Evolutionary Ecology Research, 2006, **8**: 435–454

Do elevational range size, abundance, and body size patterns mirror those documented for geographic ranges? A case study using Costa Rican rodents

Christy M. McCain

National Center for Ecological Analysis and Synthesis, University of California at Santa Barbara, 735 State Street, Suite 300, Santa Barbara, CA 93101, USA

ABSTRACT

Question: Do elevational range size, abundance, and body size patterns mirror those documented for geographic ranges?

Data studied: Local and regional elevational ranges, abundances, and body sizes of Costa Rican rodents.

Hypotheses: (1) Plotting elevational range against abundance will reveal a negative sloped, concave-upward relationship (hollow curve). (2) Elevational range sizes and geographic range sizes will be positively correlated. (3) Elevational range sizes will demonstrate a positive, linear trend with relative abundance. (4) Abundance will increase with rodent body size, and elevational range size will exhibit a triangular relationship with body size. (5) Abundances will peak near the elevational range midpoint.

Conclusions: Elevational abundances followed hollow curves, but elevational range sizes did not. Elevational and geographic range sizes were unrelated. Species with larger ranges had higher abundances, although support was stronger regionally. Body size was not related either to elevational range size or to abundance at either scale. The highest abundances generally occurred somewhere in the middle of elevational ranges, but how close to the centre was highly variable.

Keywords: abundance, body size, Costa Rica, elevation, mammals, range size, rodents.

INTRODUCTION

Many of the well-known patterns in large-scale ecology and the newly emerging field of macroecology concern geographic ranges (Brown, 1995; Brown *et al.*, 1996; Gaston and Blackburn, 2000; Gaston, 2003 and references therein). For instance, geographic range size distributions and abundance distributions exhibit strongly decreasing, concave-upward relationships (hollow curves) – that is, most species have small range sizes or low abundances and very few species have large ranges or high abundances. A positive relationship exists between geographical range sizes and abundances: small ranged species tend to be rare, whereas larger ranged species are

---

* e-mail: mccain@nceas.ucsb.edu

common. Some evidence exists for trends in body size with geographic range size (and also with abundance). And Brown (1995) has suggested that abundance across a species' geographic range tends to be highest near the range midpoint.

The mechanisms underlying these trends in the geographic ranges of species are fundamental to our understanding of evolution, range expansion and contraction, community diversity and abundance, and effects of global climate change (Brown, 1995; Gaston and Blackburn, 2000; Gaston, 2003 and references therein). However, the recent study of geographic range patterns with abundance and body size has paid much less attention to the influence of topographical variation despite its global pervasiveness. Mountains are hotspots of biodiversity and endemism, and patterns in the relationships between range size, abundance, and body size along elevational gradients may offer important insights.

Currently, we know little about whether or not patterns in elevational range mirror the relationships documented for geographic ranges. Most research on elevational gradients has focused on elevational diversity patterns (e.g. Heaney, 2001; Li *et al.*, 2003; McCain, 2005) and the possible mechanisms underlying this diversity, such as Rapoport's rule (Stevens, 1992; Ruggiero and Lawton, 1998).

In this study, using data on Costa Rican rodents, I examine how well relationships among range sizes, body sizes, and abundances on an elevational gradient agree with the same patterns documented for geographic ranges. I do this at both local and regional scales. Scale is an important aspect of geographic range patterns (see Gaston, 2003 and references therein), thus attention to scale may be critical to discern elevational patterns.

Several aspects of the relationships between range size, abundance, and body size can be assessed using the Costa Rican rodent data:

