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Extinctions of montane mammals reconsidered: putting a global-warming scenario on ice

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McDonald and Brown developed a model based on island biogeographic principles to predict the magnitude and composition of small mammal extinctions from isolated boreal habitats atop mountains of the Great Basin following global warming. The model predicts that three of 14 boreal mammals will go extinct regionally and that four of 19 mountain ranges will lose upwards of 50% of their present faunas. Here, we re-examine the model on the basis of its underlying assumptions, on the statistical and biogeographic protocols used, and on its predictive power. A key assumption, that populations of these small mammals are isolated by absolute barriers to dispersal, is challenged by published field observations and by extensive trapping records. Statistical procedures used to construct the model are questionable and the model itself yields imprecise estimates. The biogeographic principle used to identify extinction-prone species, nested subsets of species, makes predictions that are at odds with available autecological information. The demonstration of a nested pattern of species occurrences does not provide definitive evidence in resolving SLOSS – or whether a single large island or several small islands of equivalent total area will contain more species. We conclude that the model is not a reliable method for forecasting species extinctions following global warming. The final resolution of the biogeography of montane mammals (and predictive models of extinction) in the Great Basin must await a full and accurate accounting of past and present species distributions.

Keywords: biogeographic theory; global warming; montane mammals; nested species distributions; SLOSS

Introduction

McDonald and Brown (1992) describe a method based on island biogeographic theory to predict small-mammal extinctions from isolated mountaintop 'islands' of the Great Basin. Both the number and identity of species extinctions are predicted for each island following a hypothesized scenario of global-warming. In this scenario, global warming promotes species extinctions exclusively through areal reductions of suitable habitats. McDonald and Brown (1992) predict that within the next century three of 14 mammals will be lost throughout the region and four of the nineteen mountain islands will lose over 50% of their small boreal mammals.

McDonald and Brown (1992) argue that their model will serve generally to predict species loss following global climatic change. They support this argument by citing the ubiquity of the species-area relationship and nested patterns of species distributions (see

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Simberloff and Levin, 1985; Patterson and Atmar, 1986). Although the theoretical and mechanistic underpinnings of both the species-area relationship and nested patterns of species distributions have been vigorously debated (e.g., Darlington, 1957; Connor and McCoy, 1979; Gilbert, 1980; Patterson and Atmar, 1986; Simberloff and Martin, 1991; Wright and Reeves, 1992), McDonald and Brown (1992) suggest that their model yields 'highly plausible' predictions of species extinctions. In addition, they propose their model as a cost-effective alternative to traditional approaches in conservation biology, because only geographic distributions, and not detailed autecological data, are necessary to identify extinction-prone species.

Before this model is extended to other systems, or before predictions of the model influence conservation decisions involving small boreal mammals of the Great Basin (see Stolzenburg, 1992), the model should be critically examined. We base our critique of the model on an examination of the insular nature of these faunas, on the state of knowledge regarding past and present species distributions, on the predictive power of the model itself, and on the use of nestedness as a means of identifying extinction-prone species. We evaluate the model both as a general model for conservation biology and in its specific application to the boreal mammals of the Great Basin. First, we provide a brief description of the model.

The McDonald-Brown model

The McDonald-Brown model (1992) is based on earlier work by Brown and others on the biogeography of 14 species of small, boreal mammals in the mountains of the Great Basin (Brown, 1971, 1978; Brown and Gibson, 1983). By necessity our critique will include many of the assumptions and conclusions found in the original papers; therefore, we begin by outlining Brown's (1971, 1978) historical explanation and McDonald and Brown's (1992) modifications:

(i) During the late Pleistocene the entire set of small, boreal mammals colonized all of the mountain islands. Colonization was made possible by corridors of pinyon-juniper woodland that existed throughout the lower elevations of Great Basin valleys and connected the mountains of the Great Basin with the Sierra Nevada and Rocky Mountains.

(ii) Post-glacial warming caused woodland and forest habitats to recede up slope into the mountains. Boreal habitats and their associated mammals became isolated as coniferous corridors were severed.

(iii) The contemporary boreal-mammal faunas of the mountains are relicts of the post-Pleistocene fauna. These mammals are now restricted to elevations above 2286 m (7500 ft), because desert valleys are now 'virtually absolute barriers' to dispersal. The faunal composition of each mountain island is solely the result of differential extinction.

(iv) The process of differential extinction has led to a highly nested pattern of species distributions, such that faunas on small islands are proper subsets of those on larger islands.

(v) Global warming will cause the boreal habitats to recede to higher elevations in the mountains of the Great Basin, thereby reducing the size of each boreal island. Extinctions following from areal reductions will follow a predictable sequence consistent with nestedness.

(vi) Post-warming extinctions can be predicted both quantitatively and qualitatively by application of the species-area relationship in conjunction with the nested structure of the mountain fauna.

Past and present species distributions and the island metaphor

The McDonald-Brown model includes three assumptions regarding past and present distributions of small mammals in the Great Basin. The first is that all 14 species were found on all 19 mountain ranges during the Pleistocene. Upon this assumption rests the assertion that the present distribution of montane mammals is the result of differential extinctions. The second assumption is that the contemporary distributions are accurately known. Third, McDonald and Brown (1992) assume that the current faunas are isolated geographically and that boreal areas are habitat islands. We discuss these assumptions seriatim.

Grayson (1987, 1993) has raised several potential problems with Brown's (1971, 1978) reconstruction of post-Pleistocene biogeography of boreal mammals. For example, Grayson cautions that Brown's (1978) assumption that all 14 species were once present on all 19 mountain ranges during the Pleistocene is probably overstated. The paleontological evidence has established numerous distribution records of now-extripated taxa but is too spotty to establish accurately late-Quaternary distributions for the entire set of mammals. The problem here is insufficient sampling (D.K. Grayson, personal communication). In fact, the available evidence cannot eliminate the possibility of Holocene colonizations. Furthermore, the late Pleistocene and early Holocene vegetation of the intermountain region is poorly known and should not be used to infer the nature of the boreal faunas. Coniferous habitat bridges did not exist throughout the region; nevertheless, mammals typical of boreal habitats (e.g. *Phenacomys* and *Martes* spp.) were present. Finally, isolation of boreal mammals need not have been synchronous across species or across mountain ranges. Grayson (1987) concludes that significant details of the history of Great Basin mammals remain unknown.

