



# Patch occupancy of North American mammals: is patchiness in the eye of the beholder?

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## Abstract

**Aim** Intraspecific variation in patch occupancy often is related to physical features of a landscape, such as the amount and distribution of habitat. However, communities occupying patchy environments typically exhibit non-random distributions in which local assemblages of species-poor patches are nested subsets of assemblages occupying more species-rich patches. Nestedness of local communities implies interspecific differences in sensitivity to patchiness. Several hypotheses have been proposed to explain interspecific variation in responses to patchiness within a community, including differences in (1) colonization ability, (2) extinction proneness, (3) tolerance to disturbance, (4) sociality and (5) level of adaptation to prevailing environmental conditions. We used data on North American mammals to compare the performance of these ‘ecological’ hypotheses and the ‘physical landscape’ hypothesis. We then compared the best of these models against models that scaled landscape structure to ecologically relevant attributes of individual species.

**Location** North America.

**Methods** We analysed data on prevalence (i.e. proportion of patches occupied in a network of patches) and occupancy for 137 species of non-volant mammals and twenty networks consisting of four to seventy-five patches. Insular and terrestrial networks exhibited significantly different mean levels of prevalence and occupancy and thus were analysed separately. Indicator variables at ordinal and family levels were included in models to correct for effects caused by phylogeny. Akaike’s information criterion was used in conjunction with ordinary least squares and logistic regression to compare hypotheses.

**Results** A patch network’s physical structure, indexed using patch area and isolation, received the greatest support among models predicting the prevalence of species on insular networks. Niche breadth (diet and habitat) received the greatest support for predicting prevalence of species occupying terrestrial networks. For both insular and terrestrial systems, physical features (patch area and isolation) received greater support than any of the ecological hypotheses for predicting species occupancy of individual patches. For terrestrial systems, scaling patch area by its suitability to a focal species and by individual area requirements of the species, and scaling patch isolation by species-specific dispersal ability and niche breadth, resulted in models of patch occupancy that were superior to models relying solely on physical landscape features. For all selected models, unexplained levels of variation were high.

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**Main conclusions** Stochasticity dominated the systems we studied, indicating that random events are probably quite important in shaping local communities. With respect to deterministic factors, our results suggest that forces affecting species prevalence and occupancy may differ between insular and terrestrial systems. Physical features of insular systems appeared to swamp ecological differences among species in determining prevalence and occupancy, whereas species with broad niches were disproportionately represented in terrestrial networks. We hypothesize that differential extinction over long time periods in highly variable networks has driven nestedness of mammalian communities on islands, whereas differential colonization over shorter time-scales in more homogeneous networks probably governed the local structure of terrestrial communities. Our results also demonstrate that integration of a species' ecological traits with physical features of a patch network is superior to reliance on either factor separately when attempting to predict the species' probability of patch occupancy in terrestrial systems.

### Keywords

Colonization, ecological scaling, extinction, habitat fragmentation, islands, mountaintops, nested subsets, niche breadth, stochasticity, woodlots.

## INTRODUCTION

Most landscapes are patchy, inasmuch as localities vary in terms of their suitability as habitat for a species. The ecological literature is replete with examples documenting individual and population-level responses to resource heterogeneity (e.g. McGlynn *et al.*, 2002). When heterogeneity is extreme, resource patches occur as discrete entities surrounded by areas that are unsuitable for long-term persistence. Examples of such extreme patchiness include insular systems, or networks of remnant terrestrial habitat patches embedded in human-dominated landscapes of agricultural or urban areas. Field studies have documented numerous patchy landscapes in which species differ, sometimes dramatically, in their responses to resource heterogeneity (Andr n, 1994; Laurance, 1995; Bender *et al.*, 1998; Knutson *et al.*, 1999). These interspecific differences can lead to a structured gradient of local community assemblages across a landscape, as the species most sensitive to patchiness disappear from all but the largest or most well-connected patches and the least sensitive species occur ubiquitously. Such a non-random ordering of local assemblages has been termed nestedness (Patterson, 1984; Patterson & Atmar, 1986).

Nestedness is a common feature of metacommunities and tends to occur when (1) patches in a network are comparable in terms of structural and habitat features, (2) species share a similar biogeographical history, and (3) species form an ordered hierarchy in terms of ecological factors that influence incidence (Patterson & Brown, 1991; Wright *et al.*, 1998). In this paper, we examine hypotheses to explain the formation of nested assemblages of North American mammals. We then evaluate integrated hypotheses for the formation of nestedness that permit interspecific differences in perceptions of patchiness to be combined with physical attributes of a patchy system.

Phenomenological models of patchy systems (MacArthur & Wilson, 1967; Levins, 1969) have focused on colonization

and extinction dynamics of local populations. The temporal scale over which populations are tracked can have important implications for interpreting dynamics. For long-lived species with low turnover rates, long time-lags following the formation of a patchy network may be needed to approach equilibrium conditions of occupancy (Tilman *et al.*, 1994; Nagelkerke *et al.*, 2002). If observations of such systems occur after shorter lag periods, occupancy patterns may be inflated above equilibrium levels because records of occurrence will be made for local populations doomed to eventual extinction, thus yielding overly optimistic assessments of a species' likelihood of persistence in the network (Ter Braak *et al.*, 1998; Clinchy *et al.*, 2002). In this paper, we explore the effect of time since formation of patch networks on species prevalence and occupancy.

The original phenomenological models and their derivatives predict that a species' sensitivity to extreme resource patchiness generally is related to its ability to persist locally and to recolonize patches by moving across a landscape (Hanski, 1998; Etienne & Heesterbeek, 2001; Vos *et al.*, 2001). Morphological, ecological and behavioural attributes should thus interact with abiotic landscape attributes to determine the viability of populations inhabiting patchy environments (Hanski & Ovaskainen, 2000; Vos *et al.*, 2001), which in turn influences the structure of communities (Belant & Van Stappen, 2002; Swihart *et al.*, 2003). Below, we provide an overview of hypotheses linking species attributes with their sensitivities to extreme resource patchiness. We then compare the hypotheses using presence-absence data on 137 species of mammals collected from twenty patch networks in North America. Finally, we ask whether our understanding of variation in responses to resource patchiness can be improved by scaling the physical features of a landscape with ecologically relevant attributes affecting a species' colonization and extinction rates.

The models that we have tested do not comprise an exhaustive list, but instead were chosen based on prior

theoretical and empirical work suggesting their importance (Anderson *et al.*, 2000). In describing the hypotheses, we begin with a 'null' model, proceed to a model focusing exclusively on the physical environment, and then outline a series of ecological models that highlight particular species attributes. We recognize that partial overlap is possible in some of the ecological models but believe that they differ sufficiently to warrant separate consideration.

#### **Null model: phylogenetic effects**

Variation in responses to patchiness may in part be due to evolutionary constraints imposed by phylogeny. Closely related species are likely to be more similar phenotypically and in terms of ecology and life history than distantly related species, as a consequence of niche conservatism, phylogenetic time-lags, and shared constraints on adaptive responses (Harvey & Pagel, 1991). Thus, consideration of the variation attributable to phylogeny is a necessary condition for examining factors that explain variation independent of these phylogenetic effects. Our null model predicts that closely related taxa should exhibit more similar patterns of occupancy and prevalence than more distantly related taxa. Thus, we used phylogenetic effects as a baseline from which models of physical and ecological factors could be compared.

#### **Physical model: area and isolation**

Landscape ecologists have focused considerable effort on describing the complex physical structure of landscapes, with a goal of summarizing the patchiness embodied by an arrangement of spatial elements into statistics that have ecological significance (e.g. Gustafson & Parker, 1992; Schumaker, 1996; Tischendorf & Fahrig, 2000a,b; Urban & Keitt, 2001). Numerous empirical studies have documented the importance of two attributes, patch area and patch isolation, as determinants of species occupancy (e.g. Dunning *et al.*, 1995; Rosenzweig, 1995; Hanski, 1998). Support for the importance of patch area is not altogether surprising, because extinction of local populations can be influenced dramatically by stochasticity. This is especially true when populations are small (Berger, 1990). In addition, immigration to patches often can be modelled as a distance-dependent phenomenon (Hanski, 1998). The physical model thus predicts that occupancy and prevalence should be positively related to patch area and negatively related to patch isolation. Additionally, increased variation in the range of patch area and isolation within a network should result in increased nestedness of communities compared with other networks (Wright *et al.*, 1998).