- Do species' elevational ranges and abundances exhibit hollow curves as commonly documented for geographic ranges and abundances? If not, perhaps different mechanisms may drive those patterns in geographic and elevational perspectives.
- Do species with large geographical ranges have large elevational ranges? Blackburn and Ruggiero (2001) demonstrated a strong correlation between geographic and elevational range sizes in Andean passerines. Pielou (1979) also found a strong correlation for a subset of the pines in North America. And Stevens (1992) found, on average, that the highest elevational ranged species had the largest latitudinal ranges in Venezuelan birds. I know of no other analyses relating the two types of ranges.
- Do elevational range sizes correlate with relative abundances in Costa Rican rodents? Such a correlation (higher abundances of larger ranged species and lower abundances of small ranged species) has been documented for geographic ranges of many taxa across many different continents and spatial scales (Brown, 1995; Brown *et al.*, 1996; Gaston and Blackburn, 2000; Gaston, 2003 and references therein). Nonetheless, it has only been examined in one study for elevational ranges: herb and tree abundance was positively related to range size along elevational gradients in the Siskiyou Mountains and the Great Smoky Mountains (Brown, 1984).
- Are there any relationships between body size and elevational range size or abundance? How body size varies with respect to both geographic range size and abundance is equivocal. Some data exhibit support for linear or triangular patterns, but many others reveal no relationship (Brown, 1995; Gaston and Blackburn, 1996, 2000; Gaston, 2003 and references therein).
  (a) For abundance–body size relationships, both positive and negative linear trends and triangular patterns have been found in different assemblages. In the triangular

pattern tested here (Brown, 1995), the mid-sized species reach the highest abundances. Peak abundances decrease both towards the smallest and largest species. All body sizes can have low abundances. Since the Costa Rican rodents considered in this analysis are all relatively small-bodied, a positive linear trend with body size and abundance might be expected if they were part of an overall triangular abundance–body size relationship for mammals.

(b) Gaston (2003) concluded that for taxonomically and geographically constrained analyses of geographic ranges, body size and range size also tended to show a triangular pattern. In this case, species of any body size may have a large range, but the minimum range size increases with body size.

As far as I am aware, neither of the body size trends with range size or abundance has been examined for elevational ranges.

- Last, Grinnell (1917) suggested that population densities are highest at the centre of the geographical range of a species. Brown (1995) seconded that and expanded the hypothesis to include elevational ranges. The geographical pattern has been documented for many species (Hengeveld and Haeck, 1982; Brown, 1984; Gaston, 1990; Brown *et al.*, 1995, 1996; but see McGill and Collins, 2003; Gaston and Blackburn, 2000; Gaston, 2003). Meanwhile, Brown (1995) re-analysed Whittaker's plant gradient analyses along montane transects (Whittaker, 1952, 1956, 1960, 1967; Whittaker and Niering, 1965) to demonstrate it for elevational ranges. Greater population size at the centre of a species' range has several important implications for evolution, range expansion, and extinction probabilities (Channell and Lomolino, 2000a, 2000b; Gaston, 2003). To date, only Whittaker's plant data demonstrate the centred abundance pattern for elevational ranges.

The local and regional data on Costa Rican rodent abundances, range sizes, and body sizes along elevational gradients can form the basis of a preliminary investigation of the similarity of elevational and geographic range trends. Specifically, I test the following hypotheses:

1. Elevational range size and abundance distributions will exhibit hollow curves.
2. Elevational range size and geographic range sizes will be positively correlated.
3. Elevational range sizes will demonstrate a positive, linear trend with relative abundance.
4. Abundance will increase with body size, and elevational range size will exhibit a triangular relationship with body size.
5. The highest abundances will be centred near the elevation range midpoint and decline towards the range limits.