Not only are the past distributions of montane mammals in the Great Basin uncertain, so too are their present distributions. Over twenty years of research on the biogeography of montane mammals in the Great Basin has produced an evolving matrix of species-by-mountain occurrences (Fig. 1). The trend has been for an increase in the number of cells occupied, from approximately 44% of available cells in Brown (1971) to approximately 55% in Grayson and Livingston (1993). The uncertainty in the species distribution matrix is due largely to inadequate sampling and is probably best exemplified by the case of *Spermophilus beldingi*, which experienced numerous 'extinctions' and 'colonizations' during the period 1971 to 1993 (see Fig. 1). The distribution matrix has never been based on comprehensive field sampling; instead it has been pieced together from disparate literature accounts. For example, the distribution matrix presented in Brown (1971) was based primarily on literature accounts, supplemented with personal records. Small and isolated ranges did not receive equal literature coverage and so were not equally represented in Brown's (1971) matrix (Kodric-Brown and Brown, 1993). Recent sampling has increased substantially the faunal lists for these ranges. For example, Grayson and Livingston (1993) added four species to the fauna of the Roberts Creek Range, a 100% increase over that reported in McDonald and Brown (1992), and two species to the Diamond Range, a 50%

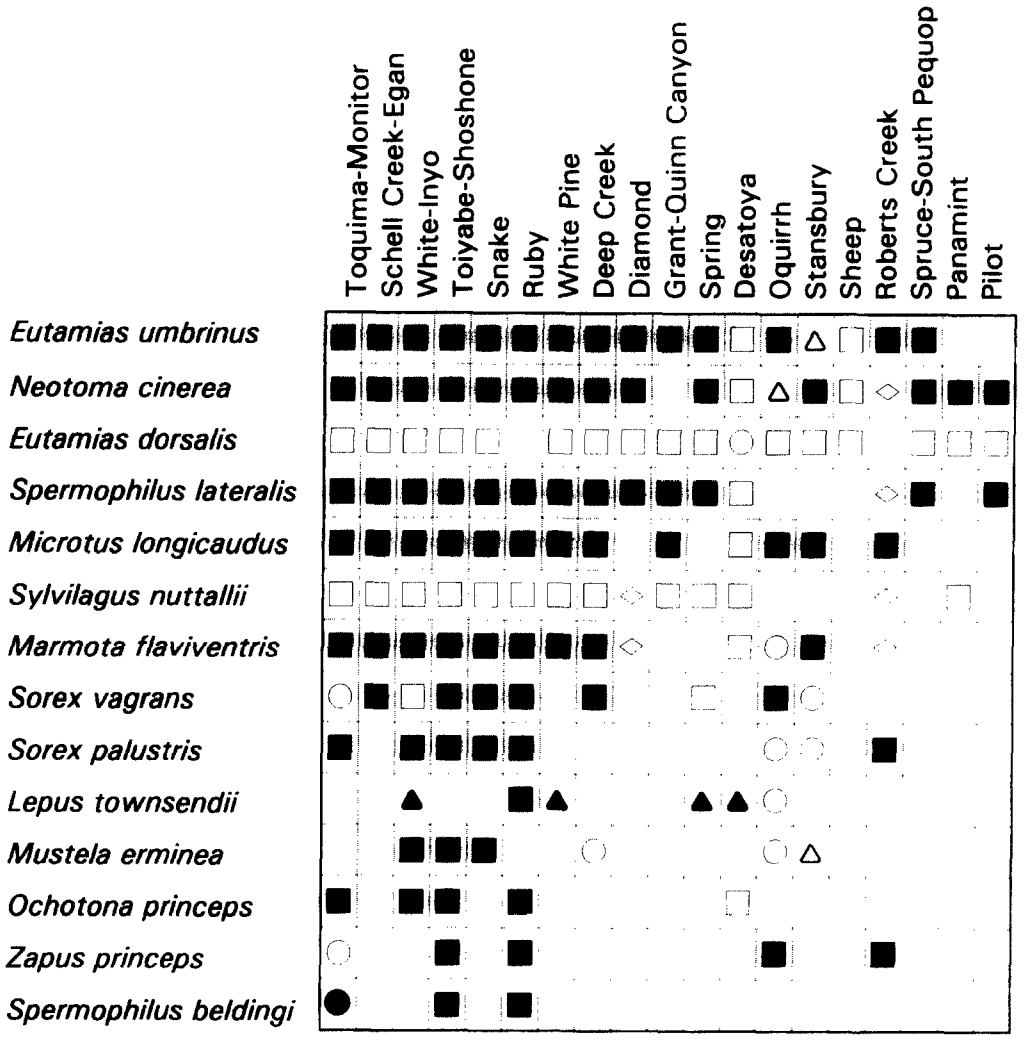

Figure 1. The distribution of 14 species of small mammals on 19 mountain ranges in the Great Basin. Black squares represent the original records of Brown (1971). □: two additional species and two mountain ranges added in Brown (1978). △: species occurrences added in Brown (1978); ○: in Brown and Gibson (1983); ◇: in Grayson and Livingston (1993). ▲: present in Grayson (1978), but absent in Grayson and Livingston (1993). ● (*Spermophilus beldingi*): present in Brown (1971), present in Brown (1978), absent in Brown and Gibson (1983), present in Grayson (1987), absent in Grayson and Livingston (1993), present in Grayson (1993), and present again in Kodric-Brown and Brown (1993).

increase, based on only two days of sampling (without trapping) and a few hours of sampling, respectively.

Continued additions to the species distribution matrix are probably best reflected in changing estimates for the parameters of the species-area relationship for the Great Basin boreal mammals. The slope of the relationship has declined steadily from 0.428 (Brown, 1971), to 0.326 (Brown, 1978), to 0.309 (McDonald and Brown, 1992), and finally to 0.282

(Grayson and Livingston, 1993; Kodric-Brown and Brown, 1993). Additions to the most recent distribution matrix will substantially lower the slope even further (T. Lawlor, personal communication). Kodric-Brown and Brown (1993) argue that results and interpretations of previous studies are not materially altered and that the 'qualitative patterns' in Brown's (1971) original model remain largely intact. On the other hand, Grayson (1993) concludes that gaps in the present species distribution matrix may reflect gaps in our knowledge as much as they reflect distributional gaps.

Another critical assumption of the McDonald-Brown model is that populations of boreal mammals in the Great Basin are isolated geographically and that the 19 mountain ranges are truly isolated habitats. Support for this assumption comes primarily from Brown's (1971, 1978) assertion that these mammals are unlikely to be found below 2286 m elevation and that desert valleys of the Great Basin constitute 'virtually absolute barriers' to dispersal. The assumption has not been tested.

However, a substantial body of empirical evidence suggests that the 2286 m elevation contour may not constitute an absolute barrier to dispersal for the majority of the 14 species modelled by McDonald and Brown (1992). Hall (1946) compiled approximately 18 000 specimen records for 111 species of Nevada mammals. Based on these extensive collections, Hall (1946) presented distribution patterns according to six major life-zones. For five of the 14 montane species, elevation ranges extended below the Pinyon-Juniper zone into the Upper Sonoran Zone dominated by sagebrush, *Artemisia tridentata* (Fig. 2A). Hall (1946) also suggested that winter snowfall in the desert valleys would allow dispersal by montane mammals among neighbouring mountain ranges that would not be possible otherwise. As a specific example, Hall (1946) noted that in winter, white-sided jackrabbits (*Lepus townsendii*), one of the 14 species in McDonald and Brown (1992), descended into lower valleys where they were absent during summer.

Hall (1946) also presented field records, including capture elevations, for 1760 collections involving the 14 species considered by McDonald and Brown (1992). For 11 of the species, the median capture elevation was below the 2286 m elevation contour (Fig. 2B). In fact, all species had at least some capture records below 1981 m (6500 ft) elevation. In addition, Egoscue (1961) reported captures of *Sorex vagrans* at 1294 m and *Sylvilagus nuttallii* at 1463 m, while Grayson and Livingston (1993) observed *Sylvilagus nuttallii* in the Ruby Valley, between the Ruby Range and the Spruce and Pequop ranges. Thus, 2286 m may not be the most conservative estimate for a dispersal barrier. However, dropping the dispersal barrier to even 1981 m (6500 ft) makes the island metaphor seem far less apt, as many islands would coalesce (Fig. 3).