#### **Ecological model 1: proximity to range edge**

A species' abundance often declines spatially from the core to the periphery of its range (Brown, 1984; Brown *et al.*, 1995). This pattern emerges because core areas of a range presumably contain more suitable habitat in terms of niche requirements and more suitable abiotic conditions for the

species' survival, resulting in lower turnover rates (Enquist *et al.*, 1995; Brown *et al.*, 1996; Pulliam, 2000). The range-boundary hypothesis thus predicts that prevalence and occupancy levels will be lower for a species near the edge of its geographical range.

#### **Ecological model 2: colonization ability**

Species perceptions of resource patchiness can differ in at least two fundamental ways, depending on variation in responses to (1) the amount and (2) the distribution of habitable sites. The colonization model focuses on the latter issue and hypothesizes that the distance a species can disperse is a critical determinant of its ability to colonize other patches. Dispersal distance is related to home-range size (Bowman *et al.*, 2002), which in turn is responsive to energetic and morphological constraints on body size, locomotion (e.g. quadrupedal, gliding, volant), or substrate use (e.g. aquatic, semi-aquatic, terrestrial) (Eisenberg, 1981; Kelt & Van Vuren, 1999, 2001; Lynam & Billick, 1999). The colonization model thus predicts greater prevalence and occupancy levels for species with well-developed dispersal capabilities.

#### **Ecological model 3: extinction proneness**

The extinction model focuses on interspecific differences in responses to the area available for occupancy by a population. For a given patch area, a greater population density is associated with a reduced risk of local extinction due to stochastic effects (Berger, 1990). Conversely, larger-bodied species are thought to exhibit greater population stability because they are better able to withstand environmental bottlenecks (see Belovsky, 1987; Goodman, 1987). The extinction model thus predicts that prevalence and occupancy should increase with population density and body size.

#### **Ecological model 4: niche breadth**

If local patches exhibit variation in resource composition, species capable of exploiting multiple resource types are less likely to be absent from any single patch. Conversely, specialists probably will be absent from patches lacking the habitat (or prey) upon which they depend. In terrestrial systems, human disturbances often result in reversion of portions of the landscape to earlier successional stages, or creation of a structurally simplified matrix separating patches of native habitat. A generalist is probably more capable than a specialist of using the human-created matrix as an alternative habitat and extracting some resources from it (Andr n, 1994; Laurance, 1995; Sarre *et al.*, 1995; Gascon *et al.*, 1999; Bentley *et al.*, 2000; Laurance *et al.*, 2002). This should be especially true of species that use early successional habitats, as evolution in these habitats favours species with larger dispersal rates or dispersal ranges (Comins *et al.*, 1980; Hanski, 1999). Finally, species that are dietary generalists should be less negatively affected by resource patchiness resulting from habitat fragmentation than dietary specialists, 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 should be less adversely affected by resource patchiness than a more stenotypic species.

### Ecological model 5: degree of sociality

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 (Smith & Peacock, 1990; Ray *et al.*, 1991; Tyutyunov *et al.*, 1996; Minchinton, 1997; Courchamp *et al.*, 1999; Lawes *et al.*, 2000). Wolff (1999) hypothesized that behavioural attributes, including sociality, may be important determinants of a species' colonization ability in fragmented landscapes. The sociality hypothesis thus predicts that highly social species should be negatively affected by habitat fragmentation, due principally to area effects that limit the carrying capacity of a patch. The result, then, is a lower threshold on sizes of patches that can be colonized.

### Joint models: ecological scaling of patchiness

The importance of physical features of patch networks to a population's persistence has theoretical (Levin, 1992; Durrett & Levin, 1994) and empirical (Debinski & Holt, 2000) support. Moreover, it seems intuitive that the scale at which resource patchiness operates is dependent upon species perceptions and responses to a patch network. Ecologically scaled landscape indices (ESLIs) (Vos *et al.*, 2001) combine physical features of a patch network with ecologically relevant characteristics of species that reflect the scales at which they respond to that network. In this paper, we evaluated the performance of the ESLIs of Vos *et al.* (2001), which combine physical metrics with individual area requirements and dispersal ability. We also evaluated ESLIs that were modified to incorporate the effects of niche breadth and habitat suitability, as described below.

### METHODS

We collected data on prevalence and occupancy of non-volant mammals from twenty patch networks across North America (Table 1). For each species, we recorded occupancy

**Table 1** Summary of patch networks included in the analysis of prevalence and occupancy for North American mammals. Min, minimum; Max, maximum

Location	Number of patches	Median patch area (km <sup>2</sup> )	Min : max area	Median nearest neighbour (km)	Min : max nearest neighbour
<b>Terrestrial networks</b>					
Great Basin mountaintops <sup>1</sup>	19	384	0.01019	15	0.050
Great Basin mountaintops <sup>2</sup>	19	384	0.01019	15	0.050
Great Basin mountaintops <sup>3</sup>	23	571	0.00781	9	< 0.0000
Southern Rocky mountains <sup>4</sup>	26	2250	0.00160	29	< 0.0000
Southern Rocky mountains <sup>5</sup>	27	107	0.00090	17	< 0.0000
Illinois woodlots <sup>6</sup>	10	0.24	0.00300	1.54	0.0011
Iowa woodlots <sup>7</sup>	11	0.0004	0.14554	0.64	< 0.0000
Indiana woodlots <sup>8</sup>	37	0.02	0.00009	0.11	0.0141
Indiana woodlots <sup>9</sup>	5	0.08	0.09612	0.21	0.3296
Wisconsin woodlots <sup>10</sup>	22	0.05	0.01000	1.6	0.2000
Indiana woodlots <sup>11</sup>	45	0.05	0.00036	0.11	0.0014
<b>Insular networks</b>					
Southern California coast <sup>12</sup>	8	105	0.01054	42	0.2841
St Lawrence River, New York <sup>13</sup>	20	0.03	0.00007	0.9	0.0020
Western Mexico coast <sup>14</sup>	4	70	0.08333	5.5	0.1875
Gulf of Maine <sup>15</sup>	24	0.67	0.00001	1.2	0.0073
	8*	27.3	0.04566	1.6	0.0125
Virginia coast <sup>16</sup>	9	5.08	0.01320	1	0.1587
Lake Michigan <sup>17</sup>	14	1.02	0.00152	3	0.0089
Alaska coast <sup>18</sup>	24	477	0.00175	6	0.0296
Sea of Cortez, Mexico <sup>19</sup>	20	20	0.00033	4	0.0417
British Columbia coast <sup>20</sup>	75	26	0.00002	2	0.0026

<sup>1</sup>McDonald & Brown (1992); <sup>2</sup>Grayson & Livingston (1993); <sup>3</sup>Brown (1978); Brown & Gibson (1983); <sup>4</sup>Patterson & Atmar (1986); <sup>5</sup>Lomolino *et al.* (1989); <sup>6</sup>Rosenblatt *et al.* (1999); <sup>7</sup>Gottfried (1979); <sup>8</sup>Nupp & Swihart (2000); <sup>9</sup>Nupp & Swihart (unpublished data); <sup>10</sup>Matthiae & Stearns (1981); <sup>11</sup>Gehring (2000); <sup>12</sup>von Bloeker (1967); <sup>13</sup>Lomolino (1986); <sup>14</sup>Wilson (1991); <sup>15</sup>Crowell (1986); <sup>16</sup>Dueser & Brown (1980); <sup>17</sup>Hatt *et al.* (1948); <sup>18</sup>Conroy *et al.* (1999); <sup>19</sup>Lawlor (1983, 1986); <sup>20</sup>McCabe & Cowan (1945); Foster (1965); Redfield (1976); Lawlor (1986).

\*Occurrence data were provided for two sets of species by Crowell (1986), with some species sampled at all twenty-four islands and others at only the eight largest islands.

as a binary variable and prevalence as the proportion of patches in a network that were occupied. Seven of the data sets were used by Wright *et al.* (1998) in their analysis of nestedness. We conducted a literature search to augment these with more recent studies and with networks not included in their analysis. Eleven studies were conducted on patch networks in which the intervening matrix consisted of terrestrial vegetation. The remaining studies were of island networks.

### Physical features of networks

For each patch in a network, we recorded the patch area ( $\text{km}^2$ ) and distance to its nearest neighbouring patch (km). Summary statistics for each network included median patch area, median distance to nearest neighbour, and the ratios minimum patch area : maximum patch area as well as minimum nearest neighbour distance : maximum nearest neighbour distance. We also recorded the types of habitat occurring on each patch, or for an entire network if patch-specific information was lacking.

### Derivation of ecological descriptor variables

For each species considered in the studies from Table 1, ecological attributes were summarized from a variety of literature sources (Appendix). Whenever possible, sources were used from regions in close proximity to patch networks. When multiple sources were available for an attribute, weighted averages were computed based on sample sizes. If data were unavailable for a species, values were imputed from the species most closely related to it, which probably exaggerate phylogenetic effects.