METHODS

Data on a local spatial scale were collected along a Caribbean elevational transect in the Tilarán mountain range in northwestern Costa Rica. All sites were within the Río Peñas Blancas watershed, which encompasses both the Monteverde Cloud Forest Reserve and the larger Bosque Eterno de Los Niños Reserve. The Caribbean slope descends quickly from the highest peak, Cerro Amigo (1840 m). The high elevations are wet, cool, cloudy, and characterized by cloud forest vegetation. The lower elevations are warm, wet, humid, and dominated by tropical wet forest. The middle elevations are a transition between these two climates – high rainfall but increasingly cooler temperatures – and between the two forest types – a habitat denoted as premontane rain forest vegetation. [Detailed descriptions of the study site and climate are available in McCain (2004).] Rodents were sampled along an elevational transect between 750 and 1840 m during three seasonal replicates in 2000–2002. Five sampling sites were surveyed: 750–800 m, 1000–1050 m, 1250–1300 m, 1500–1550 m, and 1770–1840 m [see Fig. 1; McCain (2004)]. All sampling sites were located in areas with the most undisturbed forest available at that elevation, and forest was contiguous between all sites. No large tracts of forest existed below 600 m. All five elevational sites were trapped during three seasons: late wet season, October–December 2000; early wet season, July–September 2001; and dry season, March–May 2002. Sites at the various elevations were sampled in a different order during each replicate to reduce temporal autocorrelation among sites. I used 130 traps to obtain each sample: 7 pitfalls, 10 Victor snap traps set 1–3 m above ground on vines or in trees, 40 extra-large folding Sherman live traps, and 73 large folding Sherman live traps. I trapped each elevational site for seven consecutive nights except for the early wet season transect, which I surveyed for five consecutive nights. Altogether I amassed 2350 trap-nights. Most live-trapped animals were marked with a unique toe clip or ear tag and released, but a few voucher specimens were retained. [For more details on trapping procedures, see McCain (2004).]

I defined the local elevational ranges as 'the distance between the lowest and highest captures for a species', except that these were augmented by low elevation records from specimens collected previously in the surrounding area (see McCain, 2004). Species caught only at one elevation or with most of their range at lower elevations were not included in the analyses since their abundance patterns could not be documented. I measured local abundances as 'the average number of individuals caught at each elevation per season'. Jackknife population estimates (Nichols and Conroy, 1996 and references therein) were calculated using the program CAPTURE (Rexstad and Burnham, 1991) for the species with enough recaptures for accurate estimation, but only four species met this criterion (*Peromyscus nudipes*, *Heteromys* sp., *Oryzomys albigularis* and *Scotinomys teguina*). Analyses with the population estimates for these four species produced no significant changes compared with those using simply summed individuals. Therefore, I present only the latter results.

I conducted regional spatial scale analyses using a database of 5926 rodent specimens from Costa Rica compiled from 23 collections (see Acknowledgements). All small rodents were used in the analyses except squirrels and pocket gophers, which may show misleading abundance patterns because they are not easily captured with commonly used live traps or snap traps. Other rare species may present similar problems, but we know very little about them, so I simply assumed that their low capture rates are due to their having low abundances.

I determined the regional elevational ranges from the highest and lowest elevational record in Costa Rica, including records from my Tilirán transect. Records with suspect localities, elevations, or species identifications were not used. Two species, *Heteromys* sp. and *Oligoryzomys vegetus*, are recently recognized species; thus many collections have specimens of these species misidentified as *H. desmarestianus* or *O. fulvescens*, respectively. I used the systematic monographs (Anderson and Timm, 2006; Carleton and Musser, 1995, respectively) to determine which specimens belonged to each species. I included only the specimens enumerated in the systematic revisions, those from the same localities, or those clearly above or below the elevational range of the other species in the present analysis.

I inferred relative abundances at the regional scale from the number of specimens taken from each elevational interval. Ideally, population studies across the elevational range of each species would be employed, but such data are not available for these species. Before this study, populations only of *H. desmarestianus* (Fleming, 1974), *Liomys salvini* (Fleming, 1974), and *Peromyscus nudipes* (Anderson, 1982) had been examined in short-term studies, at one site each. At present, specimen data offer the best source of data for abundance trends for tropical mammal species.

Since some elevations have been sampled more intensely than others (Fig. 1A), the abundance measures have to be adjusted for sampling effort. Unfortunately, most specimens