The elevation data described above were based on state-wide capture records. While it is clear from these data that the 2286 m contour does not absolutely bar dispersal throughout the Great Basin, it is possible that there is geographic variation in the elevation ranges of species such that mountain ranges at low latitudes are more isolated from each other than are mountain ranges at higher latitudes. The mountain ranges considered by McDonald and Brown (1992) span approximately 5° of latitude, and vary with respect to the elevations and habitats of intervening valley bottoms. In addition, the 14 species of mammals they considered may also exhibit differences in the degree of geographic variation in elevation ranges. Differences among species or among mountain ranges in the degree of isolation of adjacent populations violates a fundamental assumption of the McDonald-Brown model, which considers all species and all mountains as equivalent.

We sorted the capture records presented in Hall (1946) according to species and

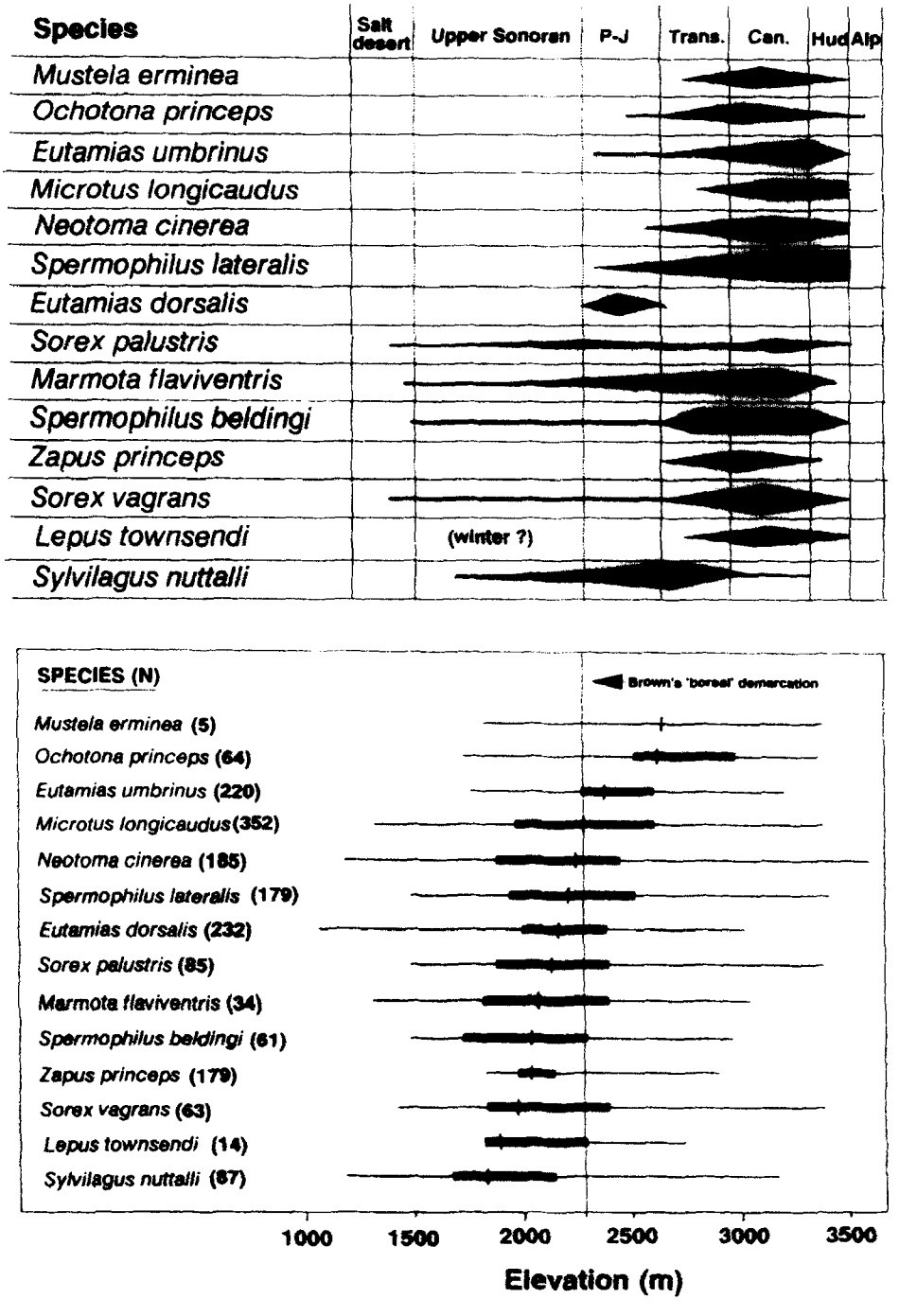

Figure 2. Elevational distribution of 14 species of montane mammals in Nevada according to five major life-zones (A). Thickness of polygons represents relative abundance (after Hall, 1946). Box and whisker plots of elevational ranges based on capture records (B). Vertical bars are medians. Numbers in parentheses are numbers of captures. Data are from Hall (1946).

