

NORTH AMERICAN DESERT RODENTS: A TEST OF THE MID-DOMAIN EFFECT IN SPECIES RICHNESS

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Many biological theories have been proposed to explain latitudinal and elevational gradients of species richness, but only recently have theories been proposed that suggest that these patterns may be due solely to geographic constraints. These null models predict mid-domain peaks in species richness as a consequence of geometric patterns resulting from overlapping species ranges between 2 geographic boundaries. Desert rodents exhibit a marked mid-domain peak in species richness for boundaries defined by the latitudinal extent of North American deserts (19°N–45°N). Empirical patterns are compared with predictions of 2 null models: an analytical–stochastic model and the binomial model. Empirical species richness occurs almost entirely within 95% prediction curves of the analytical–stochastic model. Observed species richness is highly correlated with predictions of the binomial model ($r^2 = 93\%$) but does not generally occur within 95% confidence intervals, in part because empirical range-size distributions differ from predicted distributions. Other diversity theories, species–area relationships, productivity gradients, latitudinal gradients, and Rapoport’s rule are evaluated; none is consistent with empirical patterns. These results demonstrate that the mid-domain effect is a consequence of overlap of variably sized ranges within a bounded region for both ecologically defined hard boundaries and boundaries determined by the shape of the earth. The significant deviations from null-model predictions become the biological points of interest: skewed or localized (or both) pulses or depressions of species richness. Deviations in the present analysis demonstrated a localized pulse in richness caused by a local hard boundary, the Baja peninsula.

Key words: binomial null model, bounded ranges, desert rodents, mid-domain effect, RangeModel, species richness

MacArthur (1972:1) stated, “To do science is to search for repeated patterns, not simply to accumulate facts.” MacArthur is one of many ecologists who have investigated patterns of species diversity, specifically latitudinal and elevational gradients of species richness (MacArthur 1965; Rosenzweig 1995 and references therein). The latitudinal gradient, a negative relationship between latitude and richness, with a peak in richness at the equator, is a pattern that is evinced by many taxa throughout the

world. Numerous theories have been proposed to account for the gradient (Colwell and Hurtt 1994; Kaufman 1995; Lees et al. 1999; MacArthur 1965; Osman and Whitlatch 1978; Pagel et al. 1991; Pianka 1966; Rosenzweig 1992, 1995; Stevens 1989; Terborgh 1971; Willig and Lyons 1998; Wilson 1973). The less well-documented elevational gradient of species richness can have a mid-elevation peak in species richness, and several biological theories exist to explain this pattern (Colwell and Hurtt 1994; Graham 1983; Heaney 2001; Patterson et al. 1996; Rosenzweig 1992, 1995;

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Sanchez-Cordero 2001; Stevens 1992). The majority propose that the patterns result from an underlying biological process, although no single theory has widespread acceptance (Colwell and Hurtt 1994; Kaufman 1995; Rosenzweig 1992).

Recently, several independently derived models have emerged to explain these gradients based solely on geometric constraints on species ranges, without the incorporation of underlying biological mechanisms (Colwell and Hurtt 1994; Lees et al. 1999; Willig and Lyons 1998). These null models are derived from the geometric pattern that results from random range sizes and placements between the endpoints of 2 hard boundaries, a pattern termed the mid-domain effect (Colwell and Lees 2000). Colwell and Lees (2000:72) defined the mid-domain effect as "the increasing overlap of species ranges toward the centre of a shared geographic domain due to geometric boundary constraints in relation to the distribution of species' range sizes and midpoints." Bounded range models assume that all species considered in the analysis share the same hard boundaries; therefore, all species' ranges must be entirely within the bounded domain, and large ranges must be centered near the center of the domain. This results in increasing species richness toward the midpoint of the domain. An example of geographic boundaries limiting species ranges is that of terrestrial species on an island where distinct limits to the ranges are the edges of the island. Such range constraints can exist due to geographic features, such as continental boundaries, elevational boundaries, or the perimeter or depth of a body of water. Ecological range boundaries exist where species endemic to a specific ecological biome are constrained by the biotic and abiotic distribution of that ecosystem. All proposed null models—the fully stochastic and analytical-stochastic models (Colwell and Hurtt 1994), the binomial model (Willig and Lyons 1998), and the probabilistic model (Lees et al. 1999)—predict a mid-domain effect in species rich-

ness due solely to geometric constraints, although each employs distinct mathematical frameworks (Colwell and Lees 2000).

Null models suggest that underlying patterns in latitudinal and elevational gradients of species richness are the result of geographic boundaries such as coastlines and mountains (Colwell and Hurtt 1994). A diversity peak at the equator and at middle elevations was documented before the null models of mid-domain effect were proposed; therefore, additional empirical examples of unknown species-richness patterns within bounded range limits need to be examined to test the predictions of these null models. Two studies have confirmed the mid-domain effect outside the context of latitude or elevation. Pineda and Caswell (1998) examined bathymetric gradients, and Lees et al. (1999) examined gradients across the island of Madagascar.

The North American desert biome has relatively distinct northern and southern ecological boundaries (as well as east-west boundaries) that limit the ranges of desert endemics—19°N–45°N (Fig. 1; MacMahon 1985). This ecological domain allows a valuable empirical test for null models of species richness because the latitudinal patterns of species richness within the bounded region have not been documented previously and because the North American desert biome includes taxonomic groups with numerous endemic desert taxa (e.g., Heteromyidae). Herein, these desert endemics were used in an empirical examination of the mid-domain effect. Null models predict a peak in species richness near the midpoint of the geographic limits of North American deserts, although several other patterns of species richness could be encountered. For example, if taxa were responding to environmental correlates of latitude, then species richness should increase toward lower latitudes, a pattern that has been shown for rodents in the New World (Kaufman 1995). Similarly, a uniform pattern could be encountered where species richness was uni-

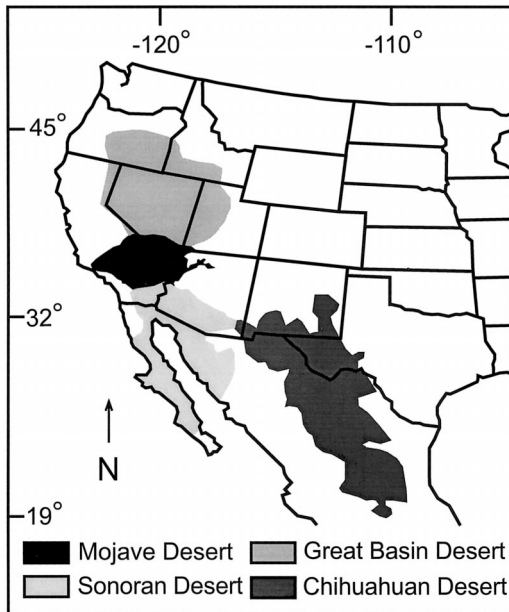


FIG. 1.—The North American desert biome including the Great Basin, Mojave, Sonoran, and Chihuahuan deserts. The biome extends from 45°N to 19°N (modified from MacMahon 1985).

formly distributed across the desert latitudinal gradient.