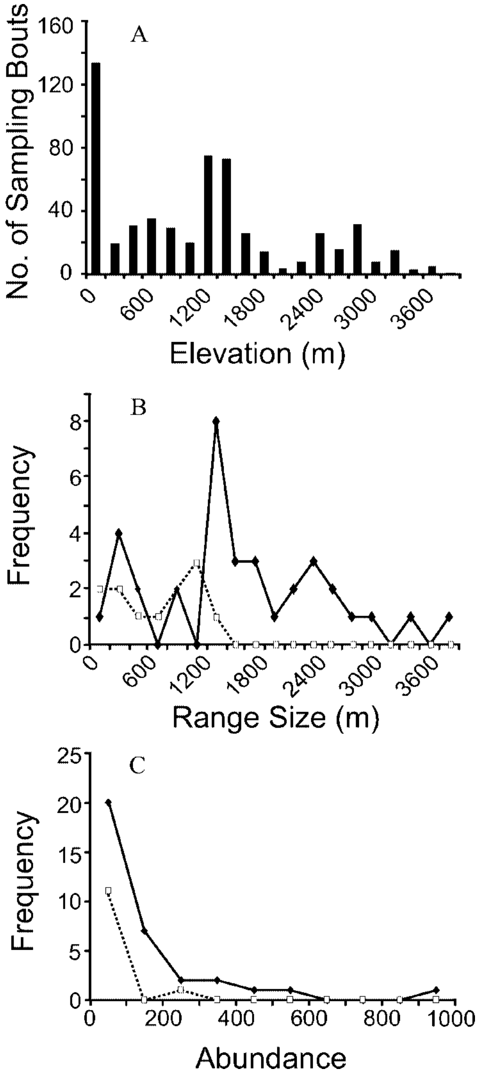

Fig. 1. (A) Number of sampling bouts for each 200 m elevational band estimated from specimen records. Range size frequency histogram (B) and abundance histogram (C) of regional elevational ranges (solid black line with black diamonds) and local elevational ranges (dotted line with open squares) of Costa Rican rodents.

are not associated with detailed descriptions of sampling methods, such as number of traps employed or sampling days. At this time, the best solution to correct for sampling with the present data is to assess the number of independent sampling bouts per elevational band (200 m). Each unique locality was considered a sampling bout. If a particular locality was visited in multiple years, I considered each unique combination of year, locality, and collector as a sampling bout. I considered collectors independent at a particular locality only if their collecting dates did not overlap dates associated with specimens from other collectors.

The numbers of specimens per species within each 200 m elevational band I multiplied by a correction factor to equalize the sampling per elevation. Because elevational bands with higher sampling may contribute more to the estimated abundance, the correction factor was simply the number of bouts in the elevational band with greatest sampling divided by the number of bouts in the elevation of interest. This procedure assumes equal sampling effort (i.e. number of traps or number of trap-nights) per sampling bout. Although equal sampling effort will not be true, we have no reason to suspect that sampling effort per bout is systematically biased elevationally.

Perhaps collections are biased towards more moderately rare species. However, such a bias is not apparent in the comparison of the summed abundances of species in both local and regional data. These are highly correlated ($r = 0.977$, $P < 0.0001$), although I examined effects of several error functions (see below).

To determine if species with larger ranges have larger abundances, I performed linear regressions of elevational range size against abundance at both the local and regional scales. Local abundance for each species was the average number of individuals captured per season summed across the five sampling localities. Regional abundance is the sum of sampling-corrected specimens for each species in Costa Rica. There were no strong differences between the statistical analyses of raw and sampling-corrected specimen numbers, so I present only the sampling-corrected results. The latitudinal range of each species (from Hall, 1981) was regressed against regional elevational range to determine the relationship between the two range measures. I used linear regressions to determine if a positive relationship exists between elevational range size and body size. I took average body size (mass in grams) of each species from the literature (Hall, 1981; Reid, 1997). Each data set was analysed for normality; non-normally distributed data were log-transformed for regression analyses.

I applied several error functions to assess how vulnerable these relationships were to error in abundance estimates and range size estimates. I assessed two types of errors for abundance estimates: uniform random and decreasing (see Table 1).

- The uniform random error was a simulation procedure to increase or decrease the sampling-corrected abundance estimate of each species randomly by a percentage of its abundance. I ran 1000 simulations each at 10, 30, 50, and 70% error in abundance estimate. Then I calculated linear regressions for each simulation with the empirical range sizes. Average r^2-values were then compared to the empirical results.
- The decreasing error estimates assumed that sampling error was greatest for rare species and decreased as abundance increased. Thus I multiplied abundances (sorted by rarest to most abundant) by different levels of linearly decreasing error functions sequentially: 5 to 1, 10 to 1, 100 to 1, and 1000 to 1. I compared linear regressions for each error transformation with empirical range sizes to the original relationships.