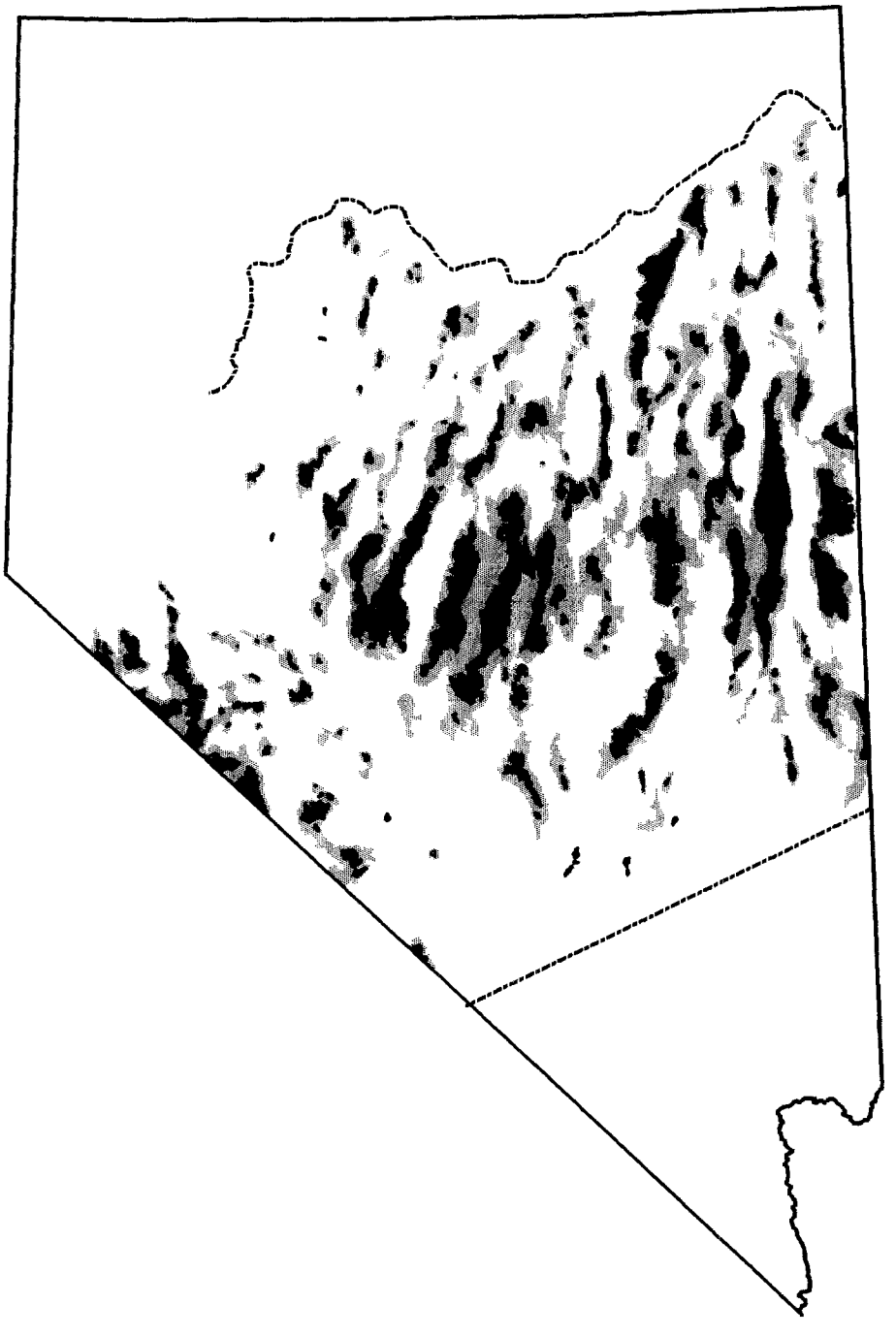

Figure 3. Montane islands in Nevada as delimited by a 2286 m elevational contour (black) and by a 1981 m contour (grey). Upper dashed line represents the Humboldt River. Omitted are the Sheep, Pilot, Stanbury, and Oquirrh Ranges, and most of the Deep Creek Range.

latitude. We next 'eye-balled' the average elevation of valley bottoms at each degree latitude from a topographic map of Nevada and plotted, for each species, capture records by latitude together with estimates of valley-bottom elevations.

We found considerable variation in the elevations of valley bottoms, and among species in the degree of geographic variation in elevation ranges (Fig. 4). Several distinct patterns emerged as depicted by the species presented in Fig. 4. We first note that 15 of 19 mountain ranges considered by McDonald and Brown (1992) occur between 38° and 41° latitude, and that three ranges are restricted below 38° latitude. Mountain ranges below 38° latitude were separated by deeper valleys than were ranges above 38° latitude. Thus, the four southernmost mountain ranges may be more isolated from each other than are the 15 northern ranges.

The pika, *Ochotoma princeps*, exhibited the highest minima in elevation range. For this species, the 2286 m contour may in fact constitute an effective dispersal barrier. A similar pattern obtained for *Marmota flaviventris*, but with only eight capture locations it was difficult to draw a definitive conclusion. In contrast, *Eutamias dorsalis* exhibited low elevation minima throughout its geographic range. Numerous capture sites were at or near the elevations of valley bottoms. Most species, such as *Sylvilagus nuttallii* and *Spermophilus lateralis*, exhibited geographic variation in minimum capture elevations, with relatively high minima at low latitudes and relatively low minima at higher latitudes. Species that demonstrated this pattern include *Eutamias umbrinus*, *Neotoma cinerea*, *Sorex vagrans*, and *Microtus longicaudus*. Several species, such as *Spermophilus beldingi*, had few capture locations south of 38° latitude; these include *Lepus townsendii*, *Zapus princeps*, *Sorex palustris*, and *Mustela erminea*. In general, these species had capture locations below the 2286 m contour, at least above 38° latitude. Thus, for two species there is evidence that the 2286 m contour may be an effective dispersal barrier, but for the majority of species, this contour does not appear to be an effective barrier, particularly for the 15 northern ranges.

We are not claiming that these capture records are conclusive evidence of inter-mountain dispersal. We simply maintain that Brown's (1971) 2286 m demarcation appears arbitrary. However, we feel that our analysis of elevation ranges is conservative, since the original sampling scheme was not designed to establish the lower limits of species elevation ranges. Demonstration of the insular nature of these faunas must await detailed population and genetic analyses.

Species-area relationship and extinction forecasts

The centrepiece of the McDonald-Brown model is the species-area relationship constructed for 14 species of boreal mammals distributed on 19 mountain ranges in the Great Basin. The expected numbers of extinctions for each mountain range are based solely on projections from this species-area relationship; no additional data, such as species' life-histories or habitat requirements, are used in forecasting numbers of extinctions. Thus, the predictive power and reliability of the model are related directly to the precision and predictive power of the underlying species-area relationship of boreal mammals. We examine McDonald and Brown's (1992) species-area relationship in terms of its construction, underlying assumptions, and predictive power.

Construction of the model

The first requirement of a species-area relationship used in the manner of the McDonald-Brown model is that the relationship describe the data. This is not so. The relationship itself is incorrectly estimated, and in two specific cases, White-Inyo and Stansbury Mounts, reported estimates cannot be reconciled with the data. The relationship described is derived from data presented in Brown (1978) and is given as

$$S = 1.188\ A^{0.326} \quad (1)$$

where area is measured in miles^2. But, as noted above, several species occurrences have been added to the distribution matrix (Fig. 1) since Brown (1978) and Brown and Gibson (1983). Consequently, the species-area relationship for the updated data matrix presented in McDonald and Brown (1992) is given by

$$S = 1.377\ A^{0.309} \quad (2)$$

for area measured in miles^2. We suspect, however, that equation (2) was actually used to estimate numbers of extinctions because the agreement with the published estimates is better for this relationship than that for the Brown (1978) and Brown and Gibson (1983) relationship.

We were unable to reproduce the estimated number of extinctions for the White-Inyo Range using either of the above species-area relationships. McDonald and Brown (1992) estimate one extinction, while we estimate three extinctions using either equation (1) or (2). All the areas presented in McDonald and Brown (1992) are incorrect owing to an improper conversion of miles^2 into km^2. (We assume throughout that the same error in unit conversion for pre-warming areas also holds for post-warming areas). Even after accounting for this error, we still cannot reproduce their estimate for White-Inyo. We also were unable to reproduce the estimated number of extinctions for the Stansbury Range using McDonald and Brown's (1992) distribution matrix. McDonald and Brown (1992) estimate two extinctions, while we estimate three extinctions using either equation (1) or (2).

McDonald and Brown (1992) use a procedure for extracting post-warming estimates of species richness from the species-area relationship of montane mammals that violates an assumption of linear regression analysis, upon which the species-area relationship is based. For each mountain range, McDonald and Brown (1992) project backwards along the area axis, but parallel to the species-area relationship, to the area of boreal habitat assumed to be remaining following global warming (Fig. 5). The estimated number of species is the corresponding value along the species axis. In other words, estimates are derived in such a way that residuals about the species-area regression are preserved. McDonald and Brown (1992) ground this approach in the belief that deviations about the contemporary species-area relationship represent deterministic characteristics of each mountain range, and that these deviations will be unaffected by large changes in area (up to 95% areal reduction) or by effects of global warming.