MATERIALS AND METHODS

An a priori delineation of North American deserts between 19°N and 45°N was based on a combination of 2 maps by MacMahon (1985). One map depicts the classical ranges of North American deserts based on climate and plant distributions, and the other was based on a combination of climate and on distributions of flora and fauna. The most expansive delineation based on these 2 maps was used in the present analysis (Fig. 1).

Thirty-seven rodent species endemic to North American deserts (Appendix I) were used in an empirical examination of the latitudinal trends of species richness. Desert endemism was defined as those species with the majority (>90%) of their range occurring within the a priori desert delineation. The list of species and their ranges was compiled by Anderson (1972), Baker (1956), Davis and Schmidly (1994), Durrant (1952), Findley et al. (1975), Hall (1981), Hoffmeister (1986), Ingles (1965), and Jameson and Peeters (1988). Taxonomy of Wilson and Reeder

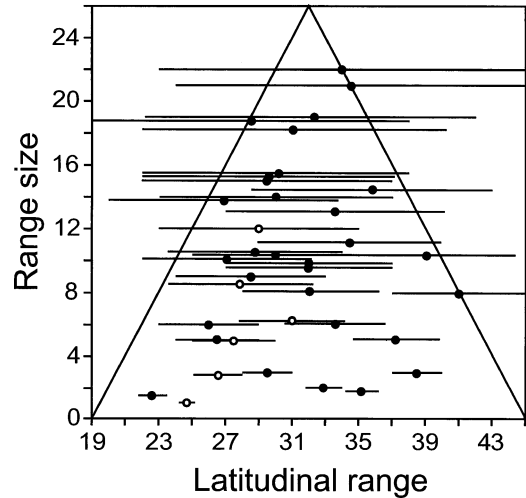


FIG. 2.—A graphical representation of range size of each desert rodent compared with range midpoint and latitudinal range in the North American desert biome. Solid circles represent continental species and open circles, Baja peninsular endemics. Horizontal lines are extent of latitudinal range for each species, and triangle represents limits of possible range midpoint for each range size.

(1993) was used to recognize species status. The latitudinal extent of the range of each species was calculated, producing 2 characteristics—the latitudinal midpoint and latitudinal range (Fig. 2). Species-richness curves were then calculated by importing the empirical range sizes and midpoints into the computer program RangeModel (RangeModel: a Monte Carlo simulation tool for assessing geometric constraints on species richness; <http://viceroy.eeb.uconn.edu/RangeModel>).

Two groupings of the desert rodent endemics were evaluated: all endemics within the continental area of the North American deserts ($n = 37$) and continental endemics excluding Baja endemics ($n = 31$). The 6 Baja endemics were excluded from the 2nd grouping to remove possible peninsular effects, which produce decreasing species richness toward the terminus of the peninsula (Brown and Lomolino 1998). Taylor and Regal (1978) detected a peninsular effect in Baja for various vertebrate groups including mammals and heteromyid rodents. Lawlor (1983) refuted these patterns for mammals in general and bats in particular but found some evidence that

heteromyid rodents may show a peninsular effect.

Empirical patterns of species richness were compared with predictions of 2 null models—Colwell and Hurtt's (1994) analytical–stochastic model and Willig and Lyons' (1998) binomial model. Colwell and Hurtt (1994) created a group of null models with different parameters; some are fully stochastic, whereas others are capable of simulations using empirical data sets (<http://viceroy.eeb.uconn.edu/RangeModel>). The 2 fully stochastic models, Models 2 and 3 of Colwell and Hurtt (1994), which correspond to the bivariate uniform range model and the uniform random range midpoint and range-size models of the RangeModel program, are incapable of using empirical data. These models assume different underlying distributions of range sizes and placements of range midpoints; thus, all variables except species number are predetermined. Model 2, the bivariate uniform model, is equivalent mathematically to the binomial model and MacArthur's two-hit broken stick model (Colwell and Lees 2000). Therefore, the ensuing discussion on the bivariate uniform model will be addressed in accordance with the binomial model. The uniform random models, 2 variations on Model 3, place 1st variable (either range size or range midpoint) within the domain boundaries according to a uniform probability distribution and then randomly draw values for the 2nd variable from geometrically feasible values within the bounded domain. These Model 3 variations are not used in the current analysis because empirical values cannot be incorporated.

Unlike Models 2 and 3, the 2 forms of Colwell's analytical–stochastic model use empirical data from a system of interest, thus making the results “conditional” on the imported variables. The analytical–stochastic models sample with replacement from imported empirical (or hypothetical) data for 1 variable and then randomize the placement of the other according to a modified uniform distribution for feasible values within 2 boundary endpoints to produce species-richness curves. The 1st analytical–stochastic model uses empirical range sizes and creates randomized placements of midpoints between the boundaries, whereas the 2nd form of the model uses the empirical midpoint locations and creates randomized range sizes constrained by the domain limits. These were the simulation models used in the current analysis because ran-

domization using empirical data is better able to assess whether under random conditions, given either known range sizes or known range midpoints, a mid-domain effect occurs.

Empirical range sizes and midpoints of desert rodents were imported into RangeModel and were used to generate 600 simulations for each species group using random placement of empirical range sizes and again of empirical midpoints. Simulation results were then used to create 95% simulation prediction curves. The empirical species-richness data were then compared with the 95% simulation prediction curves to assess the accuracy of the null-model predictions. Random simulations were limited to 600 because each successive set of 200 simulations leads to minor changes in the 95% prediction curves.