#### *Proximity to range edge*

Data for testing the range-edge hypothesis were generated from a geographical information system. We digitized range maps from Hall (1981) for each species. A digitized map of the geographical localities of the patch networks was then superimposed on each species range map. For each species recorded in a patch network, we computed the distance from the centroid of the species' range to (1) the patch network and (2) the range edge closest to the focal network. The ratio of these two measures was used to quantify proximity to a range boundary; a value of zero characterized a network falling near the centre of the species' range, whereas a value of 1 characterized a network occurring on the edge of the species' range.

#### *Colonization ability*

Two types of variables were used in conjunction with the colonization model. Indicator variables were used to designate six categories related to mode of locomotion: fossorial, gliding, semi-fossorial, semi-arboreal, semi-aquatic and terrestrial. Additionally, data on maximum dispersal distance ( $d_{\text{max}}$  in km) were available for forty-four of the 137 species in our study (Sutherland *et al.*, 2000). These data were used to establish a nonlinear predictive equation relating  $d_{\text{max}}$  to

published and unpublished data on home-range area (HR in  $\text{km}^2$ , Appendix). The model producing the best fit was

$$d_{\text{max}} = 22.5 \text{HR}^{0.29} \quad (1)$$

( $r^2 = 0.45$ ). Home-range areas for the remaining species were then used in the regression model to compute predicted values of  $d_{\text{max}}$  for species lacking observed values of  $d_{\text{max}}$ .

#### *Extinction proneness*

Body size was indexed using data on adult body mass (kg), averaged between the sexes. Local population density (individuals  $\text{km}^{-2}$ ) was taken from studies reporting density directly, or from studies for which estimates could be derived from data on individuals captured and area sampled.

#### *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. We estimated niche breadth along two dimensions, habitat and diet. 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. Consequently, we relied only on used resources in our computations.

Each species was assigned a dietary breadth rating on a scale of 1–5. Species receiving a rank of 1 were considered extreme specialists that feed only on one or a few taxa within a dietary class. Species receiving a rank of 2 were specialists, restricted to a single dietary class but feeding on several taxa within that class. Species assigned a rank of 3 were facultative specialists that usually feed on items from a single dietary class but rarely would feed on other dietary classes. Species assigned a rank of 4 were generalists and differed from facultative specialists in commonly feeding on dietary classes other than the predominant class. Species receiving a rank of 5 were considered extreme generalists that feed opportunistically on foods of more than one dietary class.

In a similar fashion, each species was assigned a habitat breadth score on a scale of 1–15, with 15 representing the greatest variety of habitats used. The fifteen habitat classes considered in assigning scores for habitat breadth were temperate deciduous forest, temperate coniferous forest, temperate mixed deciduous–coniferous forest, temperate grassland, temperate savanna, temperate shrub-scrub, wetlands, Mediterranean shrub, Mediterranean savanna, xeric shrub-scrub, xeric desert, taiga, tundra, tropical moist broadleaf forest, and tropical dry broadleaf forest (Ricketts *et al.*, 1999).

A single niche-breadth variable with a mean of zero and a standard deviation of 1 was derived as

$$Z_{H+D} = \frac{Z_H + Z_D}{s_{(Z_H + Z_D)}},$$

where  $Z_H$  and  $Z_D$  are standardized (zero mean, unit variance) variables for the dietary and habitat breadth scores, respectively, and the denominator is the standard deviation of the sum of these variables.

In an attempt to provide a crude summary of niche breadth, we also categorized each species in terms of (1) whether it was omnivorous and (2) whether its habitat requirements matched the availability of a particular patch (or patch network). The former variable was a binary indicator variable, whereas the latter variable, labelled  $h$ , was estimated on an interval scale 0–1, with 0 representing the absence of suitable habitat and 1 representing ample suitable habitat. For networks lacking information regarding the habitat of specific patches, a single value of  $h$  was used for all patches in the network. These two variables, together with  $Z_{H+D}$ , formed the basis for assessing the niche-breadth model.

#### Degree of sociality

Sociality was indexed on a scale of 0–4. Species received a rating of 0 if they were asocial and exhibited no male care of offspring. Species were assigned a rating of 1 if they exhibited rudimentary sociality (e.g. huddling, overlap of home ranges) but no male care. Species received a rating of 2 if they formed matrilineal groups or other kin groups but no male care. A rating of 3 was assigned to monogamous species in which males provided some care of offspring. Finally, a rating of 4 was assigned to species consisting of communal groups and in which cooperative foraging and offspring care had been documented. Sociality clearly is a phenotypically flexible trait (Swihart, 1992; Revilla & Palomares, 2002); thus, when multiple sources reported different social structures, we used the study that was closest to the focal network(s). Otherwise, ratings from the different studies were averaged.

#### Ecological scaling of patchiness

We used two methods to scale patch networks according to ecological attributes of species. Metapopulation theory provided the basis for both approaches. The incidence of a species in a patch,  $P$ , is given by  $P = C/(C + E)$ , where  $C$  and  $E$  are colonization and extinction rates, respectively (Hanski, 1994). The viability of a metapopulation is determined by the ratio  $C/E$ , which for many species are isolation-dependent ( $C$ ) and area-dependent ( $E$ ) processes; thus, ecological scaling of patchiness addressed these two critical parameters.

The first method was developed by Vos *et al.* (2001). They linked landscape structural features with ecologically relevant measures of a species' sensitivity to isolation and area effects by defining the carrying capacity (2) and connectivity (3) of patch  $i$ :

$$ESLI_{K_i} = \frac{A_i}{IAR_i}, \quad (2)$$

$$ESLI_{C_i} = \sum_{\text{all } j \neq i}^n A_j e^{-\alpha d_{ij}}. \quad (3)$$

In equation 2,  $A_i$  is the area of patch  $i$  and  $IAR_i$  is the area in patch  $i$  required by one reproductive unit of a species. In equation 3,  $d_{ij}$  is the distance between focal patch  $i$  and another patch  $j$ , and  $1/\alpha$  is the mean dispersal distance for the species. Limitations on the data available to us necessitated the following changes to the indices of Vos *et al.* (2001). We substituted local population density,  $D$ , for  $IAR_i^{-1}$  when calculating  $ESLI_{K_i}$ . For  $ESLI_{C_i}$  we restricted our attention to the nearest neighbouring patch rather than all other patches in the network. Also, because we had more data on maximum dispersal distances than on mean (or median) distances, we calculated the dispersal parameter such that it occurred at the 0.999 quantile of the negative exponential distribution; i.e.  $\alpha = -\ln(0.001)/d_{\max}$ . We used observed values of  $d_{\max}$  when available, and values predicted from equation 1 for all other species. An alternative approach to calculating the dispersal parameter using the median ( $d_{\text{med}}$ ) would have resulted in  $\alpha = -\ln(0.5)/d_{\text{med}}$ . For the thirteen species of mammals in our data set with both median and maximum dispersal distances, the values of  $\alpha$  were highly correlated ( $r = 0.97$ ,  $P < 0.001$ ) and comparable in magnitude (paired  $t = 0.58$ ,  $P = 0.57$ ).

The ecological scaling of patches developed by Vos *et al.* (2001) does not explicitly address variation in quality of patches or factors unrelated to distance that could affect connectivity. Our second method of scaling patchiness addressed these issues by defining a modified carrying capacity (4) and connectivity (5) for patch  $i$ :

$$ESLI_{K_i}^* = h_i A_i D, \quad (4)$$

$$ESLI_{C_i}^* = A_i e^{-\alpha^* d_{ij}}. \quad (5)$$

Patch carrying capacity was modified to include a variable,  $h_i$ , representing the quality of the patch in terms of meeting the habitat needs of the focal species. The variable  $h_i$  was scaled from 0 to 1, such that carrying capacity was 0 if the patch contained no suitable habitat for the focal species, and equalled the original index of Vos *et al.* (2001) when  $h_i = 1$ . Patch connectivity was modified via the dispersal parameter. We reasoned that estimates of dispersal distance might be improved by considering the ease with which individuals of a species might traverse or extract resources from the matrix separating patches. For terrestrial networks of patches, species with broad niches probably find areas between patches less hostile than species with narrow, specialized resource requirements. For terrestrial patch networks, we therefore modified equation 1 to include a linear relationship with standardized niche breadth,  $NB_z$ , yielding

$$d_{\max}^* = 20.86 \text{ HR}^{0.31} + (8.48 \text{ NB}_z - 1.27) \quad (6)$$

with  $r^2 = 0.49$ . As equation 6 conceivably could yield negative values of  $d_{\max}^*$  for specialists with small home ranges, we used 1 home-range diameter as a minimum  $d_{\max}^*$  value. For insular systems, isolation effects are probably more

pronounced for species with limited abilities for travelling through water or over ice. For island studies, we estimated  $d_{\max}^*$  using equation 1 for semi-aquatic mammals and mammals with a terrestrial mode of locomotion occupying systems where travelling across ice was a possibility. For all other cases, maximum dispersal distance was the minimum of  $d_{\max}^*$  or island diameter (estimated by assuming a circular shape).