Table 1. Abundance error estimates: effects of different levels and functions of errors in abundances on the r^2-values in linear regressions of abundance and elevational range size

		r^2-values	
Error function	Error level	Local	Regional
Empirical		0.296$^{\#}$	0.402***
Uniform Random	10%	0.275	0.400
Uniform Random	30%	0.273	0.391
Uniform Random	50%	0.255	0.366
Uniform Random	70%	0.217	0.332
Decreasing	5 to 1	0.313$^{\#}$	0.383***
Decreasing	10 to 1	0.308$^{\#}$	0.362***
Decreasing	100 to 1	0.225	0.226**
Decreasing	1000 to 1	0.078	0.081
Random		0.086	0.028

Note: Empirical = no error; Uniform Random = randomly ± a percentage of the empirical abundance per species (average r^2 of 1000 simulations; no P-values); Decreasing = decreasing function of multiplicative value with increasing abundance; Random = abundances randomly generated between 1 and summed abundance (average r^2 of 1000 simulations; no P-values). *** $P \leq 0.0001$; ** $P \leq 0.001$; * $P \leq 0.05$; $^{\#}$ $P \leq 0.07$.

I also applied two error methodologies to range size estimates: graduated uniform and decreasing (see Table 2).

- Graduated uniform error in range sizes assumes that smaller ranges had more error than larger ranges. I increased each third of range sizes by adding a percentage of its range for several error levels: [10, 0, 0%]; [30, 10, 0%]; [50, 30, 10%]; and [70, 50, 30%].
- The decreasing methodology was the same as that for decreasing error in abundances, but reflected the smaller error possible due to the height limit of the mountains, thus the decreasing error functions were multiplications by 2 to 1, 3 to 1, 5 to 1, and 7 to 1. I performed linear regressions for each range size error transformation with empirical abundances.

Last, I used each error function and corresponding level for both abundance and range size to calculate combined error effects on the range size–abundance relationship (see Table 2). To ensure that relationships in range size and abundance were significantly different from random, I ran 1000 simulations with random abundances (between 1 and the summed empirical abundance) and empirical range sizes, and with empirical abundances versus simulated range sizes (between 100 m and the mountain top).

I assigned the abundance pattern for local and regional (sampling-corrected) data across the elevational range for each species to one of five descriptive categories: (1) decreasing with elevation, (2) peak shifted towards lower elevations, (3) peak centred near elevational range midpoint, (4) peak shifted towards higher elevations, and (5) increasing with elevation. I based the descriptive category for regional data on LOWESS curves from SYSTAT

Table 2. Range size error estimates: effects of different levels and functions of errors in range size on the r^2-values in linear regressions of abundance and elevational range size

		r^2-values	
Error function	Error level	Local	Regional
Empirical		0.296$^{\#}$	0.402***
Graduated Uniform	10%, 0, 0	0.298$^{\#}$	0.401***
Graduated Uniform	30%, 10%, 0	0.286	0.412***
Graduated Uniform	50%, 30%, 10%	0.271	0.419***
Graduated Uniform	70%, 50%, 30%	0.256	0.407***
Decreasing	2 to 1	0.307$^{\#}$ (0.321$^{\#}$)	0.376*** (0.364***)
Decreasing	3 to 1	0.270 (0.306$^{\#}$)	0.292** (0.286**)
Decreasing	5 to 1	0.249 (0.323$^{\#}$)	0.161* (0.141*)
Decreasing	7 to 1	0.249 (0.199)	0.145* (0.090)
Random		0.088	0.098

Note: Empirical = no error; Graduated Uniform = range size increased by a percentage graduated by each third of ranges sizes; Decreasing = decreasing function of multiplicative value with increasing range size (limit in range size = mountain top); Random = range sizes randomly generated between 100 m and the mountain top (average r^2 of 1000 simulations; no P-values). Effect of a combination of error level in abundance and range size in parentheses. *** $P \leq 0.0001$; ** $P \leq 0.001$; *$P \leq 0.05$; $^{\#}$ $P \leq 0.07$.