The binomial null model is based on the joint probabilities of choosing 2 random points on a number line between 0 and 1, such that the range spans a sampling point, p , on the unit domain (Willig and Lyons 1998). The probability of a randomly chosen range spanning the sampling point is $2pq$, where $q = 1 - p$. The resulting species-richness curve has a mid-domain effect with the highest species richness at $p = 0.5$, with the predicted species richness being half the total number of species in the analysis. This model allows the calculation of standard deviations and 95% confidence intervals using a corrected version of the formula presented by Willig and Lyons (1998, pers. comm.) as follows: $\text{var}(2pqS) = \{2(S - 1)/S^3\}\{(3 - 2S)(1 - 2pq)^2 + 2(S - 2)(p^3 + q^3) + (1 - 2pq)\}$ from Nei (1975) and Nei and Roychoudhury (1974), where S is the number of range termini or twice the number of species in the analysis. Two standard deviations multiplied by species richness then give values to add and subtract from the predicted values to delineate approximate 95% confidence intervals of the binomial model predictions. Following Willig and Lyons (1998), I also tested for a linear association between richness and $2pq$. The empirical values of species richness at each latitudinal degree of the desert domain were regressed against $2pq$, and r^2 and 95% prediction curves were calculated to show how well the empirical data conform to the null model.

The binomial null model predicts not only a mid-domain effect but also an implicit distribution of range sizes based on the joint probability density function of pairs of uniformly distributed

variables that delimit species' latitudinal ranges. This implicit frequency distribution of range sizes is a decreasing function from small to large ranges, thus implying that empirical species-richness patterns that fit the binomial null model should consist of many small-ranged species, few mid-ranged species, and very few large-ranged species. This was tested by comparing the cumulative number of range sizes produced by the null model with the cumulative distribution of range sizes in the empirical data using a Kolmogorov–Smirnov goodness-of-fit test (MINITAB 1996). This requirement of a particular distribution of range sizes is shared by MacArthur's two-hit broken stick model and the bivariate uniform random model (Colwell and Lees 2000) but not with the analytical–stochastic models. When the empirical distribution of range sizes differs from the underlying binomial model distribution (i.e., more larger-ranged species), the empirical species-richness curve will diverge from the predicted curve.

Species richness frequently is correlated positively with area (Rosenzweig 1995). The North American desert biome does not have equal area throughout its latitudinal extent. An estimate of area per latitudinal degree was calculated by digitizing the desert boundaries into a geographic information system using the latest version of ArcInfo 8.1 (ESRI 2001). The area estimates were based on the Albers equal-area conic projections using 24°N and 41°N as the standard parallels that support a north–south extent of up to 30–35° (25° extent for present analysis). The effect of area on the species-richness pattern was assessed using regression analyses (MINITAB 1996). Species richness was regressed against 2pq alone, 2pq with area, and area alone. Experimental lack-of-fit tests (MINITAB 1996) produced no evidence for curvilinearity ($P > 0.10$) in regressions including 2pq with or without area.

RESULTS

Both species-richness curves showed a strong mid-domain effect (Fig. 3). The concentration of small-ranged species endemic to the Baja Peninsula ($n = 6$) created a slight skew in the peak of species richness at 28°N but otherwise was indistinguishable from the purely continental pattern. The continental species-richness gradient also

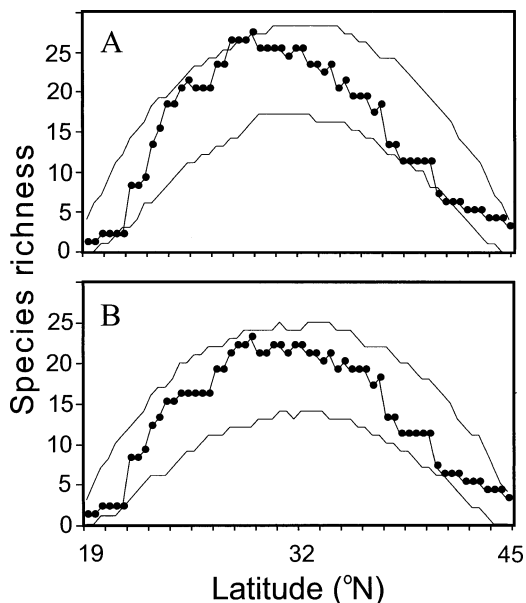


FIG. 3.—Empirical species-richness curves for North American desert rodent endemics plotted with 95% simulation prediction curves from RangeModel (<http://viceroy.eeb.uconn.edu/RangeModel>) based on empirical range sizes. Curves for A) all species ($n = 37$) and B) excluding Baja peninsular endemics ($n = 31$).

had a marked mid-domain peak, with the highest richness close to the center of the latitudinal domain at about 32°.

Six hundred RangeModel simulations using the empirical range sizes for each species grouping and randomized placement of midpoints resulted in a mid-domain peak in species richness. A comparison of the empirical data with the 95% simulation prediction curves showed that the majority of empirical points (116/120) occurred within the predicted range of the analytical–stochastic null model (Fig. 3). The 600 RangeModel simulations with empirical range midpoints for each species grouping and randomized placement of range sizes also resulted in a mid-domain peaks in species richness. Again, the majority of empirical points (119/120) occurred within the 95% simulation prediction curves of the analytical–stochastic null model (Fig. 4).

Regressions of species richness per lati-

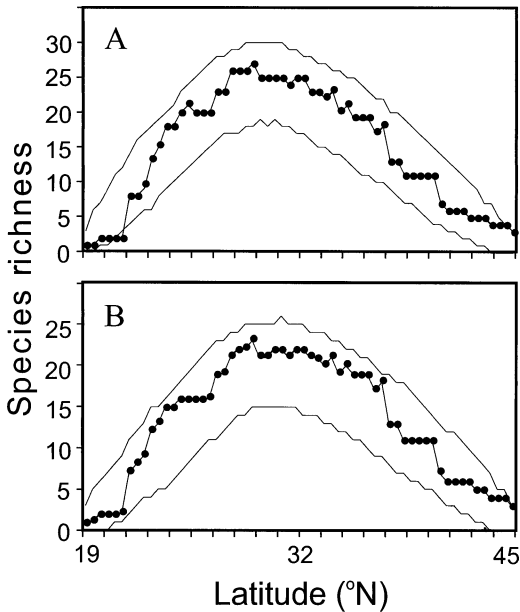


FIG. 4.—Empirical species-richness curves for North American desert rodent endemics plotted with 95% simulation prediction curves from RangeModel (<http://viceroy.eeb.uconn.edu/Range-Model>) based on empirical range midpoints. Curves for A) all species ($n = 37$) and B) excluding Baja peninsular endemics ($n = 31$).