### Statistical analysis

The forces structuring insular and terrestrial networks may be quite different, in part because of the different time-scales over which patchiness typically operates in the two situations (Hubbell, 2001). In addition, true islands have discrete boundaries and are surrounded by uninhabitable matrix, whereas edges of terrestrial patches often are less distinct and the intervening matrix can exhibit varying levels of habitability. Because of these differences, we tested our hypotheses separately for insular and terrestrial networks. Multiple linear regression was used with data on prevalence, and multiple logistic regression was used with data on patch occupancy. Before analyses, logarithmic transformations were performed on patch area, nearest-neighbour distance, body size, dispersal distance, population density, and ESLs. Prevalence data were subjected to a variance-stabilizing arcsine-square root transformation (Draper & Smith, 1998). Methods for comparing models are described below.

To remove covariation in responses that were due to phylogenetic similarity, we constructed a set of nineteen phylogenetic indicator variables, five for ordinal contrasts and fourteen for contrasts of families within orders (Harvey & Pagel, 1991, p. 130). For analysis of prevalence, we conducted a multiple regression against the phylogenetic variables to remove phylogenetic effects. Subsequently, regression models were constructed using the residuals from the phylogeny regression to test hypotheses. For analysis of occupancy, we included phylogenetic indicator variables in all logistic models. We also included indicator variables for patch networks to remove variability caused by differences among networks in the number of patches.

Akaike's information criterion (AIC) links the information lost because of reliance on an approximating model to the method of maximum likelihood (Burnham & Anderson, 1998). The model with a minimum AIC among a candidate set of models is judged as the 'best' model, in the sense of maximizing model likelihood in a parsimonious manner. We compared our hypotheses using AIC corrected for sample size,  $AIC_c$  (Burnham & Anderson, 1998; Anderson *et al.*, 2000). To easily assess evidence for the alternative models, we rescaled the  $AIC_c$  values by subtracting from each the minimum  $AIC_c$ . The resulting values,  $\Delta_i$ , were scaled such that  $\Delta_i = 0$  for the model with minimum  $AIC_c$ . Rules of thumb provided by Burnham & Anderson (1998, p. 123) suggest that models with  $\Delta_i \leq 7$  probably will 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 best model. Results for all models were presented following the suggestions of Anderson & Burnham (2002). After the models with greatest support had been selected using  $AIC_c$ , we estimated their parameters and goodness-of-fit.

## RESULTS

Terrestrial and insular networks did not differ in average median area or nearest-neighbour distance ( $P > 0.35$  for both  $t$  tests). Mean ( $\pm$ SE) ratios of minimum and maximum patch areas were smaller for insular systems ( $0.005 \pm 0.001$ ) than for terrestrial networks ( $0.012 \pm 0.002$ ) ( $t = 2.88$ , d.f. = 264,  $P = 0.004$ ). Similarly, mean ratios of minimum and maximum nearest-neighbour distances were smaller for insular systems ( $0.41 \pm 0.03$ ) than for terrestrial networks ( $0.66 \pm 0.06$ ) ( $t = 3.80$ , d.f. = 248,  $P < 0.001$ ). Within terrestrial networks, montane networks and networks of woodland remnants differed significantly ( $P \leq 0.002$  for all tests), with montane networks exhibiting larger patches, greater nearest-neighbour distances, and greater variation in patch area and isolation.

### Species prevalence in patch networks

Species occupying terrestrial networks exhibited a greater mean level of prevalence ( $0.40 \pm 0.02$ ) than species occupying insular systems ( $0.27 \pm 0.02$ ) ( $t = 3.85$ , d.f. = 332,  $P < 0.001$ ). Likewise, mean prevalence of species occupying forest remnants in agricultural landscapes ( $0.48 \pm 0.04$ ) was greater than for species in montane regions ( $0.35 \pm 0.03$ ) ( $t = 2.37$ , d.f. = 104,  $P = 0.02$ ).

For insular systems, ordinal and familial effects accounted for 14.8% of the variation in prevalence ( $F = 1.46$ , d.f. = 17, 142,  $P = 0.12$ ). For terrestrial systems, 17.8% of the variation in prevalence ( $F = 2.47$ , d.f. = 14, 174,  $P = 0.003$ ) was explained by phylogeny at the order and family level. Subsequent model comparisons were made using residuals from these regressions.

Comparison of the ecological models with the physical model produced contrasting results for the two systems. For insular systems, the model receiving the greatest support (i.e. lowest  $AIC_c$ ) was the physical model, with ecological models highly unlikely to be the best model in the set (Table 2). For terrestrial networks, the niche-breadth model received the greatest support, with a modest likelihood that range edge also could be the best model. The physical model was highly unlikely to be the best model for terrestrial networks (Table 2).

The fitted model for physical features of insular systems accounted for 6.7% of the residual variation in prevalence ( $F = 2.79$ , d.f. = 4, 159,  $P = 0.03$ ), after removing phylogenetic effects. Of the four explanatory variables included in the fitted model, only the coefficient for the ratio of minimum : maximum island area was significantly different from zero ( $t = 2.13$ ,  $P = 0.03$ ). The coefficient was positive, indicating an increase in prevalence with a smaller range of island areas within an insular system. For terrestrial

Model	Sum of squared errors	Number of parameters	AIC <sub>c</sub>	$\Delta_i$	$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$
Island ( $n = 161$ )					
Physical features	16.02	6	905.8	0	0.9968
Range edge	17.06	3	919.5	13.8	0.0010
Colonization ability	16.80	8	925.4	19.6	0.0000
Extinction proneness	17.09	4	922.3	16.5	0.0003
Niche breadth	16.80	5	918.8	13.0	0.0015
Degree of sociality	17.15	3	921.3	15.4	0.0004
Terrestrial ( $n = 176$ )					
Physical features	22.98	6	1116.0	34.7	0.0000
Range edge	21.65	3	1088.6	7.3	0.0253
Colonization ability	22.93	8	1119.5	38.2	0.0000
Extinction proneness	23.64	4	1121.6	40.4	0.0000
Niche breadth	20.95	5	1081.2	0	0.9747
Degree of sociality	23.49	3	1117.2	36.0	0.0000

**Table 2** Results of model selection for prevalence of non-volant mammals on patch networks, based on least squares regression. Separate analyses were conducted for insular systems and terrestrial patch networks. Akaike weights ( $w_i$ ) are given as a means of comparing the relative likelihoods of the competing models; the weights are normalized to sum to 1 (Burnham & Anderson, 1998)

Model	$-2\log_e(L)$	Number of parameters	AIC <sub>c</sub>	$\Delta_i$	$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^R \exp(-\frac{1}{2}\Delta_r)}$
Island ( $n = 4598$ )					
Physical features	3786	28	3842	0	1.0000
Range edge	4138	27	4192	350	0.0000
Colonization ability	4079	32	4143	301	0.0000
Extinction proneness	4104	28	4160	318	0.0000
Niche breadth	4092	29	4150	308	0.0000
Degree of sociality	4139	27	4194	351	0.0000
Terrestrial ( $n = 3252$ )					
Physical features	3626	24	3674	0	0.9797
Range edge	3820	23	3867	192	0.0000
Colonization ability	3863	27	3918	281	0.0000
Extinction proneness	3897	24	3946	271	0.0000
Niche breadth	3632	25	3682	7.8	0.0203
Degree of sociality	3888	23	3934	260	0.0000

**Table 3** Results of model selection for probability of occupancy on individual patches, based on logistic regression. Separate analyses were conducted for islands and terrestrial patches. Akaike weights ( $w_i$ ) are defined in Table 2.  $L$  refers to the maximized likelihood for the model after inclusion of phylogenetic and study site effects, given the data (Burnham & Anderson, 1998)

networks, the fitted model for niche breadth explained 11.5% of the residual variation ( $F = 7.37$ , d.f. = 3, 171,  $P < 0.001$ ). Two of the three explanatory variables in the fitted model differed significantly from zero;  $Z_{H+D}$  ( $t = 2.55$ ,  $P = 0.01$ ) and  $b$  ( $t = 3.70$ ,  $P < 0.001$ ) were both positively associated with prevalence. The fitted model for range boundary explained 8.5% of the residual variation ( $F = 16.08$ , d.f. = 1, 173,  $P < 0.001$ ), revealing that species prevalence declined in patch networks nearer the range periphery.