(1998). The LOWESS function (I set it at a tension of 3.5) produces a conservative estimate of the elevational abundance pattern given spatial sampling error. I examined only species with more than 10 captures at the local scale or 20 specimens at the regional scale, because less than this does not allow meaningful discernment of pattern.

RESULTS

Elevational range size and range limits were variable across both the local and regional scales among species (see Appendix). Elevational range size varied from 100 to 1340 m at the local scale ($n = 12$ species) and 150 to 3800 m at the regional scale ($n = 35$ species). The range size frequency distributions differ from the right-skewed, hollow curve commonly documented for many species assemblages geographically (Fig. 1B) (Gaston, 2003). Abundances were highly variable also (Table 1): four species are known from fewer than five individuals on the local elevational transect, whereas *Peromyscus nudipes*, the most common species, had 859 individuals caught in the same sampling period (average abundance per season = 287). A similar spread in abundances appeared in the regional data. Eight species are known in Costa Rica from fewer than 10 specimens; others are very common in collections (e.g. *P. nudipes* = 990 specimens). The raw abundances of species that occur both locally and regionally were highly correlated between scales ($r = 0.977$, $P < 0.001$). The abundance pattern at both scales follows the commonly documented right-skewed, hollow-curve distribution (Fig. 1C) (Gaston, 2003).

No linear relationship was observed between regional elevational range size and geographical range size ($r^2 = 0.045$, $P = 0.222$, $n = 35$), or regional abundance (log) and geographical range size ($r^2 = 0.024$, $P = 0.369$, $n = 35$). The linear regression of log-abundance by elevational range size was not significant at the local scale, although nearly so ($r^2 = 0.296$, $P = 0.067$, $n = 12$; Fig. 2A). It was significant at the regional scale ($r^2 = 0.402$, $P < 0.001$, $n = 35$; Fig. 2B). Even with substantial amounts of error in abundance and/or range sizes, the positive linear relationships were consistent at both scales (Tables 1 and 2). Only the most extreme sampling errors – the 1000 to 1 function of multiplication of abundances and 5 to 1 and 7 to 1 functions in range size – decreased the r^2-values substantially. Many of the error adjustments led to increased r^2-values, most notably so in the combined error for local data and graduated uniform procedures for regional data (Table 2). Positive, linear trends did not appear if abundances or range sizes were completely randomized (Tables 1 and 2).

Log body size and log abundance appear unrelated at both the local ($r^2 = 0.002$, $P = 0.881$, $n = 12$; Fig. 3A) and regional scales ($r^2 = 0.092$, $P = 0.087$, $n = 33$; Fig. 3B). Neither scale supports the triangular pattern, as abundance does not appear to increase with body size at small sizes (Fig. 3A, B). No significant relationship was found between log body size and elevational range size at the local ($r^2 = 0.185$, $P = 0.163$, $n = 12$; Fig. 3C) or regional scale ($r^2 = 0.073$, $P = 0.128$, $n = 33$; Fig. 3D). The slope was positive in the local analysis, but negative in the regional analysis. However, in both cases, the regressions were heavily influenced by one or two relatively large-bodied species (Fig. 3C, D); without them, no appreciable pattern in elevational range size with body size was evident for these rodent species.

Local abundance across each elevational range was highly variable, although some species did tend towards higher abundances at mid-range (Fig. 4, solid lines). None of the species followed a normal curve. Abundance trends were relatively consistent among