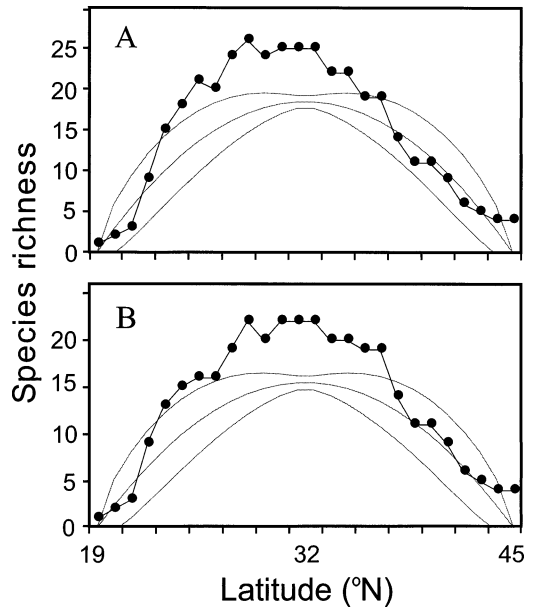


FIG. 5.—Empirical species-richness curves for North American desert rodent endemics plotted with 95% confidence interval from the binomial null model (Willig and Lyons 1998). Curves for A) all species ($n = 37$) and B) excluding Baja peninsular endemics ($n = 31$).

tudinal degree predicted by the binomial null model ($2pq$) against empirical values resulted in high r^2 values for both species groupings: all desert rodent endemics, $r^2 = 0.88$; species excluding Baja peninsular endemics, $r^2 = 0.93$. Even when all rodent species inhabiting the North American deserts were included in the analyses ($n = 53$, including 22 non-endemics), a strong mid-domain effect still was observed ($r^2 = 0.90$). Regression analysis demonstrated high correlation between the observed and the predicted species-richness values because all empirical data occurred within the 95% regression prediction curves (curves based solely on regression analysis). The empirical distributions did not coincide, however, with the specific predicted values of species richness because 60% of the empirical data occurred outside the 95% confidence intervals based on the calculations

of variance, which include the restrictions of underlying range distribution (Fig. 5). Observed species richness was higher than predicted by the binomial null model. This was partially a result of the deviation of the empirical range-size distribution from that predicted by the binomial model. Although not significantly different in cumulative deviations (all species: $P > 0.2$; without Baja peninsular endemics: $P > 0.2$), the desert species had fewer small ranges and more intermediate and large range sizes than predicted (Fig. 6). The small increase in numbers of species with larger-range sizes leads to the peak in species richness deviating from the predicted value of $n/2$.

The area estimates for each degree of latitude were not equal for all the latitudinal bands within North American deserts (Fig. 7A) or for the distribution excluding Baja (Fig. 7B). The greatest area occurred where the Sonoran and Chihuahuan deserts overlapped between 29°N and 33°N , with a low-

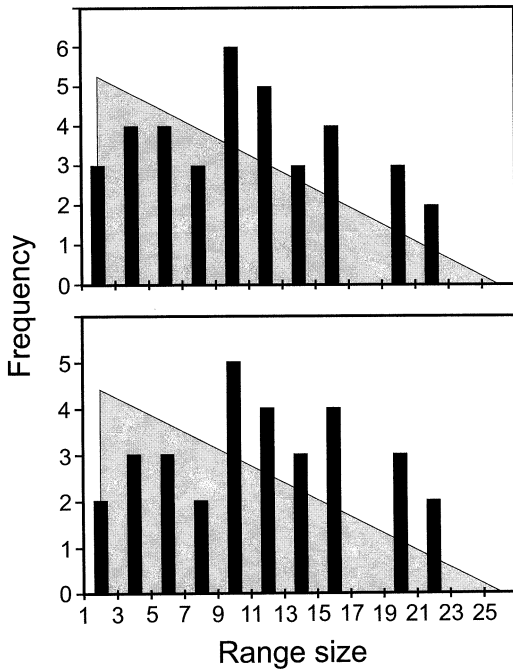


FIG. 6.—Probability density functions for range sizes of the binomial model compared with empirical distribution of range size for North American desert rodents. Probability density function (gray) and empirical range sizes (black) for (upper) all rodent endemics and (lower) excluding Baja peninsular endemics.

er peak in area within the Great Basin Desert (39°N–42°N). Plots of latitude versus area had 2 peaks, whereas curves of species richness showed a single peak (Fig. 7). The regressions using 2pq alone to predict species richness had r^2 values identical to values of regressions including both 2pq and area (all species, 0.88 and 0.88; and species excluding Baja endemics, 0.93 and 0.93). The regression using area alone to predict species richness resulted in much lower r^2 values (all species, 0.47; and species excluding Baja endemics, 0.37).

DISCUSSION

Evaluation of null models supported the conclusion that the pattern of species richness for North American desert rodent endemics was a consequence of geometric

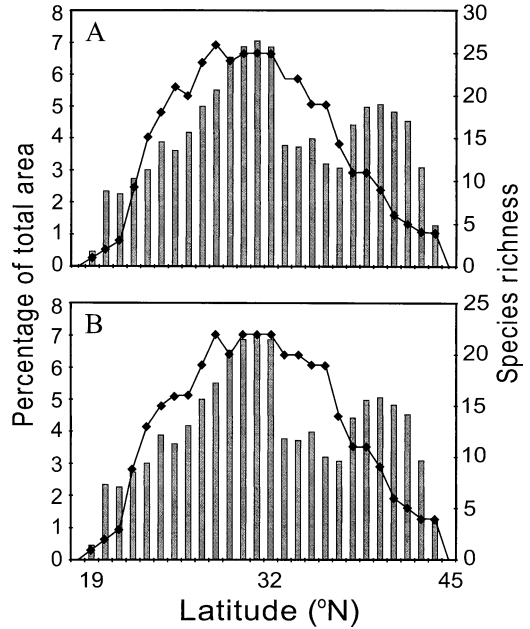


FIG. 7.—Comparison between species-richness curves of desert rodents and area associated with each degree of latitude for geographical distribution of North American deserts. Area and richness of species for A) all deserts and B) deserts excluding Baja peninsula.

constraints within a bounded environmental domain. A comparison of the predictions and deviations based on the 2 null models tested illustrated the differences between and strengths of the 2 models.

