and mammalian mesopredators, respectively (Kolozsvary & Swihart, 1999; Nupp & Swihart, 2000; Gehring & Swihart, 2002). Within each functional group, species exhibited substantial variation in sensitivity to habitat fragmentation (Table 4). Ubiquitous species included *Peromyscus leucopus*, *Bufo americanus*, and *Hyla versicolor* (Table 4). In contrast, one salamander (*Ambystoma maculatum*) and one anuran (*Rana sylvatica*) were not recorded during our sampling,

even though they have been recorded in the area in previous decades (Minton, 1972). Several other species were encountered rarely during sampling. Of 2307 rodents captured, *Tamiasciurus hudsonicus* and *Glaucomys volans* comprised only 1.34% and 2.51% of the total, respectively. Of 882 scent station visits, *Mustela nivalis* and *M. vison* accounted for only 0.45% and 0.79% of the total, respectively. Of 1804 amphibians captured in pitfall traps, *Eurycea cirrigera*, *Bufo woodhousii fowleri*, and *Ambystoma laterale-jeffersonianum* accounted for only 0.17%, 0.50%, and 0.78%, respectively.

Comparison of Δ_i values for the single-process models (hypotheses 1–5) indicated that models 4 (niche breadth) and 5 (proximity to geographical range boundary) had the greatest support (Table 5). Akaike weights indicated that the niche-breadth model was approximately six times more likely given the sample data collected (0.8620/0.1364 = 6.3,

Table 5 Comparison of models derived from a priori hypotheses about processes capable of influencing sensitivities of species to habitat loss and fragmentation. Models were fitted using least squares regression. For each candidate model, the number of parameters (K), sample-size adjusted Akaike's Information Criterion rescaled from a minimum of zero (Δ_i), and Akaike weights (w_i) are presented. In model 8, nw = dummy variable for species on north or west range margin, and se = dummy variable for species on south or east range margin

Model	K	Δ_i	w_i
Single-process models			
1: body size	3	15.40	0.0004
2: morphology and ontogeny	3	16.11	0.0003
3: behavioural attributes	5	13.81	0.0009
4: niche breadth	3	0	0.8620
5: geographical range boundary	3	3.69	0.1364
Single- and multiple-process models			
1: body size (bs)	3	25.22	0.0000
2: morphology and ontogeny (mo)	3	25.92	0.0000
3: behavioural attributes (ba)	5	23.62	0.0000
4: niche breadth (nb)	3	9.81	0.0070
5: geographical range boundary (grb)	3	13.50	0.0011
6: bs + mo + bs*mo	5	26.59	0.0000
7: nb + grb	4	0	0.9418
8: nb + nw + se + nb* nw + nb*se	7	5.86	0.0501

Fig. 1 Relation between niche breadth and species' occurrence in an agricultural landscape in Indiana, USA. Niche breadth was standardized to a zero mean and unit variance within each of the three functional groups of species. For amphibians and small forest rodents, the fraction of patches occupied by each species was plotted on the ordinate. For mammalian mesopredators, the fraction of scent station visits occurring in agricultural fields was plotted on the ordinate as a measure of tolerance to habitat fragmentation.

Table 5). Niche breadth was positively related to species' tolerance of habitat alteration for all functional groups (Fig. 1), whereas proximity of a species to its geographical range boundary was associated with reduced tolerance to habitat alteration.