### Species occupancy of patches

For both insular and terrestrial systems, the physical model received greater support than any of the five ecological models. For insular systems, no ecological model was deemed remotely likely to be the best model, with values of  $\Delta_i > 300$  (Table 3). For terrestrial networks, the niche-

breadth model received a modest amount of support (Table 3).

The physical model yielded a reasonable fit when applied to occupancy data from islands (Nagelkerke's  $R^2 = 0.26$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 11.94$ , d.f. = 8,  $P = 0.15$ ). The model correctly classified 80.7% of 4598 cases. It also reduced the rate of type II error, i.e. misclassification of an occupied island as unoccupied, by 21.9% compared with the model containing only phylogeny and study site variables. Estimated coefficients indicated that probability of occupancy increased with island area ( $z = 17.35$ ,  $P < 0.001$ ) and declined with distance to nearest-neighbouring islands ( $z = -3.07$ ,  $P = 0.002$ ). Results for terrestrial patches were similar. Fit of the physical model was reasonable (Nagelkerke's  $R^2 = 0.24$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 11.50$ , d.f. = 8,  $P = 0.18$ ), and 71.4% of 3252 cases were classified correctly. Type II error was reduced by 26.7% compared with the phylogeny study



site model. Predicted probability of occupancy increased with patch area ( $z = 13.23$ ,  $P < 0.001$ ) and declined with distance to the nearest neighbouring patch ( $z = -2.44$ ,  $P = 0.02$ ). The fit for the model of niche breadth was poor (Nagelkerke's  $R^2 = 0.24$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 31.11$ , d.f. = 8,  $P < 0.001$ ), although all three explanatory variables ( $b$ ,  $Z_{H+D}$ , omnivory) displayed a significant positive association with probability of occupancy ( $P < 0.001$  in all cases).

### Ecological scaling of patchiness

For insular systems, neither the ESLIs of Vos *et al.* (2001, see equations 2 and 3) nor our modifications to incorporate habitat suitability and ability to disperse across an aquatic medium improved on the performance of the more parsimonious physical model (Table 4). It is possible, but not probable, that the modified ESLI model could be the best of this candidate set ( $\Delta_i = 5.2$ ). Interestingly, *post-hoc* fitting of island occupancy data to the niche-based definition of  $ESLI_{C_i}^*$  used for terrestrial networks (equations 5 and 6) resulted in a model  $AIC_c$  value 29 units less than the value for the model containing only physical features, indicating a superior model (Table 4). A different story emerged for mammals occupying terrestrial networks. Although the ESLI model of Vos *et al.* (2001) offered no improvement on the physical model, the modified ESLI model (equations 4 and 5) received much greater support than the physical model (Table 4).

The fit of the modified ESLI model to data on island occupancy was reasonable (Nagelkerke's  $R^2 = 0.26$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 11.37$ , d.f. = 8,  $P = 0.18$ ) and indicated that probability of occupancy was positively associated with  $ESLI_{K_i}^*$  ( $z = 17.13$ ,  $P < 0.001$ ) and  $ESLI_{C_i}^*$  ( $z = 3.00$ ,  $P = 0.002$ ). A 21.4% reduction in type II error was evident for the model relative to the phylogeny study site model, and 81.1% of cases were classified correctly. The fit of the *post-hoc* model also was good (Nagelkerke's  $R^2 = 0.27$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 11.75$ , d.f. = 8,  $P = 0.17$ ) and indicated that probability of occupancy was positively associated with  $ESLI_{K_i}^*$  ( $z = 17.68$ ,  $P < 0.001$ ) and  $ESLI_{C_i}^*$  ( $z = 6.59$ ,  $P < 0.001$ ). A 21.9% reduction in type II error was evident for the model relative to the phylogeny study site model, and

81.2% of cases were classified correctly. The fit of the modified ESLI model was also acceptable for data on terrestrial patch occupancy (Nagelkerke's  $R^2 = 0.26$ , Hosmer and Lemeshow goodness-of-fit  $\chi^2 = 12.78$ , d.f. = 8,  $P = 0.12$ ), and 72% of cases were classified correctly. Notably, a reduction in type II error of 28.7% was observed, the largest reduction for any model. As with island data, probability of patch occupancy was positively associated with  $ESLI_{K_i}^*$  ( $z = 13.93$ ,  $P < 0.001$ ) and  $ESLI_{C_i}^*$  ( $z = 6.23$ ,  $P < 0.001$ ).

## DISCUSSION

### Patterns of prevalence and occupancy

On average, insular systems were more sparsely occupied by mammals than were more recently formed montane networks, which were more sparsely occupied than woodlot remnants formed during the last two centuries. Faunal relaxation resulting from stochastic extinction events could have contributed to this pattern. Unfortunately, isolation time covaried with physical features of the networks in our study. Thus, it is impossible to disentangle the effect on prevalence of time since formation and variation in patch area or isolation. In all likelihood, the effects of this covariation in temporal and spatial scales have acted together to produce the patterns of prevalence we observed. Likewise, our results suggest that if two networks are comparable in mean patch size and isolation but differ in their ratios of minimum : maximum patch area and isolation, the network with greater variation in patch size and isolation will be subjected to greater extinction and lower colonization rates. Thus, populations occupying insular systems, which are characterized by longer timespans since formation and greater variation in patch size and isolation than terrestrial networks, presumably have suffered from faunal relaxation accentuated by variation in the physical landscape. Less severe faunal relaxation appears to have contributed to the lower prevalence on mountaintops relative to forest remnants in farmland.

Prevalence of mammal species was most closely linked to physical features of insular systems, which is reasonable if long time periods enhance the effects of catastrophes and environmental stochasticity on persistence (Lande, 1993).

**Table 4** Results of model selection for probability of occupancy of non-volant mammals on individual patches, based on logistic regression. Separate analyses were conducted for islands and terrestrial patches. The models with the lowest  $AIC_c$  scores from Table 3 were compared with models containing ESLI (equations 2 and 3, with modifications described in text) and  $ESLI^*$  (equations 4 and 5). Akaike weights ( $w_i$ ) are defined in Table 2.  $L$  refers to the maximized likelihood for the model after inclusion of phylogenetic and study site effects, given the data (Burnham & Anderson, 1998)

Model	$-2\log_e(L)$	Number of parameters	$AIC_c$	$\Delta_i$	$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{i=1}^R \exp(-\frac{1}{2}\Delta_i)}$
Island ( $n = 4598$ )					
Physical features	3786	28	3842	0	0.9268
ESLI	3796	28	3852	10	0.0056
$ESLI^*$	3791	28	3847	5	0.0676
$ESLI^*$ (as in terrestrial) <sup>†</sup>	3757	28	3813	-29	-
Terrestrial ( $n = 3252$ )					
Physical features	3626	24	3674	51	0.0000
ESLI	3716	24	3764	141	0.0000
$ESLI^*$	3575	24	3623	0	1.0000

<sup>†</sup>*Post-hoc* modelling effort; not used in selection procedure (Anderson & Burnham, 2002).

Interestingly, variation in island area was the sole significant predictor of prevalence. This result suggests that extinction is of greater importance than colonization in determining the structure of insular communities, and that variation in island area is important in the absence of any effect of average island size.

In contrast, prevalence of mammal species on terrestrial networks was not associated with physical features. Rather, ecological attributes associated with niche breadth and levels of adaptation to local conditions received the greatest support (Table 2). A separate analysis of thirty-two species of amphibians and mammals in an agricultural landscape revealed a similar pattern (Swihart *et al.*, 2003). We believe the strength of these correlates with prevalence is tied principally to their influence on dispersal ability. Generalists presumably view the areas separating patches of preferred habitat as less hostile, and hence are more likely to travel through these areas than are specialists. Indeed, the success of generalists in human-altered landscapes has been tied to their ability to travel through or extract resources from the human matrix that separates native habitat remnants (Laurance, 1991; Andr en, 1994; Laurance *et al.*, 2002). In contrast, specialists appear sensitive to structural and compositional differences between preferred habitat and matrix habitat (Lomolino & Perault, 2001). Our measures of niche breadth were derived from studies conducted across a species' geographical range and thus lend support to the notion that broad-scale measures of niche breadth are useful indicators of a single population's ability to respond to resource heterogeneity. Close proximity of a species to its geographical range boundary had a negative influence on prevalence, as predicted if core areas of a range are more suitable for occupancy and lead to lower turnover rates (Enquist *et al.*, 1995; Pulliam, 2000). The lower prevalence of species near range boundaries has important implications for conservation, especially in areas subjected to human disturbance (Channell & Lomolino, 2000). Recovery plans that do not account for geographical effects on occupancy may fail if efforts are focused on populations that are responding principally to adaptive regimes at a geographical scale rather than local disturbances. Our results for mammals support the notion 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 (Gaston *et al.*, 2001).