RangeModel null model.—Empirical patterns of species richness agree closely with predictions of analytical–stochastic models constrained by empirical range sizes or empirical range midpoints, with only 5 out of 240 data points occurring outside the 95% prediction limits (Figs. 3 and 4). All 5 outliers were associated with the curve that included the Baja peninsular endemics. The range midpoint simulations produced slightly lower richness than predicted toward the extreme limits of the desert latitudinal extent, and the range-size simulations showed slightly higher than expected richness at 28°N. The peninsular effect could bias data sets that included peninsular species by creating an exaggerated decrease

in species richness along the extent of the peninsula. Therefore, species-richness curves including peninsular endemics may deviate from null-model predictions at the southern extent of the peninsula. This was not the case in empirical analysis. The deviations of lower richness were outside the extent of the peninsula.

The influence of peninsular endemics was to shift the peak in richness toward the south because the Baja endemics were all clustered within a small extent of the desert distribution. This is the likely reason for a slight deviation of higher than expected richness at 28°N and slightly lower than expected toward the extremes of the distribution. In a comparison of the 2 simulation sets, this reasoning becomes apparent because the simulations using observed range sizes with random midpoint placement did not predict a cluster of species but a more even dispersion within the desert domain, whereas the simulations using empirical midpoint distributions, with the cluster of peninsular midpoints, predicted higher richness slightly south of the center. The lack of a peninsular effect for the desert endemics confirms the suspicions of Lawlor (1983) that the suggestion there is a peninsular effect in rodents is unfounded and that only weak patterns exist for heteromyid rodents. A more accurate description of Baja peninsula is that of a local hard boundary at the southern end of the peninsula. In such cases, a smaller, localized mid-domain peak would be expected toward the center of the local domain, which may create pulses of higher richness in a broader diversity pattern. The local hard boundary at the southern end of Baja leads to more Baja endemics overlapping toward the center of Baja, thus creating a localized pulse in richness, which led to the deviations from predictions across the entire desert domain.

In this analysis, a priori knowledge of the peninsular effect allowed explicit evaluation of the factor. Analyses of patterns of species richness in less intensely investigated regions might identify such unusual

patterns as significant deviations from predictions of the null model. Recognition of local hard boundaries within broader domains may clarify localized pulses in richness that appear in the analysis as deviations. A comparison of the simulations separately constrained by observed range sizes and observed range midpoints enables a more comprehensive evaluation of possible causes of divergent patterns than would use of models not constrained in such a manner (i.e., binomial model).

Binomial null model.—The binomial model serves as a null model for the mid-domain effect, as does the analytical–stochastic model of Colwell and Hurtt (1994), but the binomial has more specific predictions about the range-size distribution. The generalized mid-domain effect predicts the shape of the richness gradient between 2 distinct domain boundaries. It predicts peak richness at the center of the domain, with species richness decreasing toward the limits of the domain, but it does not assume any specific distribution of range sizes or any specific species-richness values. All distributions of variable range sizes can produce mid-domain effects but of different magnitude of curvature. A distribution of variable small range sizes placed randomly, but in a uniform distribution across the domain, will create a mid-domain peak with a flat and low curvature. A distribution of variable large and intermediate range sizes will produce a steep curve in species richness, with a distinct peak. Colwell's models allow the testing for these different distributions of range sizes through simple dummy data sets imported into his RangeModel program.

Using confidence intervals from the variance calculation of $2pq$ (Willig and Lyons 1998) tests not only for a mid-domain effect but also for a specific number of species at that peak and elsewhere ($R_{\text{predicted}} = 2pqR_{\text{total}}$; R = species richness; i.e., peak species richness = $R_{\text{total}}/2$). The strict form of the model assumes a triangular distribution of range sizes (Fig. 6), such that the

majority of range sizes are small, few are intermediate, and very few are large. Such a distribution of range sizes between the 2 range constraints creates a mid-domain species-richness curve of a standardized low curvature, constraining the peak to be half the total species richness. The more large and intermediate range sizes in the distribution, the greater the overlap of ranges toward the center of the domain, leading to a higher peak and a more pronounced curvature to the species-richness pattern. This relationship between range sizes and curve shape is demonstrated clearly by both Colwell and Hurtt (1994) and Colwell and Lees (2000).

Therefore, empirical species-richness patterns may be completely congruent with the null-model predictions based on the geometric effects of bounded ranges but may not fall within the confidence intervals of the binomial model if the empirical distribution of range sizes includes more intermediate or large-sized ranges than the underlying distribution of the binomial model. This was the case with the desert rodent species-richness pattern (as well as the species-richness patterns for bats of Willig and Lyons 1998) because all indications supported the mid-domain effect, whereas the 95% confidence intervals were consistently lower than the empirical curves. The distribution of range sizes for desert rodent endemics included more (but not significantly more) intermediate to large range sizes than predicted by the binomial distribution, resulting in more than half the species being present at mid-domain. By overlaying the 95% simulation prediction curves of the RangeModel and the predicted curve and associated 95% confidence curves of the binomial model, it is apparent that the binomial species-richness predictions are low because the binomial prediction curve corresponds closely with the lower 95% simulation prediction curve of RangeModel. Additionally, half the points of the lower-binomial 95% confidence

curve were outside RangeModel predictions.

According to range-size theory, many distributions of range sizes are strongly right-skewed and generally follow a log-normal distribution, although few empirical cases have been tested for fit to a log-normal distribution. Of those that have, many deviate significantly from this distribution (Gaston 1996). The binomial model assumes a triangular distribution of range sizes—a linearly decreasing function of sizes—although this is not a frequently cited distribution (Gaston 1996). Because the range-size distribution has received relatively little investigation and because the universality of a single range-size distribution among variously sized groups of taxa has yet to be shown, the assumption of the triangular range-size distribution of the binomial model cannot yet be verified.