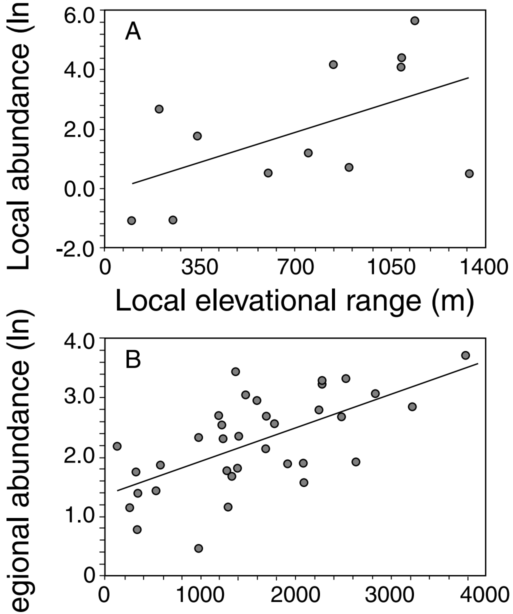

Fig. 2. Linear relationships between log abundance and elevational range size for rodents in Costa Rica at (A) the local scale ($r^2 = 0.296$, $P = 0.0673$) and (B) the regional scale (sampling-corrected; $r^2 = 0.402$, $P < 0.0001$).

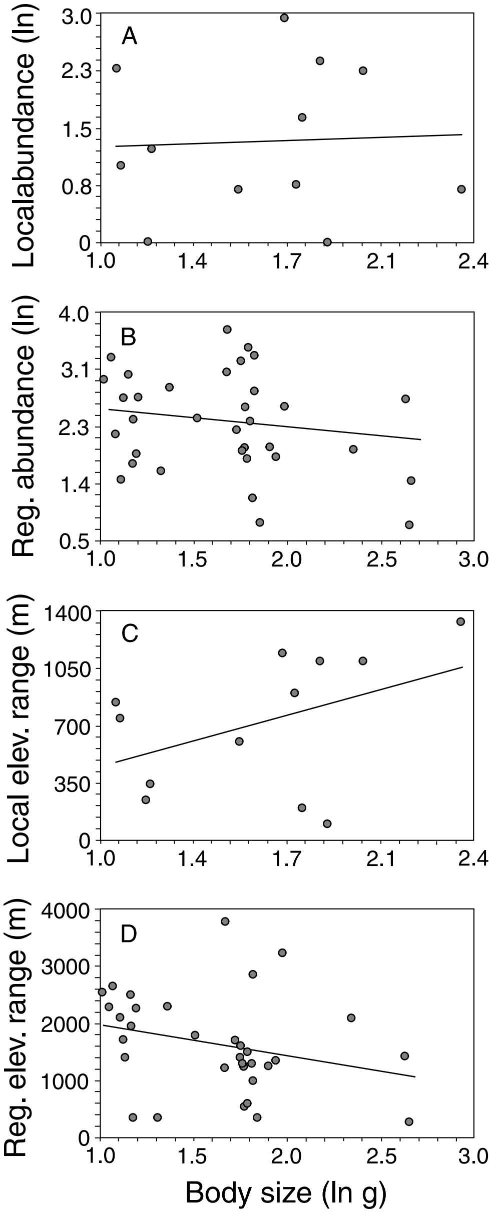

Fig. 3. Linear relationships between log body size and log abundance at (A) the local scale ($r^2 = 0.002$, $P = 0.881$) and (B) the regional scale ($r^2 = 0.092$, $P = 0.087$), and log body size and elevational range size at (C) the local scale ($r^2 = 0.185$, $P = 0.163$) and (d) the regional scale ($r^2 = 0.073$, $P = 0.128$) for rodents in Costa Rica.

seasons at each elevation (bars; Fig. 4), although variability in abundance across the elevations was common. The highest abundances were shifted towards higher elevations for *P. nudipes* and *Reithrodontomys gracilis* (Fig. 4C, E). *Oryzomys albigularis* (Fig. 4B)