Simultaneous consideration of single- (1–5) and multiple-process (6–8) models indicated that the models incorporating niche breadth alone or in combination with geographical range margin were superior (Table 5). Comparing the Akaike weights (Table 5), the normalized likelihood was 0.9418 for the model jointly considering niche breadth and range boundary (model 7), 0.0501 for the model incorporating niche breadth, range boundary and boundary type (model 8), 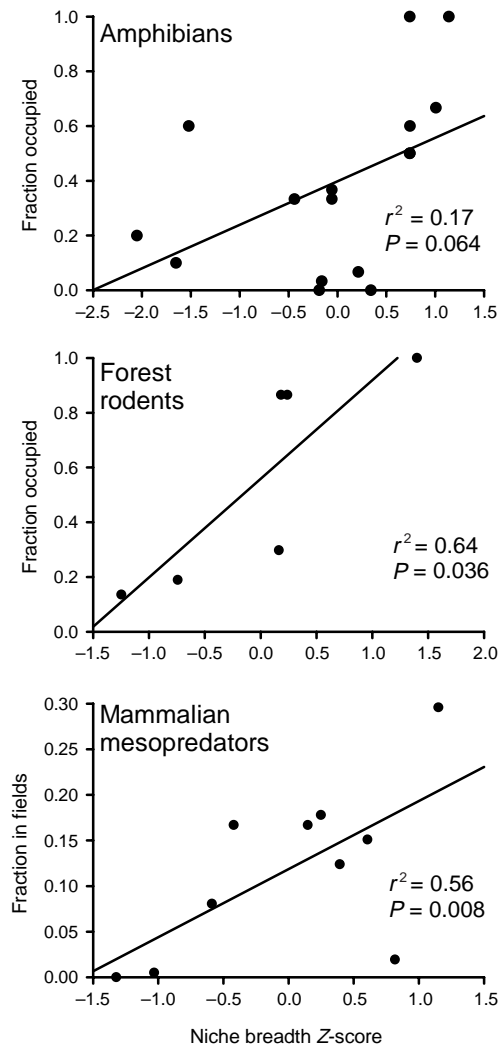and 0.0070 for niche breadth alone (model 4). The dual process model incorporating niche breadth and proximity to the edge of a species' geographical range was roughly 19 times more suitable than the model specifying the type of range margin encountered
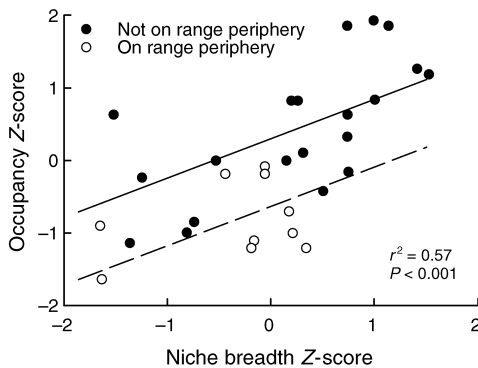
Fig. 2 Joint effects of niche breadth and proximity to the boundary of a geographical range on species' responses to habitat loss and fragmentation. Standardized measures of niche breadth are plotted on the abscissa, and standardized measures of species' tolerance of habitat alteration are represented on the ordinate. The dashed line depicts the predicted tolerance for species on the periphery of their ranges (open circles), whereas the solid line represents the increased tolerance conveyed by being more centrally located within a species' geographical range (solid circles).

(0.9418/0.0501 = 18.8). Our analysis provided strong evidence that the niche breadth-range periphery model was the best of the candidate models we examined. The regression of this 'best' model was highly significant (F = 21.44, 2, 29 d.f., P < 0.001) and explained 56.9% of the variation in standardized measures of species occurrence data (Fig. 2).

DISCUSSION

The Indiana landscape in which our study was conducted has been subjected to widespread alteration by humans for 150 years. The most dramatic initial changes were clearing of forest, followed by draining of wetlands, and more recently by exurban development. Populations thus have been subjected to human stressors for dozens of generations, and the most sensitive species disappeared decades ago (see Mumford & Whitaker, 1982). Surviving species therefore represent a subset of the original species pool that presumably are more resistant to human disturbance generally and habitat loss and

fragmentation specifically (Rosenblatt *et al.*, 1999). Even so, our results provide convincing evidence that extant species exhibit considerable interspecific variation in sensitivity to habitat alteration, even after 150 years. Moreover, niche breadth appears to be a primary determinant of a species' tolerance to loss and fragmentation of habitat. A species' ability to rely upon a broad array of food and habitat types across its geographical range was associated with tolerance to habitat alteration by humans at the population level, irrespective of taxonomic affiliation. For instance, the most tolerant species in each group (Table 4: *Peromyscus leucopus*, *Canis latrans*, *Bufo americanus*) also were the species with the greatest niche scores. Conversely, the most sensitive species in each group (Table 4: *Glaucomys volans*, *Mustela nivalis*, *Rana catesbeiana*) had the lowest niche scores. In an interspecific context, flexibility in resource use may be an inferior strategy at a local level (e.g. Scriber & Feeney, 1979) but provide an advantage at a regional scale by permitting populations of generalists to respond to environmental changes (Ricklefs, 1990: 746), including human-induced disturbance. We focused on resource axes (diet, habitat) because these data were most readily available in the literature. Clearly, other characterizations of niche space (e.g. physiological tolerances, hunting or antipredator strategies) could be considered as well.

The proximity of a species to its geographical range boundary was a significant predictor of tolerance to habitat fragmentation (t = −3.34, P = 0.002) and ranked second among the five single-process models (Table 5). Abiotic conditions associated with species' range limits appear to be responsible for most of the response we observed. Proximity to a range edge probably formed in response to abiotic factors corresponded with a significant decline in occupancy (t = −3.75, P = 0.001), whereas the effect of proximity to a range edge probably formed in response to biotic factors was weaker (t = −1.74, P = 0.094; Table 6). Of the 10 species for which the study site was located in proximity to their range boundary, eight were amphibians. Amphibians are likely to be especially sensitive to habitat alteration at the edge of their range, because many species rely on both wetlands and terrestrial habitats to complete their lifecycles. Thus, they face double the challenges of a homeothermic mammal with

Table 6 Estimates of parameters ($\hat{\beta}$) and standard errors (s.e.) for the three most plausible models from Table 5, as judged using Akaike's Information Criterion. All regressions were highly significant ($P < 0.001$), with adjusted coefficients of determination (R^2) of 0.569 (model 7), 0.566 (model 4), and 0.385 (model 8). Abbreviations are as in Table 5