Biological theories.—Several biological theories have been proposed that also could produce peaks in species richness within a range domain, namely the species–area relationship, latitudinal gradients, productivity gradients, Rapoport's rule, habitat complexity, and inadequate sampling. As stated earlier, the species–area relationship is a pattern of increasing species richness with increasing area (Lees et al. 1999; Rosenzweig 1992, 1995; Willig and Lyons 1998). This pattern could produce a mid-domain peak in species richness if the greatest area were found toward the center of the distribution and tapers to the extremes. In North American deserts, the area effect was small and insignificant. Therefore, the species–area relationship or longitude (Bokma and Monkkonen 2000; Bokma et al. 2001) cannot be the primary underlying cause of the desert rodent species-richness pattern.

With respect to the latitudinal species-richness gradient, the desert species-richness pattern clearly does not follow a trend toward increasing richness with decreasing latitude because the lowest species richness was at the southernmost latitudes. Kaufman (1995) examined the latitudinal gradients of

mammals by taxonomic orders, and the trend for all mammals was a strong peak in species richness at the equator. The pattern for rodents was an irregular hump-shaped curve with a general trend toward higher species richness near the equator but with several peaks and valleys between 45°N and 45°S (Fig. 5; Kaufman 1995). Between 19°N and 45°N, her curve for rodents is concave, with the lowest local diversity at about 30°. This is opposite of the pattern demonstrated in this study for the desert rodents at these latitudes, further indicating that the desert pattern is divergent from the overall rodent diversity gradient.

Productivity gradients frequently show hump-shaped relationships with species richness, with peaks in richness at intermediate productivity levels along a gradient from low to high productivity (Mittelbach et al. 2001; Rosenzweig 1992, 1995; Waide et al. 1999), although other studies show trends of increasing or decreasing species diversity with increasing productivity (Brown 1975; Mittelbach et al. 2001; Rosenzweig 1992, 1995; Waide et al. 1999). For deserts, productivity is relatively low, ranging from 0 to 600 g m⁻² year⁻¹ but has been shown to be highly variable spatially and temporally (Brown 1975; Waide et al. 1999). According to Waide et al. (1999), the relationship in arid ecosystems has not been investigated specifically, but they did note 2 general trends of particular value. They found that, for large-scale patterns among deserts across the world, those deserts with low to zero productivity have low species richness for various groups of taxa, whereas those with relatively high productivity have high species richness. However, at smaller scales, i.e., deserts within the same region, they did not find increased species richness with productivity (Fig. 8; Waide et al. 1999). In North America for instance, the Mojave Desert has the lowest productivity but high species richness, whereas the Chihuahuan Desert has the highest productivity estimates but lower richness. If productivity were the primary underlying cause of the

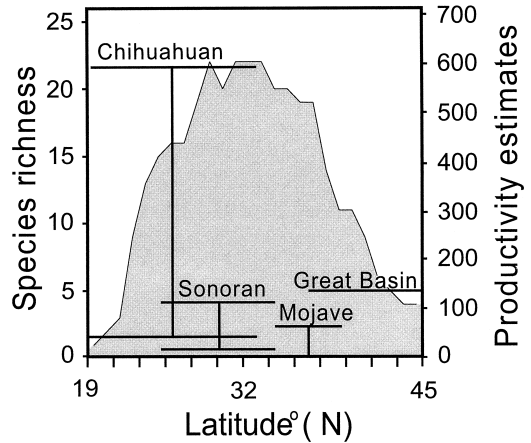


FIG. 8.—Range of estimates of primary productivity (g m⁻² year⁻¹) for each desert within the North American desert ecosystem compared with species richness of desert rodent endemics (data from Waide et al. 1999 and references therein). Extent of each desert shown with horizontal bars. Range of productivity estimates shown with vertical bars (with only a single estimate for the Great Basin).

mid-domain peak in species richness in the North American deserts, then the prediction would be that either there is highest richness at intermediate productivity levels or there is highest richness at high productivity levels. Neither of these cases is supported with the present productivity estimates available on the regional scale. Productivity–diversity trends appear to be strongly scale dependent (Mittelbach et al. 2001; Scheiner et al. 2000; Waide et al. 1999), and therefore productivity–diversity patterns at local scales may show divergent patterns from the regional scale studied here.

Rapoport's rule, the tendency for mean sizes of species ranges to decrease toward the equator and toward mid-elevations, predicts that as species richness increases range sizes decrease (Stevens 1989, 1992). Recently, Rapoport's rule has caused a flurry of investigative effort applied to understanding species-richness gradients, including a test of the universality of the pattern (Lyons and Willig 1997) and theoretical

modeling (Colwell and Hurtt 1994; Taylor and Gaines 1999). These studies suggest that the universality and robustness of Rapoport's rule are questionable. Similarly, Rapoport's rule was not corroborated in the present analysis because small range sizes were not clustered toward the area of highest species richness (Fig. 2).

Inadequate sampling has been shown to affect richness trends (Colwell and Hurtt 1994; Lees et al. 1999), although this most often is the case for tropical regions where species are not well documented and ranges may be far from accurate. In this case, the majority of species used in the study have been known since the beginning of the 1900s, and most have well-known ranges (Hall 1981). Thus, none of inadequate sampling, area, latitudinal species gradient, productivity, and Rapoport's rule appears to explain the unimodal pattern of species richness observed for desert rodents.

Some authors assert that latitudinal, elevational, and even desert mid-domain peaks in species richness are the result of increased habitat complexity (MacArthur 1964; Pianka 1966). If habitat complexity is the result of higher diversity of plants and plant forms, and plant diversity is also highest at mid-domain, that pattern may just be a coincident mid-domain species-richness peak for plant endemics bounded by the same geographic or ecological boundaries as the animal kingdom. Thus, an interesting prediction of the mid-domain effect is that patterns of habitat complexity or plant species richness also would reflect geometric constraints. Of course, habitat complexity also may involve relationships with climatic variables and be intertwined with productivity hypotheses. To understand the explanatory power of these hypotheses, detailed empirical analyses are needed.

It has been suggested that the mid-domain null model limits analyses to endemics within the boundaries of specified limits and has biased the results by not including non-endemics, generalists of the same taxa also present within the same region (R.

Holt, and J. Brown, pers. comm.). Some critics argue that the mid-domain effect may be a result of this culling of the data set and predict divergent patterns of species richness in analyses that include all species inhabiting the region. But when all rodent species inhabiting the North American deserts were included in the analyses ($n = 53$, including 22 non-endemics), a strong mid-domain effect still was observed ($r^2 = 0.90$). Because non-endemic species tend to be generalists, they have larger ranges that encompass more of the extent of the domain, which leads to a similarly shaped, but elevated, species richness curve with increased richness throughout the curve but particularly pronounced toward the center of the domain. Thus, adding non-endemics to the analysis does not lead to divergent patterns from the predictions of the null models.