For both insular and terrestrial networks, probability of occupancy was linked more closely to patch area and isolation than to ecological factors. Thus, results from our single-factor models supported the ties between extinction-colonization dynamics and area-isolation attributes assumed by classical island biogeography and metapopulation paradigms (MacArthur & Wilson, 1967; Hanski, 1994).

### Ecological scaling of patchiness

Can the distributional patterns in our study be explained more readily by models that unite physical features of

patch networks with ecological attributes of species? For terrestrial networks the answer is unequivocally 'yes'. The evidence is less convincing for insular systems, although it is possible that the ESLI model modified by species abilities to travel through water or over ice was superior to the physical model (Table 4). We did not attempt to differentiate species by swimming or rafting ability, attributes which may be tied to colonization ability in insular systems. We do not have an explanation for the superior fit of the *post-hoc* model incorporating the modified connectivity of equations 5 and 6, although it is possible that home-range size or niche breadth are related generally to travel across inhospitable environments, including water.

In constructing a species-based model of insular zoogeography that was conceptually similar to the ESLIs of Vos *et al.* (2001) Lomolino (2000) noted that the validity of comparisons among networks relies on an ability to account for differences in the intervening matrix and in carrying capacities. By combining physical landscape features with ecological measures of area sensitivity (individual resource requirements and availability) and isolation sensitivity (dispersal ability mediated by niche breadth), we obtained models with greater predictive ability than the models relying solely on physical features. Specifically, species with large resource requirements or poor matches to available habitat occupied correspondingly larger patches than species with more modest resource requirements or good matches to available habitat. Likewise, mobile species with broad niches were more likely to occupy isolated patches than less mobile specialists. Our analysis thus provides additional evidence that ESLIs are superior in many instances to traditional landscape indices when the objective is predicting species occupancy (Vos *et al.*, 2001; Opdam *et al.*, 2002; Swihart & Verboom, 2003).

### The role of stochasticity

Our results support and extend the conclusions of studies on fewer networks and species; namely, that patterns of prevalence and occupancy in insular communities can result from non-random variation in ecological traits among species (Lomolino, 2000; Vos *et al.*, 2001; Swihart *et al.*, 2003; Swihart & Verboom, 2003). However, stochasticity appears to play a dominant role in shaping these communities. Although the regression models best describing prevalence and occupancy provided reasonable fits to the data for both insular and terrestrial systems, the majority of variation in these response variables remained unexplained.

The residual variation in our models can be partitioned into two origins, natural and methodological. Addressing the former, Hubbell (2001) suggested that stochastic events are largely responsible for patterns of species prevalence and occupancy in meta and local communities. He argued that ecological drift and random dispersal were key processes governing species richness across taxa and scales, and that niche differentiation among species yielded individuals that

were equivalent in per capita fitness. This ecological equivalence results from constraints imposed by universal scaling laws and trade-offs in life-history invariants, and serves to equalize relative fitness between species. Thus, ecological drift may override species-specific attributes in dictating patterns of species abundance in communities. Recent analyses of birds do not support the notion that ecological drift is more powerful than non-random mechanisms in shaping communities (McGill, 2003).

Several methodological issues could potentially explain some of the residual variation in our models. First, the variable sampling methods used during surveys can influence the probability of detecting a species in a patch. An important challenge awaiting future biogeographical studies is to incorporate methods of correcting for site and species differences in detection uncertainty (MacKenzie *et al.*, 2002). Secondly, the level of phylogenetic differentiation used in our contrasts was coarse. Subfamily, tribal and generic affinities were not included in the analysis but could be important in explaining variation in patterns of occupancy or prevalence. Thirdly, no attempt was made to incorporate nonlinearities in the variables for describing the effects of a species' position within its geographical range. Theoretical models of niche shifts as a function of spatial position within a range (e.g. Pulliam, 2000) could be used to incorporate predicted nonlinear responses. Fourthly, interspecific interactions can be strong determinants of community structure at local levels and thus may explain a species' absence in suitable patches or presence in poorly suited patches (e.g. Hanski & Zhang, 1993; Swihart *et al.*, 2001). Many biogeographical analyses, including ours, suffer from an inability to adequately assess the role of interspecific interactions in shaping patterns of occupancy. Potential competing species covaried positively on patches in our study, rather than negatively as expected (Diamond, 1975; Lomolino, 2000). We could not examine patterns of covariation for predator-prey dyads, as most studies forming our data base focused exclusively on one trophic group. A more accurate determination of the role of stochastic events relative to deterministic factors will require improved specification of species-based models, including a consideration of inter-specific interactions.

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**Appendix** Biological attributes for species of North American mammals used in occupancy and prevalence analyses. Scientific names follow Wilson & Reeder (1993). Ter, terrestrial; Saq, semi-aquatic; Sar, semi-arboreal; Sfo, semi-fossorial; Gli, gliding. A species receiving a value of zero for all five variables was designated as fossorial

Species	Ter	Saq	Sar	Sfo	Gli	Dispersal (km)	Home range (km <sup>2</sup> )	Body size (kg)	Population density (individuals km <sup>-2</sup> )	Sociality	Habitats	Diet
<i>Alces alces</i>	1	0	0	0	0	118	47	600	1.5	1	3	2
<i>Ammospermophilus leucurus</i>	0	0	0	1	0		0.06167	0.10585	20.5	0	4	5
<i>Aplodontia rufa</i>	0	0	0	0	0		0.00183	0.806	946	0	3	2
<i>Bassariscus astutus</i>	1	0	0	0	0		0.5	0.94	3.5	1	4	5
<i>Blarina brevicauda</i>	0	0	0	1	0		0.025	0.016	3925	1	5	4
<i>Canis latrans</i>	1	0	0	0	0	176	10.5	14.5	0.7	3	10	5
<i>Canis lupus</i>	1	0	0	0	0	79	65	28	0.02	3	4	2
<i>Castor canadensis</i>	0	1	0	0	0	40.6	0.1108	18.5	3.6	3	7	2
<i>Cervus elaphus</i>	1	0	0	0	0	18.5	159	280	13.5	2	4	3
<i>Chaetodipus arenarius</i>	1	0	0	0	0		0.003	0.0185	1551	0	1	4
<i>Chaetodipus baileyi</i>	1	0	0	0	0		0.003	0.0264	4085	0	2	4
<i>Chaetodipus fallax</i>	1	0	0	0	0		0.003	0.0195	1785	0	2	4
<i>Chaetodipus intermedius</i>	1	0	0	0	0		0.003	0.0152	235	0	2	4
<i>Chaetodipus penicillatus</i>	1	0	0	0	0		0.003	0.016	98	0	2	4
<i>Chaetodipus spinatus</i>	1	0	0	0	0		0.003	0.0155	1551	0	2	4
<i>Clethrionomys gapperi</i>	1	0	0	0	0		0.0077	0.0275	1000	0	2	2
<i>Clethrionomys rutilus</i>	1	0	0	0	0		0.003	0.03	1331	0	2	3.5
<i>Condylura cristata</i>	0	1	0	0	0		0.004	0.056	2500	3	2	2
<i>Cryptotis parva</i>	0	0	0	1	0		0.000023	0.004	1798	3	4	3
<i>Didelphis virginiana</i>	1	0	0	0	0	4.3	0.2	3.75	26	0	4	5
<i>Dipodomys merriami</i>	1	0	0	0	0	0.2	0.00125	0.04315	1100	1	3	4
<i>Erethizon dorsatum</i>	0	0	1	0	0		1.5712	6.8	5.1	1	6	2
<i>Felis concolor</i>	1	0	0	0	0	155	409	43.7	0.02	0	5	3
<i>Glaucomys sabrinus</i>	0	0	0	0	1		0.01	0.107	550	1	3	4
<i>Glaucomys volans</i>	0	0	0	0	1		0.0114	0.07	700	1	4	4
<i>Gulo gulo</i>	1	0	0	0	0	300	374	14.5	0.005	0	1	3
<i>Lepus alleni</i>	1	0	0	0	0		6.428	3.783	18.8	1	2	2
<i>Lepus americanus</i>	1	0	0	0	0	20.1	0.088	1.7	2000	0	3	2
<i>Lepus californicus</i>	1	0	0	0	0	45	0.8	2.4	92.5	0	2	2
<i>Lepus townsendii</i>	1	0	0	0	0		19.63	3.262	5.73	1	4	2
<i>Lontra canadensis*</i>	0	1	0	0	0	42	15	8.4	0.28	2.5	2	3
<i>Lynx canadensis</i>	1	0	0	0	0	9.7	155	10	0.06	1	2	2
<i>Lynx rufus</i>	1	0	0	0	0	56	38.4	8.2	0.03	0	8	2
<i>Marmosa canescens</i>	0	0	1	0	0		0.002	0.725	128	0	2	5
<i>Marmota flaviventris</i>	0	0	0	1	0	1.4	0.00575	4	8.5	2	5	4
<i>Marmota monax</i>	0	0	0	1	0	0.7	0.03412	3.676	148	1	4	2
<i>Marmota vancouverensis</i>	0	0	0	1	0		0.00575	4	0.5	3	1	2
<i>Martes americana</i>	0	0	1	0	0	61	12.1	1	1.1	0	3	3
<i>Martes pennanti</i>	0	0	1	0	0	22.6	25	3.5	0.10	0	4	3
<i>Mephitis mephitis</i>	1	0	0	0	0	21.7	2.08	1.6	3.3	1	4	5
<i>Microsorex hoyi</i>	1	0	0	0	0		0.003	0.0035	520	1	4	3
<i>Microtus californicus</i>	1	0	0	0	0		0.0055	0.062	5250	2	4	3
<i>Microtus longicaudus</i>	1	0	0	0	0		0.00882	0.047	2572	0	6	3
<i>Microtus mexicanus</i>	1	0	0	0	0		0.001	0.0385	7700	0	2	2
<i>Microtus montanus</i>	1	0	0	0	0		0.00015	0.059	31250	2	4	2
<i>Microtus ochrogaster</i>	1	0	0	0	0	0.1	0.00165	0.042	5373	3	2	2
<i>Microtus oeconomus</i>	1	0	0	0	0	1	0.0025	0.062	3750	1.5	3	2
<i>Microtus oregoni</i>	0	0	0	1	0		0.00068	0.021	2213	1.5	3	3
<i>Microtus pennsylvanicus</i>	1	0	0	0	0	0.2	0.00179	0.0441	12202	1	4	2
<i>Microtus pinetorum</i>	0	0	0	1	0		0.0001	0.02345	730	2	3	3
<i>Microtus richardsoni</i>	1	0	0	0	0		0.00177	0.107	1041	0	2	2
<i>Microtus townsendii</i>	1	0	0	0	0	0.1	0.00017	0.046	11400	2.5	2	2
<i>Mustela erminea</i>	1	0	0	0	0	1	0.5875	0.061	1.32	0	5	1