Assumptions of the model

The assumption of deterministic deviations about the species-area relationship is problematic. First, the theoretical basis of the McDonald-Brown model is the dynamic equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967). Yet, the model envisaged by MacArthur and Wilson (1963) posits a dynamic equilibrium of species

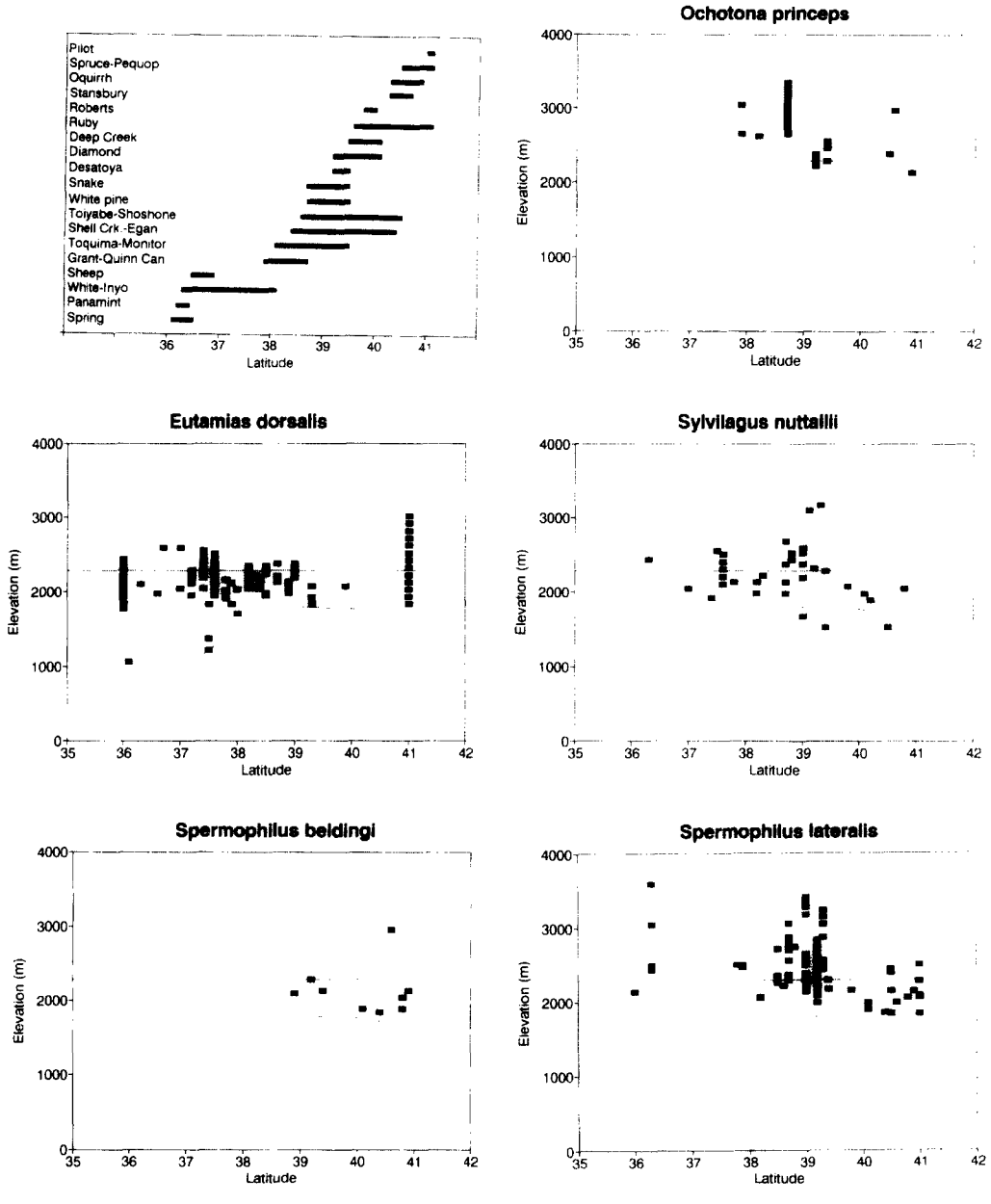

Figure 4. Geographic range of 19 mountain ranges in Nevada considered by McDonald and Brown (1992), and elevations of capture locations by species and latitude. Horizontal line represents the 2286 m contour, while the curved line represents estimates of average valley-bottom elevations. Data from Hall (1946).

richness, determined, in part, by stochastic immigration and extinction dynamics that yield an expected species richness with an associated variance (see Simberloff, 1969). Thus, random deviations about the species-area relationship are to be expected owing to the vagaries of immigration and extinction.

Second, if the McDonald and Brown (1992) model is to be used generally to predict species extinctions following global warming, the assumption of deterministic deviation must be extended to other systems. Yet, a fully deterministic accounting of patterns of species richness has eluded biogeographers. In fact, the species-area relationship itself may not be determinate, as the passive sampling hypothesis (Connor and McCoy, 1979) and the random placement hypothesis (Coleman *et al.*, 1982) posit statistical mechanisms to account for the relationship.

Whatever the theoretical basis for the species-area relationship, the relationship itself is probably best viewed as a statistical model (Connor and McCoy, 1979). Species-area relationships have been constructed for hundreds of systems, with area alone typically explaining only about half the variation in species numbers (Connor and McCoy, 1979; Boecklen and Gotelli, 1984). Inclusion of multiple independent variables has often significantly increased the explanatory power of models (e.g. Hamilton and Armstrong, 1965; Johnson and Simberloff, 1974), but never has all variation in species numbers been explained.

Our knowledge of the causes of species richness is incomplete, but even less is known about how patterns of covariation among the determinants of species richness will be affected by large changes in area or by direct and indirect effects of global warming. What little we do know suggests that covariance patterns will be affected. For example, changes in habitat heterogeneity, which most biogeographers consider an important determinant of species richness (e.g. Wiliams, 1964; MacArthur and Wilson, 1967; Abbott, 1978; Connor and McCoy, 1979), can directly affect the parameters of the species-area relationship itself (Boecklen, 1986). Thus, as area and, concomitantly, habitat diversity are reduced following global warming, it is unlikely that deviations from contemporary species-area relationships will be preserved when the species-area relationship itself may be altered.