The mid-domain effect.—The mid-domain effect is an unavoidable consequence of bounded ranges of variable sizes. This is true for bounded latitudinal ranges as well as for longitudinal or 3-dimensional ranges. As in any null model, it is the basis with which novel species-richness patterns should be compared. Significant deviations from the null model could then be biologically interesting patterns and indicate the need for analysis of such factors as distribution of abiotic resources, competition, evolutionary history, ecological history, and biome shifts.

Empirical diversity patterns that conform to predictions of the mid-domain effect based on randomizations of the empirical range sizes and midpoints do not signify that the diversity pattern is random. The empirical pattern consists of a distribution of species with different-sized overlapping ranges within limited boundaries that result in the mid-domain peak in species richness. Any random grouping of species with variably sized ranges within boundaries will show a mid-domain peak. The biological requirements and evolutionary history of each species have determined its range size

and location within the bounded range of the North American deserts. The partitioning of the desert domain by each species and reasons for individual range distributions are biologically interesting on a finer community scale. Osman and Whitlatch (1978:52) addressed this general issue, that diversity patterns "can exist regardless of any assumptions concerning the importance of competition, predation, species packing, niche characteristics, species ability to adapt, etc. Certainly, processes such as competition and predation may be important in determining the co-occurrence of particular suites of species. . . , but a diversity pattern could have resulted independent of these." Therefore, in the scope of the mid-domain effect, the diversity pattern may be a result of geometric boundaries, but species diversity in patches of the domain (alpha diversity) may be controlled by very different phenomena that are predominately biological.

RESUMEN

Se han propuesto numerosas teorías para explicar el gradiente latitudinal y altitudinal de la riqueza de especies. Teorías recientes sugieren que estos patrones pueden deberse únicamente a limitaciones geográficas. Estos modelos nulos predicen picos de dominio medio en la riqueza de especies, como consecuencia de los patrones geométricos resultantes del solapamiento en el rango de las especies entre dos límites geográficas. Los roedores de los desiertos exhiben un pico de dominio medio en riqueza de especies en los límites definidos por la extensión latitudinal de los desiertos norteamericanos (19°N a 45°N). Los patrones empíricos se comparan con las predicciones de 2 modelos nulos: un modelo analítico-estocástico y el modelo binomial. La mayoría de la riqueza de especies empírica se observa dentro del 95% de las curvas de predicción del modelo analítico-estocástico. La riqueza de especies observada está altamente correlacionada con las predicciones del modelo binomial ($r^2 = 93\%$) pero ge-

neralmente no está incluida en los intervalos de confianza de 95%; esto se debe, en parte, a que el tamaño del rango de distribución empírica es diferente al de las distribuciones predichas. Otras teorías de diversidad, relaciones especies-área, gradientes de productividad, gradientes latitudinales y Regla de Rapoport, son evaluadas; ninguna de estas es consistente con los patrones empíricos. Estos resultados demuestran que el efecto de dominio medio es una consecuencia del solapamiento de rangos de tamaño variable en un region restringida por fuertes límites definidos ecológicamente así como límites definidos por la topografía de la tierra. Las desviaciones significativas de las predicciones del modelo nulo son los puntos de interés biológico: pulsos sesgados y/o localizados o disminución de la riqueza de especies. Las desviaciones en el presente análisis demostraron un pulso localizado en riqueza causado por un fuerte límite local, la Península de Baja California.

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LITERATURE CITED

- ANDERSON, S. 1972. Mammals of Chihuahua: taxonomy and distribution. *Bulletin of the American Museum of Natural History* 148:151-410.
BAKER, R. H. 1956. Mammals of Coahuila, México.