## Appendix continued

Species	Ter	Saq	Sar	Sfo	Gli	Dispersal (km)	Home range (km <sup>2</sup> )	Body size (kg)	Population density (individuals km <sup>-2</sup> )	Sociality	Habitats	Diet
<i>Mustela frenata</i>	1	0	0	0	0		1.16	0.205	0.22	0	12	1
<i>Mustela nivalis</i>	1	0	0	0	0		0.015	0.0375	10.5	0	8	1
<i>Mustela vison</i>	1	1	0	0	0	45	3.8	0.792	4.2	0	1	3
<i>Napaeozapus insignis</i>	1	0	0	0	0		0.0175	0.0215	1304	1	3	4
<i>Neotoma albigula</i>	1	0	0	0	0		0.0486	0.18905	583	0	3	3
<i>Neotoma cinerea</i>	1	0	0	0	0	2.2	0.055	0.36	400	1	4	4
<i>Neotoma lepida</i>	1	0	0	0	0		0.00053	0.137	365	0	3	2
<i>Neotoma mexicana</i>	1	0	0	0	0		0.055	0.33	400	0	4	4
<i>Neurotrichus gibbsii</i>	1	0	0	0	0		0.00633	0.00945	1350	4	4	2
<i>Notiosorex crawfordi</i>	1	0	0	0	0		0.00446	0.00592	2400	0	8	2
<i>Ochotona princeps</i>	1	0	0	0	0	0.4	1.5655	0.1485	592	1	1	2
<i>Odocoileus hemionus</i>	1	0	0	0	0	7.3	2.11	86	22	2	10	3
<i>Odocoileus virginianus</i>	1	0	0	0	0	11.7	2.895	87	15	2	11	3
<i>Ondatra zibethicus</i>	0	1	0	0	0	3.4	0.0028	1.1	4150	0	1	3
<i>Oreamnos americana</i>	1	0	0	0	0		18	90	0.7	2	3	3
<i>Oryzomys nelsoni</i>	0	1	0	0	0		0.003	0.069	1000	0	1	5
<i>Oryzomys palustris</i>	0	1	0	0	0		0.003	0.052	1350	0	2	5
<i>Parascalops breweri</i>	0	0	0	0	0		0.000003	0.04845	300	1	4	2
<i>Peromyscus crinitus</i>	1	0	0	0	0		0.0036	0.0165	1519	0	1	5
<i>Peromyscus eremicus</i>	1	0	0	0	0		0.003	0.02	32	0	5	4
<i>Peromyscus keeni</i>	1	0	0	0	0		0.003	0.02	500	1	3	4
<i>Peromyscus leucopus</i>	0	0	1	0	0	1	0.0025	0.023	1250	1	9	4.5
<i>Peromyscus madrensis</i>	0	0	1	0	0		0.00057	0.0217	3002	1	4	3
<i>Peromyscus maniculatus</i>	1	0	0	0	0	0.9	0.007	0.02	2200	1	10	5
<i>Phenacomys intermedius</i>	1	0	0	0	0		0.002	0.027	549	1	5	4
<i>Procyon lotor</i>	1	0	0	0	0	265.5*	0.7	5.72	20	0.5	10	5
<i>Rangifer tarandus</i>	1	0	0	0	0		711	105	1.02	2	2	3
<i>Reithrodontomys megalotis</i>	1	0	0	0	0		0.0095	0.015	2530	1	7	2
<i>Scalopus aquaticus</i>	0	0	0	0	0		0.0109	0.1035	373	1	3	3
<i>Sciurus aberti</i>	0	0	1	0	0		0.06395	0.794	38.2	1	3	2
<i>Sciurus carolinensis</i>	0	0	1	0	0		0.018	0.533	500	1	4	2
<i>Sciurus niger</i>	0	0	1	0	0	3.4	0.15598	0.9	289	1	4	2
<i>Sorex cinereus</i>	1	0	0	0	0		0.006	0.0036	948	0	4	2
<i>Sorex fumeus</i>	1	0	0	0	0		0.02353	0.0075	5967	0	2	2
<i>Sorex longirostris</i>	1	0	0	0	0		0.00637	0.0039	3700	0	4	3
<i>Sorex lyelli</i>	1	0	0	0	0		0.00709	0.0045	1500	0	2	2
<i>Sorex merriami</i>	1	0	0	0	0		0.00869	0.0059	1200	0	3	2
<i>Sorex monticolus</i>	1	0	0	0	0		0.03514	0.00666	1200	0	2	3
<i>Sorex nanus</i>	1	0	0	0	0		0.003	0.0025	500	0	4	2
<i>Sorex ornatus</i>	1	0	0	0	0		0.0004	0.00512	11100	2	2	2
<i>Sorex palustris</i>	0	1	0	0	0		0.0025	0.01385	180	0	1	2
<i>Sorex tenellus</i>	1	0	0	0	0		0.003	0.00375	1000	0	3	2
<i>Sorex trowbridgii</i>	0	0	0	1	0		0.024	0.0075	4784	0	3	4
<i>Sorex vagrans</i>	1	0	0	0	0		0.02234	0.007	1200	0	1	3
<i>Spermophilus armatus</i>	0	0	0	1	0		0.00303	0.425	8200	1	2	4
<i>Spermophilus beecheyi</i>	0	0	0	1	0	1.3	0.005	0.7265	450	1	4	5
<i>Spermophilus beldingi</i>	0	0	0	1	0	0.3	0.0005	0.35	15260	2	4	3
<i>Spermophilus elegans</i>	0	0	0	1	0		0.00055	0.3485	2340	2	2	2
<i>Spermophilus lateralis</i>	0	0	0	1	0		0.007	0.2625	2050	1	4	5
<i>Spermophilus tereticaudus</i>	0	0	0	1	0		0.003	0.125	530	2	2	4
<i>Spermophilus variegatus</i>	0	0	0	1	0		0.00295	0.69133	690	2	3	5
<i>Spilogale gracilis</i>	1	0	0	0	0		0.64	0.432	5	1	4	4
<i>Sylvilagus bachmani</i>	1	0	0	0	0	0.4	0.0025	0.7	450	0	1	2
<i>Sylvilagus floridanus</i>	1	0	0	0	0	2.3	0.0295	1.1892	954	0	6	2
<i>Sylvilagus graysoni</i>	1	0	0	0	0		0.02476	1.4725	75	0	3	2
<i>Sylvilagus nuttallii</i>	1	0	0	0	0		0.015	0.755	150	0	1	2
<i>Sylvilagus transitionalis</i>	1	0	0	0	0		0.0045	0.89	150	0	2	2
<i>Synaptomys borealis</i>	1	0	0	0	0		0.001	0.0305	1333	0	3	2