(Model Table 5)	Intercept $\hat{\beta}$	SE	nb $\hat{\beta}$	SE	grb $\hat{\beta}$	SE	nw $\hat{\beta}$	SE	se $\hat{\beta}$	SE	nb*nw $\hat{\beta}$	SE	nb*se $\hat{\beta}$	SE
7	0.299	0.138	0.542	0.124	−0.934	0.252								
8	0.290	0.138	0.608	0.137			−1.127	0.300	−0.798	0.459	−0.695	0.421	0.055	0.481
4	0.009	0.135	0.652	0.144										

respect to adapting to inhospitable conditions (i.e. both aquatic breeding and terrestrial adult conditions). The extent to which the importance of geographical range boundaries apply to taxa other than amphibians must await examination in other systems. For birds, Blackburn & Duncan (2001) demonstrated that abiotic factors are more important than biotic resistance in determining successful establishment of introduced exotics. Regardless of the relative importance of abiotic and biotic forces, our findings suggest that conservation strategies failing to account for geographical effects on occupancy may expend limited financial resources inefficiently if efforts are focused on populations which are responding principally to adaptive regimes at a geographical scale rather than disturbance regimes imposed by humans. Our results support the observation by Gaston *et al.* (2001) that selection of a core reserve network based on minimum complementary sets of species will be inadequate if several species are represented in marginal or peripheral areas of their ranges.

The use of standardized scores for niche breadth and for responses to habitat alteration permits comparison of species groups for which data are collected differently or for which responses to alteration are distinctive. If the distribution of standardized response variables is known or assumed, quantitative estimation of effects of independent variables are possible. For instance, in our data proximity to the edge of a species' geographical range was associated with a predicted decline in standardized response scores of 0.8 standard deviation units (Fig. 2). Assuming a normal distribution, this corresponds to a 29% decline in the distribution of tolerances to habitat loss and fragmentation relative to species in the core of their ranges.

An important assumption in our analysis is that patch occupancy rates reflect responses to human-induced changes in landscapes and provide a useful predictor of a population's viability. Interspecific comparisons have revealed a strong degree of nestedness in the amphibian and rodent assemblages studied (Kolozsvary & Swihart, 1999; Nupp & Swihart, 2000). In both assemblages, occurrences were related principally to the spatial or temporal extent of a patch; local extinctions were more likely in smaller or less permanent patches. Because human disturbance often results in patches that are smaller or more ephemeral, we believe that the patch occupancy rates we observed do indeed reflect responses to habitat loss and fragmentation. Moreover, levels of patch occupancy likely were reasonable indicators of viability. Patch-occupancy models are based on this notion and have received empirical support (Hanski, 1994, 1998). Vos *et al.* (2001) proposed, based on extensive simulations for hypothetical species with varying ecological profiles, that patch occupancy of less than 0.5 might serve as a universal indicator of serious conservation risks imposed by habitat fragmentation. Applying this criterion, several of the species we studied (e.g. *Sciurus carolinensis*, *Glaucomys volans*, *Rana pipiens*) may be steadily declining and present today only as ghosts of a prior landscape rather than as an indication of an established equilibrium with the current landscape (Tilman *et al.*, 1994; Ter Braak *et al.*, 1998). Of course, consideration of the historical and ecological context of species occupancy is preferable to blind adherence to a universal indicator, as numerous factors can influence the robustness of the indicator (Vos *et al.* 2001). For instance, some species occurring at relatively low levels of patch occupancy in our system (e.g. *Tamiasciurus hudsonicus*) actually appear to be

increasing relative to past conditions, due in part to altered interspecific interactions (Nupp & Swihart, 2001; Goheen, 2002).

Although development of predictive models was not our goal, it is instructive to compute estimated responses of species native to the region but extirpated before 1900 by human activity. Several forest-dwelling mammals, including porcupine (*Erethizon dorsatum*), grey wolf (*Canis lupus*), mountain lion (*Felis concolor*), black bear (*Ursus americanus*) and fisher (*Martes pennanti*) were extirpated from Indiana over a century ago, coincident with widespread logging (Mumford & Whitaker, 1982). High sensitivity to habitat loss and fragmentation should be reflected in low predicted Z scores for these species. Conversely, Z scores from the central portion of the distribution would suggest that other factors, such as human persecution, probably were more important in the species' demise. Using the Kullback–Leibler best model (Table 6), we computed predicted Z scores for porcupine (-1.53), grey wolf (-1.14), mountain lion (-0.45), fisher (-0.73) and black bear (0.00). These findings suggest that restricted niche breadth or proximity to historical range boundaries were contributors to the local extinction of porcupine, and perhaps grey wolf. However, the fact that the predicted values were well within the range of values observed for extant species (Table 4) suggests that factors such as reductions in prey (Fuller & Sievert 2001) or mortality due to increased contact with humans (Johnson *et al.* 2001) may have been more important in the disappearance of relatively large, mobile predators such as wolf, mountain lion, fisher and black bear from Indiana.

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