- University of Kansas Publications, Museum of Natural History 9:125–335.
- BOKMA, F., J. BOKMA, AND M. MONKKONEN. 2001. Random processes and geographic species richness patterns: why so few species in the north? *Ecography* 24:43–49.
- BOKMA, F., AND M. MONKKONEN. 2000. The mid-domain effect and the longitudinal dimension of continents. *Trends in Ecology and Evolution* 15:288–289.
- BROWN, J. H. 1975. Geographical ecology of desert rodents. Pp. 315–341 in *Ecology and evolution of communities* (M. L. Cody and J. M. Diamond, eds.). Harvard University Press, Cambridge, Massachusetts.
- BROWN, J. H., AND M. V. LOMOLINO. 1998. *Biogeography*. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- COLWELL, R. K., AND G. C. HURTT. 1994. Nonbiological gradients in species richness and a spurious rapoport effect. *American Naturalist* 144:570–595.
- COLWELL, R. K., AND D. C. LEES. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15:70–76.
- DAVIS, W. B., AND D. J. SCHMIDLY. 1994. *The mammals of Texas*. Texas Parks and Wildlife Press, Austin.
- DURRANT, S. D. 1952. *The mammals of Utah: taxonomy and distribution*. University of Kansas Publications, Museum of Natural History 6:1–549.
- ESRI: ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE. 2001. ArcInfo Version 8.1. Redlands, California.
- FINDLEY, J. S., A. H. HARRIS, D. E. WILSON, AND C. JONES. 1975. *Mammals of New Mexico*. University of New Mexico Press, Albuquerque.
- GASTON, K. J. 1996. Species-range size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution* 11:197–201.
- GRAHAM, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64:559–571.
- HALL, E. R. 1981. *The mammals of North America*. 2nd ed. John Wiley & Sons, Inc., New York 1:1–600 + 90, 2:601–1181 + 90.
- HEANEY, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecology and Biogeography* 10:15–39.
- HOFFMEISTER, D. F. 1986. *Mammals of Arizona*. University of Arizona Press and the Arizona Game and Fish Department, Phoenix.
- INGLES, L. G. 1965. *Mammals of the Pacific States: California, Oregon and Washington*. Stanford University Press, Stanford, California.
- JAMESON, E. W., JR., AND H. J. PEETERS. 1988. *California mammals*. University of California Press, Berkeley.
- KAUFMAN, D. M. 1995. Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy* 76:322–334.
- LAWLOR, T. E. 1983. The peninsular effect on mammalian species diversity in Baja California. *American Naturalist* 121:432–439.
- LEES, D. C., C. KREMEN, AND L. ANDRIAMAMPANINA. 1999. A null model for species richness gradients: bounded range overlap of butterflies and other rain-forest endemics in Madagascar. *Biological Journal of the Linnean Society* 67:529–584.
- LYONS, S. K., AND M. R. WILLIG. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos* 79:568–580.
- MACARTHUR, R. H. 1964. Environmental factors affecting bird species diversity. *American Naturalist* 98:387–398.
- MACARTHUR, R. H. 1965. Patterns of species diversity. *Biological Review* 40:510–533.
- MACARTHUR, R. H. 1972. *Geographical ecology*. Princeton University Press, Princeton, New Jersey.
- MACMAHON, J. A. 1985. *Deserts*. Chanticleer Press, New York.
- MINITAB, INC. 1996. *MINITAB Reference Manual*. Release 11. Minitab Inc., State College, Pennsylvania.
- MITTELBACH, G. G., ET AL. 2001. What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396.
- NEI, M. 1975. *Molecular population genetics and evolution*. North-Holland Publishing Co., Amsterdam, The Netherlands.
- NEI, M., AND A. K. ROYCHOUDHURY. 1974. Sampling variances of heterozygosity and genetic distance. *Genetics* 76:379–390.
- OSMAN, R. W., AND R. B. WHITLATCH. 1978. Patterns of species diversity: fact or artifact? *Paleobiology* 4: 41–54.
- PAGEL, M. D., R. M. MAY, AND A. R. COLLIE. 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. *American Naturalist* 137:791–815.
- PATTERSON, B. D., V. PACHECO, AND S. SOLARI. 1996. Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology (London)* 240:637–658.
- PIANKA, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist* 100:33–46.
- PINEDA, J., AND H. CASWELL. 1998. Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. *Deep-Sea Research II* 45:83–101.
- ROSENZWEIG, M. L. 1992. Species diversity gradients: we know more and less than we thought. *Journal of Mammalogy* 73:715–730.
- ROSENZWEIG, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, Massachusetts.
- SANCHEZ-CORDERO, V. 2001. Elevation gradients of diversity for rodents and bats in Oaxaca, Mexico. *Global Ecology and Biogeography* 10:63–76.
- SCHEINER, S. M., S. B. COX, M. WILLIG, G. G. MITTELBACH, C. OSENBURG, AND M. KASPARI. 2000. Species richness, species-area curves and Simpson's paradox. *Evolutionary Ecology Research* 2:791–802.
- STEVENS, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist* 133:240–256.

- STEVENS, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *American Naturalist* 140:893–911.
- TAYLOR, P. H., AND S. D. GAINES. 1999. Can Rapoport's rule be rescued? Modeling causes of the latitudinal gradient in species richness. *Ecology* 80:2474–2482.
- TAYLOR, R. L., AND P. J. REGAL. 1978. The peninsular effect on species diversity and the biogeography of Baja California. *American Naturalist* 112:583–593.
- TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23–40.
- WAIDE, R. B., ET AL. 1999. The relationship between productivity and species richness. *Annual Review of Ecology and Systematics* 30:257–300.
- WILLIG, M. R., AND S. K. LYONS. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. *Oikos* 81:93–98.
- WILSON, D. E., AND D. M. REEDER. 1993. *Mammal species of the world: a taxonomic and geographic reference*. 2nd ed. Smithsonian Institution Press, Washington, D.C.
- WILSON, J. W., III. 1973. Analytical zoogeography of North American mammals. *Evolution* 28:124–140.
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- APPENDIX I
- Rodent species endemic to North American deserts including desert affiliation (GB = Great Basin Desert, M = Mojave Desert, S = Sonoran Desert, C = Chihuahuan Desert) and latitudinal range limits (degrees and minutes N). Species endemic to the Baja Peninsula indicated by Baja in parentheses after latitudinal range.
- Sciuridae.—*Spermophilus atricapillus*, S, 25°10'–28°00' (Baja); *S. mohavensis*, M, 34°20'–36°10'; *S. tereticaudus*, M, S, 27°00'–37°00'; *Ammospermophilus harrisi*, S, 28°00'–36°10'; *A. interpres*, C, 25°00'–35°00'; *A. leucurus*, GB, M, 24°00'–45°00'.
- Geomyidae.—*Geomys arenarius*, C, 31°50'–34°00'; *Pappogeomys castanops*, C, 22°30'–38°00'.
- Heteromyidae.—*Dipodomys agilis*, S, 25°00'–30°00' (Baja); *D. deserti*, GB, M, S, 29°00'–40°10'; *D. merriami*, GB, M, S, C, 22°00'–41°50'; *D. microps*, GB, 34°00'–44°20'; *D. nelsoni*, C, 24°00'–29°00'; *D. panamintinus*, GB, M, S, 34°40'–39°50'; *D. spectabilis*, S, C, 22°00'–37°00'; *Microdipodops megacephalus*, GB, 37°00'–45°00'; *M. pallidus*, GB, 37°00'–40°00'; *Chaetodipus arenarius*, S, 23°30'–32°10' (Baja); *C. baileyi*, S, 23°30'–34°00'; *C. fallax*, M, S, 27°50'–34°10' (Baja); *C. formosus*, GB, M, S, 27°00'–40°10'; *C. intermedius*, S, C, 27°00'–37°00'; *C. lineatus*, S, 21°50'–23°30'; *C. nelsoni*, C, 22°00'–32°10'; *C. penicillatus*, M, S, C, 23°00'–37°00'; *C. spinatus*, S, 23°00'–35°00' (Baja); *Perognathus amplus*, S, 30°30'–36°40'; *P. longimembris*, GB, M, S, 28°30'–43°00'.
- Muridae.—*Neotoma albigula*, C, 19°00'–38°00'; *N. goldmani*, C, 23°00'–29°00'; *N. lepida*, GB, M, 23°00'–45°00'; *Onychomys torridus*, GB, M, S, C, 22°00'–40°20'; *Peromyscus eremicus*, M, S, C, 22°00'–37°10'; *P. eva*, S, 24°10'–25°20' (Baja); *P. merriami*, S, 24°00'–33°00'; *P. pectoralis*, C, 20°00'–33°50'; *P. polius*, C, 28°00'–31°00'.