Predictive power of the model

The predictive performance of a species-area relationship can be assessed according to well-established statistical criteria, perhaps the most important being the size of prediction intervals constructed about point estimates (see Boecklen and Gotelli, 1984; Boecklen and Simberloff, 1986). However, McDonald and Brown's (1992) treatment of residuals as fixed precludes an evaluation of the precision of their model by established methods. Any model can produce estimates, but only those models that give precise and reliable estimates should be applied to conservation practice (see Boecklen and Gotelli, 1984; Boecklen and Simberloff, 1986). We evaluate the precision of the McDonald-Brown model by first relaxing the assumption of deterministic deviations and then constructing a simultaneous 95% prediction interval (see Weisberg, 1980). Many of the point estimates change substantially. For example, McDonald and Brown (1992) estimate that 5 species will remain in the Schell Creek Range following global warming, while we estimate approximately eight species (Table 1). For the Toiyabe Range, McDonald and Brown (1992) estimate 11 species remaining; we estimate approximately eight species. The simultaneous 95% prediction interval for the species-area relationship of boreal mammals

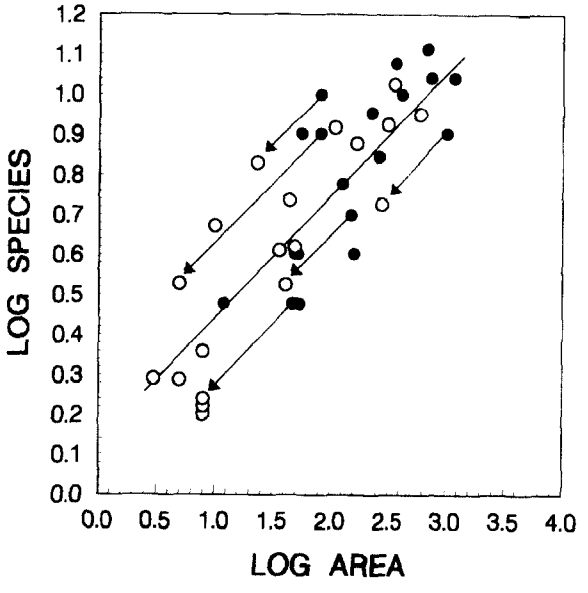

Figure 5. Estimates of post-warming species richness on 19 isolated mountain ranges in the Great Basin, as predicted by McDonald and Brown (1992). Closed circles represent contemporary areas of boreal habitat on each mountain range, while open circles are predicted areas of boreal habitat following global warming. Post-warming species numbers are estimated by projecting backwards along, but parallel to, the contemporary species-area relationship (see arrows).

routinely spans nearly an order of magnitude (Fig. 6). Consequently, 95% prediction intervals for individual mountain ranges exhibit 6–10-fold ranges in species richness. For example, McDonald and Brown (1992) predict that nine species will remain on the Toquima Range following global warming. The underlying species-area relationships predicts that 3.8–25.7 species, or 34.5–233.6% of the original species assemblage, will remain with a 95% level of confidence (Table 1).

The level of precision exhibited by the model is far too low to warrant specific recommendations regarding reserve design or management practice even for the Great Basin mammals under the assumed scenario of global warming. The typical predictive performance of species-area relationships, roughly half the variation in species numbers explained (Boecklen and Gotelli, 1984), suggests that equally low levels of precision will result if the McDonald-Brown model was to be applied to other systems.

Nested subsets, extinction-prone species, and SLOSS

Once they obtained estimates of the number of extinctions for each mountain range, McDonald and Brown (1992) examined the species distribution matrix to determine which species would most probably be lost from each mountain island. The nested structure of this species occurrence matrix had been interpreted as extinction generated (Brown and

Gibson, 1983) and predictable (Cutler, 1991). Therefore, McDonald and Brown (1992) selected extinction candidates in a manner that preserved the nested structure (Fig. 7). Predictions derived with this method may be incorrect, however, as mechanisms other than differential extinction may generate nestedness, and the method itself is insensitive to species' autecologies.

Darlington (1957) hypothesized that predictable (nested) distribution patterns among islands resulted from immigration processes, irregular distributions from faunal relaxation, and that present faunas likely result from a mixture of both processes. In contrast, Patterson and Atmar (1986) invoked selective extinction as the primary mechanism responsible for highly nested patterns. However, Simberloff and Martin (1991) noted that in most cases faunal relaxation is hypothesized, and the assumption that a common set of species originally occupied all islands may be invalid (see also Patterson, 1987). Moreover, Simberloff and Martin (1991) argue that a given species distribution pattern is probably the result of several factors operating simultaneously, including extinction and colonization events, as well as historical factors and distributions of habitats and resources (see also Ward and Lakhani, 1977). Thus, the demonstration of a nested pattern of species occurrences is insufficient evidence of differential extinction as the responsible mechanism (Simberloff and Levin, 1985; Patterson, 1987; Simberloff and Martin, 1991) and does not warrant projections based on the assumption that future extinctions will follow a nested pattern (see also Doak and Mills, 1994).

Degrees of nestedness and their meaning can vary among methods. For example, the

Table 1. Numbers of species predicted by McDonald and Brown (1992) to be remaining on 19 mountain ranges in the Great Basin following a scenario of global warming. Numbers of species estimated and 95% prediction intervals are derived from standard linear regression procedures

Mountain range	Number of species		95% prediction interval
	Predicted	Estimated	
Toquima	9	9.9	3.8–25.7
Schell	5	7.8	3.1–19.8
White-Inyo	10	8.1	3.2–20.7
Toiyabe	11	8.4	3.3–21.6
Snake	8	6.7	2.6–16.9
Ruby	8	5.9	2.3–14.8
White Pine	4	4.6	1.8–11.8
Deep Creek	5	4.4	1.7–11.5
Diamond	2	2.6	0.9– 7.5
Grant	3	4.3	1.7–11.3
Spring	4	4.2	1.6–10.9
Desatoya	3	2.3	0.8– 6.8
Oquirrh	7	3.6	1.4– 9.7
Stansbury	6	2.8	1.0– 7.9
Sheep	2	2.6	0.9– 7.5
Roberts Creek	2	2.3	0.8– 6.8
Spruce	2	2.6	0.9– 7.5
Panamint	2	2.6	0.9– 7.5
Pilot	2	2.0	0.6– 6.1

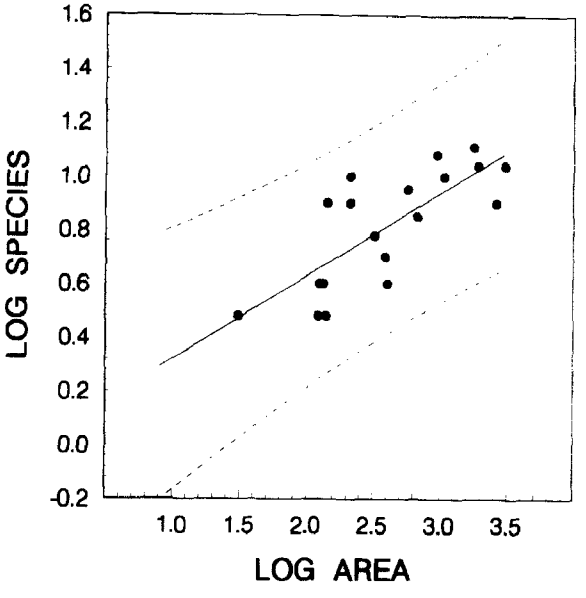

Figure 6. Species-area relationship and simultaneous 95% prediction interval for 14 species of small mammals distributed on 19 mountain ranges in the Great Basin. Data are from McDonald and Brown (1992). The regression equation is given by log S = 0.010 + 0.309* log A, where area is measured in km^2 (R^2 = 57.9%; $p < 0.001$).

degree of nestedness of a set of islands ranked by area generally can be increased if islands are instead ranked by species richness (Simberloff and Martin, 1991). In addition, community-wide measures of nestedness can mask individual species patterns (Simberloff and Martin, 1991). McDonald and Brown (1992) cite analyses by Patterson and Atmar (1986) and Cutler (1992) as evidence that boreal mammals in the Great Basin exhibit a significantly nested pattern of distribution. However, Patterson and Atmar (1986) examined a different data set. Cutler's (1992) analysis was at the community level, and ordered mountain ranges by species richness. Perhaps, for purposes of conservation planning, a more appropriate analysis of nestedness would rank mountains by area, as the McDonald-Brown model is area-based and most conservation strategies have areal considerations. In addition, a species-by-species analysis may be more appropriate, since the object is to identify extinction-prone species and species may differ in their adherence to nestedness.