## Appendix continued

Species	Ter	Saq	Sar	Sfo	Gli	Dispersal (km)	Home range (km <sup>2</sup> )	Body size (kg)	Population density (individuals km <sup>-2</sup> )	Sociality	Habitats	Diet
<i>Synaptomys cooperi</i>	1	0	0	0	0		0.001	0.035	1333	0	2	2
<i>Tamias alpinus</i>	1	0	0	0	0		0.0126	0.036	814	0	1	4
<i>Tamias amoenus</i>	0	0	0	1	0		0.022	0.051	125	0	3	5
<i>Tamias canipes</i>	0	0	0	1	0		0.016	0.07	650	0	3	5
<i>Tamias cinereicollis</i>	0	0	1	0	0		0.016	0.062	650	0	2	4
<i>Tamias dorsalis</i>	1	0	0	0	0		0.011	0.07	650	0	3	4
<i>Tamias minimus</i>	0	0	0	1	0		0.001	0.041	902.5	0	6	4
<i>Tamias panamintinus</i>	1	0	0	0	0		0.016	0.051	375	0	2	4
<i>Tamias quadrimaculatus</i>	1	0	0	0	0		0.0068	0.087	70	0	1	4
<i>Tamias quadrivittatus</i>	0	0	0	1	0		0.0197	0.067	130	0	2	4
<i>Tamias speciosus</i>	0	0	0	1	0		0.01385	0.0555	58.5	0	2	4
<i>Tamias striatus</i>	0	0	0	1	0	0.9	0.0022	0.096	4000	0	1	4
<i>Tamias townsendii</i>	0	0	1	0	0		0.008	0.08	260	0	2	4
<i>Tamias umbrinus</i>	0	0	0	1	0		0.0195	0.0625	336	0	2	4
<i>Tamiasciurus douglasii</i>	0	0	1	0	0		0.00417	0.2265	23.7	0	2	5
<i>Tamiasciurus hudsonicus</i>	0	0	1	0	0	0.6	0.00575	0.2	115	0	3	5
<i>Thomomys bottae</i>	0	0	0	0	0	0.3	0.00038	0.15	860	0	9	2
<i>Thomomys talpoides</i>	0	0	0	0	0	0.1	0.00014	0.11	32.7	0	5	2
<i>Urocyon cinereoargenteus</i>	1	0	0	0	0	83.7	3.5	3.07	1.65	3	6	5
<i>Urocyon littoralis</i>	1	0	0	0	0		0.3	1.95	2.7	3	2	4
<i>Ursus americanus</i>	1	0	0	0	0	28.8	45.5	77.27	3.17	0	7	4
<i>Ursus arctos</i>	1	0	0	0	0	82	550	202.5	0.02	0	2	4
<i>Vulpes vulpes</i>	1	0	0	0	0	302*	3.885	5.2	3	3	8	4
<i>Zapus hudsonius</i>	1	0	0	0	0		0.005	0.018	1713	0	3	4
<i>Zapus princeps</i>	1	0	0	0	0		0.0025	0.0275	256	0	3	3
<i>Zapus trinotatus</i>	1	0	0	0	0		0.0025	0.0275	305	0	4	4

\*An extreme value from the study of Sutherland *et al.* (2000); not used in formulating predictive relations between home range and dispersal distance in the present study.

Sources: Anderson and Wallmo (1984), Anthony *et al.* (1987), Armstrong & Jones (1971, 1972), Baker (1983), Bandoli (1987), Barash (1989), Bartels & Thompson (1993), Bear (1989), Bekoff (1977), Belk & Smith (1991), Beneski & Stinson (1987) Bergstrom (1988), Best (1996), Best & Henry (1993), Best *et al.* (1992), Best *et al.* (1994a,b,c), Boonstra *et al.* (1987), Brown & Heske (1990), Carraway & Verts (1985, 1991a,b, 1993), Cervantes (1997), Chapman (1974, 1975a,b), Chapman & Feldhamer (1982), Chapman *et al.* (1980), Churchfield (1990), Clark *et al.* (1987), Clawson *et al.* (1994a,b), Cole *et al.* (1998), Cornely & Baker (1986), Cornely & Verts (1988), Cunningham (1990), Currier (1983), Demarais & Krausman (2000), Demarchi *et al.* (2000), Dolan & Carter (1977), Douglas (1976), Doyle (1990), Eadie (1939), Eisenberg (1981), Ernest & Mares (1987), Franzmann (1981), Frase & Hoffmann (1980), French (1980), Fritzell & Haroldson (1982), Fuller & Sievert (2001), Galindo & Krebs (1985), Gannon (1988), Gehring & Swihart (2003), George (1989), George *et al.* (1986), Gilbert & Krebs (1991), Gliwicz (1997), Goheen (2002), Gomez & Anthony (1998), Gorman & Stone (1980), Hall (1981), Hallett (1978), Hanski *et al.* (1991), Hart (1992), Hartman & Krenz (1993), Hayes & Harestad (2000), Hays & Lidicker (2000), Hilton & Best (1993), Hoffmann & Owen (1980), Holling (1992), Ivan & Swihart (2000), Jenkins & Busher (1979), Jenkins & Eshelman (1984), Johnson & Armstrong (1987), King (1983, 1989), Kinlaw (1995), Kirkland & Layne (1989), Koprowski (1994), Krebs & Wingate (1985), Kurta (1995), Kwiecinski (1998), Lackey (1991a,b, 1996), Lackey *et al.* (1985), Lambin & Krebs (1991, 1993), Lambin *et al.* (1992), Lapasha & Powell (1994), Larivière & Pasitschniak-Arts (1996), Larivière & Walton (1997, 1998), Lim (1987), Linzey (1983), Long (1974), Lotze & Anderson (1979), Ludwig (1984), MacCracken *et al.* (1985), McAllister & Hoffmann (1988), McComb *et al.* (1993), McCorquodale *et al.* (1989), McManus (1974), Macêdo & Mares (1988), Mech (1970, 1974), Merritt (1981), Moore & Collins (1995), Mumford & Whitaker (1982), Murie & Michener (1984), Nagorsen (1987), Nash & Seaman (1977), Negus *et al.* (1986), Novikov & Moshkin (1998), Oaks *et al.* (1987), Olding & Cockrum (1977), Owen & Hoffmann (1983), Pasitschniak-Arts (1993), Pasitschniak-Arts & Larivière (1995), Paulson (1988), Petersen & Yates (1980), Pinter (1988), Poglajen-Neuwall & Towell (1988), Powell (1981, 1993), Redfield (1976), Reich (1981), Reid *et al.* (1994), Richens (1974), Rickart & Heaney (2001), Rideout & Hoffmann (1975), Ruggiero *et al.* (1994), Schweiger & Boutin (1995), Schwilk & Keeley (1998), Sheffield & King (1994), Sheffield & Thomas (1997), Sheperd & Swihart (1995), Slough & Mowat (1996), Smith (1991), Smith (1997), Smith & Belk (1996), Smith & Weston (1990), Smolen (1981), Smolen & Keller (1987), Snyder (1982), Stalling (1990), Steele (1998), Stuart-Smith *et al.* (1997), Sullivan *et al.* (1997, 2001), Sutton (1992, 1993), Swihart (1992), Tamarin (1985), Thompson (1982), Ticul & Arroyo-Cabrales (1990), Tumilson (1987), Veal & Caire (1979), Verts & Carraway (2002), Viitala (1994), Wade-Smith & Verts (1982), Webster & Jones (1982), Wells-Gosling & Heaney (1984), Wheatley (1997), Whitaker (1972, 1974), Whitaker & Wrigley (1972), Williams (1984), Willner *et al.* (1980), Wilson & Ruff (1999), Wolfe (1982), Woods (1973), Yates & Schmidly (1978), Zegers (1984).