We reanalysed the distribution matrix presented by McDonald and Brown (1992) for nestedness as follows. First, we ranked the McDonald-Brown matrix by area, then we tested the distributions of individual species against a null hypothesis of random distribution by using the Wilcoxon 2-sample rank-sum statistic, as outlined in Simberloff and Levin (1985) and Simberloff and Martin (1991). We found that seven of 14 species exhibited significant patterns of nestedness, while for the remaining seven species, we failed to reject the null hypothesis of random distribution (Table 2). Thus, we found substantial variation among species in their adherence to nestedness. These results suggest

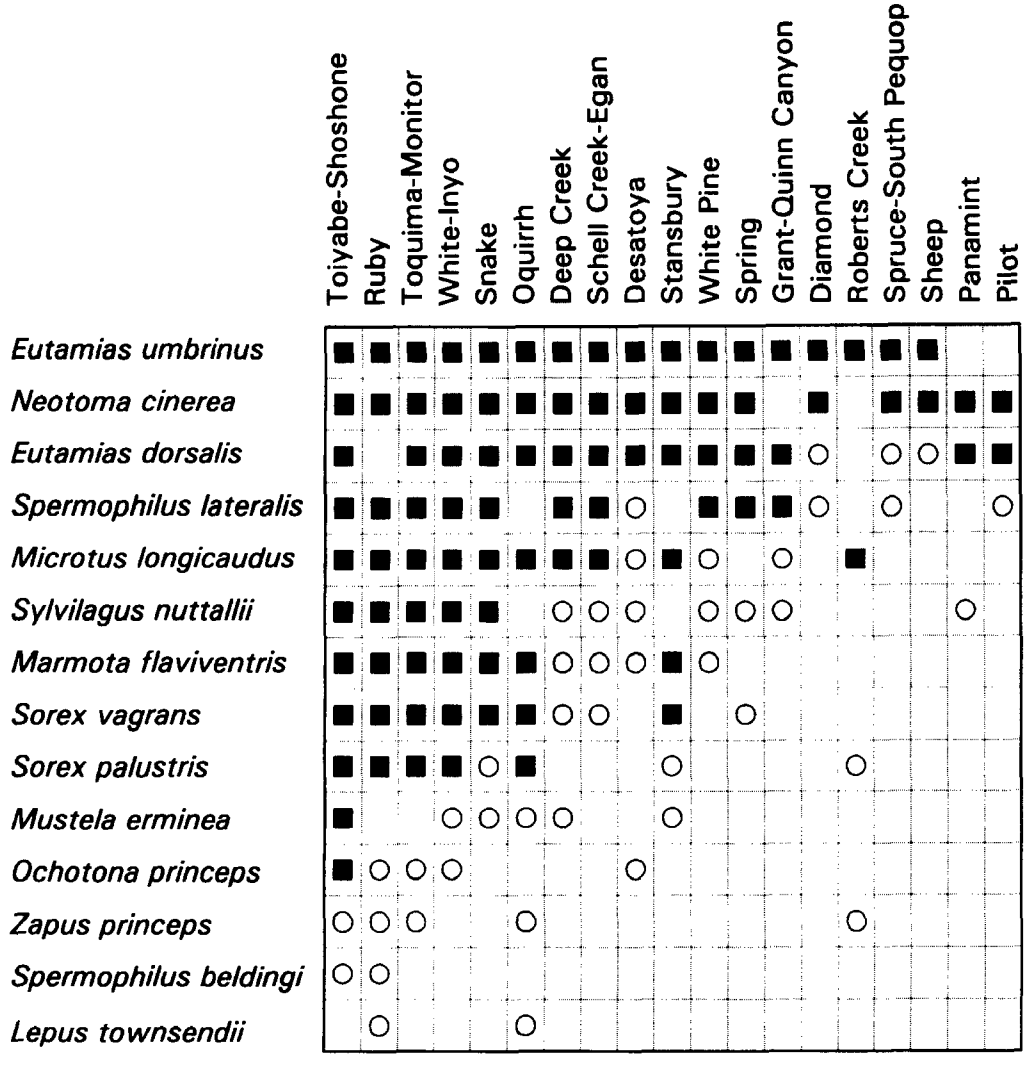

Figure 7. Extinctions of montane mammals in Great Basin mountain ranges as predicted by McDonald and Brown (1992). Open circles represent predicted extinctions.

that a variety of factors, not just differential extinction, may contribute to the distribution of boreal mammals in the Great Basin. It appears unlikely that all 14 species would respond to global warming similarly. Species differences argue strongly that the course of extinctions is not highly predictable by reference to nestedness alone.

We find some specific extinction events predicted by McDonald and Brown (1992) counterintuitive. For example, approximately 44% of all predicted extinctions are of species that failed to exhibit a significant pattern of nestedness. In addition, McDonald and Brown's (1992) global-warming scenario has habitats receding upslope 430 m. We assume this would mean high-elevation Hudsonian and Canadian habitats and their associated faunas will be eliminated before lower Transitional or Upper Sonoran habitats and their species (see Fig. 2). Thus, we might expect that, in mountain ranges where they occur

together, *Microtus longicaudus*, *Eutamias umbrinus*, and *Neotoma cinerea* would be lost before *Eutamias dorsalis*, *Marmota flaviventris*, *Sylvilagus nuttallii*, or *Spermophilus beldingi* were. Yet 15 of 18 extinctions predicted for these species would occur in the lower-elevation group (see Fig. 7). McDonald and Brown (1992) predict that *Spermophilus lateralis* will be lost from the Desatoya, Diamond, Spruce, and Pilot Ranges (all ranges north of 38° latitude) but will not be lost from the White-Inyo and Spring Ranges (both largely south of 38° latitude). Yet, *Spermophilus lateralis* exhibited geographic variation in elevation range such that southern ranges appeared to be more isolated from each other than were northern ranges (see Fig. 4). Likewise, McDonald and Brown (1992) predict that *Sylvilagus nuttallii*, which exhibited geographic variation in elevation range similar to that of *Spermophilus lateralis*, will persist in the White-Inyo Range, but will be lost from the Deep Creek, Schell Creek-Egan, Desatoya, White Pine, and Grant-Quinn Canyon Ranges.

The demonstration of a significant pattern of nestedness in species distributions has been adduced as conclusive evidence in resolving the SLOSS debate – or whether a single large or several small reserves will contain more species (Brown, 1986; Patterson and Atmar, 1986; Bolger *et al.*, 1991; Patterson, 1991; Cutler, 1992; Atmar and Patterson, 1993). In particular, Kodric-Brown and Brown (1993) argue that the pattern of nestedness exhibited by boreal mammals in the Great Basin indicates the importance of the largest ranges in any regional conservation strategy. Of course, with perfect nestedness a single large island (or reserve) will always contain more species than will several small islands of equivalent total area. Rarely, however, do natural systems exhibit perfect nestedness. In fact, the relationship between nestedness and SLOSS appears to be equivocal, as several small areas may still contain more species than would a single large area of equal total area, even when species exhibit a significantly nested pattern of occurrences (see Wright and Reeves, 1992; Beckon, 1993).

We examined the relationship between nestedness and SLOSS for the boreal mammals

Table 2. Tests of nestedness based on the Wilcoxon 2-sample rank-sum statistic (one-tailed tests)

Species	*p*-value
Eutamias umbrinus	0.014
Neotoma cinerea	0.233
Eutamias dorsalis	0.421
Spermophilus lateralis	0.009
Microtus longicaudus	0.006
Sylvilagus nuttallii	0.003
Marmota flaviventris	0.002
Sorex vagrans	0.004
Sorex palustris	0.075
Lepus townsendii	0.474
Mustela erminea	0.137
Ochotona princeps	0.015
Zapus princeps	0.190
Spermophilus beldingi	0.104

of the Great Basin as follows. We first used a computer algorithm to elucidate all combinations of size 2, 3, and 4 that can be constructed from the 19 mountain ranges. We then eliminated all subsets (combinations) with a combined area outside the range of areas observed in the original data. For the remaining subsets, we calculated total species richness based on the distribution matrices presented in McDonald and Brown (1992) and Grayson and Livingston (1993). Finally, we estimated species-area relationships for subsets of a given size for both the McDonald and Brown (1992) and Grayson and Livingston (1993) data sets.

Our analyses indicate a monotonically increasing relationship between the number of areas combined and the intercept of the corresponding species-area relationship (Fig. 8). Consequently, sets of small mountain ranges combined as pairs, triplets, or quartets contain more species, on average, than does a single range of equal total area. The species additions presented in Grayson and Livingston (1993) increase the level of nestedness within the species distribution matrix (see Grayson and Livingston, 1993; Kodric-Brown and Brown, 1993). However, even with this more nested structure, several small ranges still contain more species, on average, than do single large ranges of equivalent area (Fig. 8B). These results demonstrate that the existence of a nested pattern of species occurrences alone yields no unique recommendation regarding SLOSS.

Discussion

Island biogeographic theory has had a profound effect on conservation biology since its initial applications nearly two decades ago (i.e., Terborgh, 1974; Diamond, 1975; Wilson and Willis, 1975). Arguably, its major contribution has been to motivate much discussion among ecologists, population biologists, and conservation biologists on the factors and mechanisms that place small populations at risk of extinction (reviewed by Simberloff, 1988). The application of biogeographic theory has been less successful in producing a set of theoretical models that yield unambiguous recommendations regarding reserve design

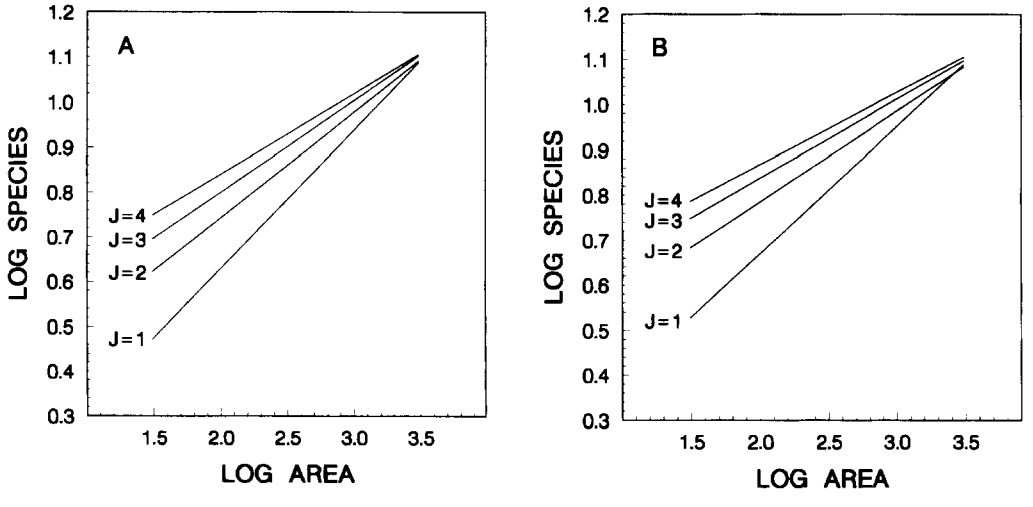

Figure 8. Species-area relationships for Great Basin boreal mammals when mountain ranges area combined into subsets of size J. Data are from (A) McDonald and Brown (1992) and from (B) Grayson and Livingston (1993).

or management practice (reviewed by Boecklen, 1991), or in producing a set of empirical models that reliably predict species numbers or minimal areas, or predict the course of extinctions in reserves owing to fragmentation and isolation (see Boecklen and Gotelli, 1984; Boecklen and Simberloff, 1986; Boecklen and Bell, 1987).

The McDonald-Brown model shares many characteristics with other biogeographic models applied to conservation biology: questionable assumptions, low predictive power, and ambiguous recommendations regarding key issues in reserve design and management practice. Insofar as the model generates discussion (or criticism) regarding the conservation of boreal mammals in the Great Basin, it can be considered a success. As a theoretical or empirical model, it has numerous shortcomings that disqualify it as a useful conservation tool. Chief among these are its untenable assumptions and inadequate data base. In particular, the model can give misleading estimates of the number of extinctions in a given area and can misidentify the most extinction-prone species in a given fauna.

McDonald and Brown (1992) offered their model as a cost-effective alternative to traditional approaches in conservation biology that emphasize detailed knowledge of the biology of targeted species. Yet, underlying assumptions necessitate that exhaustive (and probably unattainable) information on the ecology, distribution, and population structure of all species in a targeted fauna be compiled in order to make the model operational in a given application. For example, in order to validate a key assumption of the model, a conservation strategist could gather detailed information on the paleonotological record, on the habitat requirements of species, on dispersal patterns, on the distribution of suitable habitats, and on population dynamics of species, and still not be certain that deviations about a species-area relationship represent deterministic factors that will be unaffected by areal reduction or by direct and indirect effects of global warming. In addition, a detailed genetic analysis would probably be required to determine whether populations were truly isolated. For a conservation biologist already armed with this information, it is hard to imagine what additional contribution the McDonald-Brown model would make in devising a conservation strategy.

In sum, the McDonald-Brown model is not a general or reliable method for forecasting species extinctions following global warming. We must agree with Kodric-Brown and Brown (1993) that in matters of conservation strategy there is '...no substitute for a detailed knowledge of both the organisms and their habitats.'

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