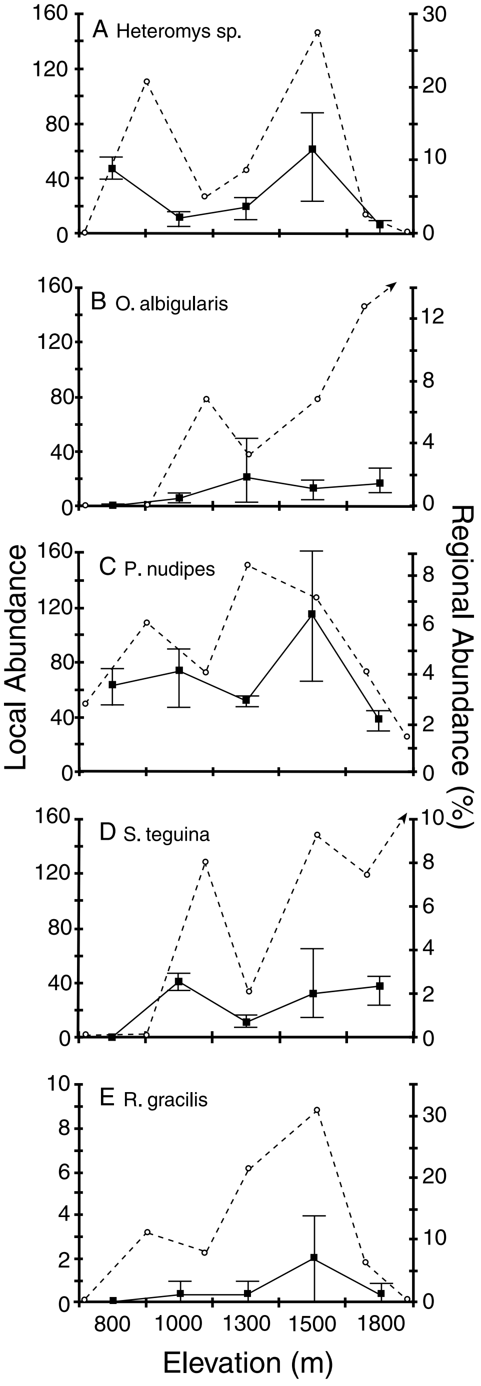

Fig. 4. Average abundance for five elevations on a Caribbean transect in the Tilarán mountain range for five rodent species: (A) *Heteromys* sp., (B) *Oryzomys albigularis*, (C) *Peromyscus nudipes*, (D) *Scotinomys teguina,* and (E) *Reithrodontomys gracilis* (solid lines). Ranges of abundances among seasons depicted with horizontal bars around abundance average. Regional abundances (sampling-corrected; % of specimens) across sampled local elevations displayed with dashed lines.

appeared to have increasing abundance, whereas the *Heteromys* sp. and *Scotinomys teguina* data suggest a bimodal pattern (Fig. 4A, D). Similar trends in abundance were seen at the regional scale (sampling-corrected) and in the abbreviated range of elevations for the local transect, although *O. albigularis* and *R. gracilis* had much stronger increasing trends regionally (Fig. 4, dashed lines). Overall, abundance patterns across the ranges of the 12 locally documented species included two skewed towards higher elevations, perhaps two bimodal patterns, and two that increased with elevation (includes *Reithrodontomys* new sp., previously only found at ~1800 m). Six species had no discernible pattern because they were caught too infrequently or at only one elevation.

The majority of species in the regional analysis (17 of 22) had highest abundances (sampling-corrected, LOWESS curves) at mid-range (e.g. Fig. 5, dashed lines). Of those, four species had their peak abundances shifted towards higher elevations and two species towards lower elevations. Five species had their highest abundance at the lowest elevations in the range (e.g. Fig. 5E). Again, the most conspicuous aspects of the elevational pattern of abundances were the variability in location of peak abundance and the variability in abundance among elevations.

DISCUSSION

The distribution of elevational abundances followed the commonly documented hollow curve, but elevational range sizes did not (Fig. 1B, C). Instead, intermediate range sizes were most common at both the local and regional scales. Perhaps the mechanisms underlying range size distributions differ for elevational and geographical ranges. The range sizes of Costa Rican rodents were elevationally and geographically unrelated ($r^2 = 0.045$, $P = 0.222$). Species with large elevational ranges did not necessarily have large geographic ranges (latitudinal extent). However, Blackburn and Ruggiero (2001) documented such a positive relationship for Andean passerine birds, and Pielou (1979) for a subset of North American pines. Also, Stevens (1992) found that on average the highest elevational ranged species had the largest latitudinal ranges in Venezuelan birds. Clearly, more than these few analyses are needed to identify any generalities.

Most studies of geographic range size and abundance across taxonomic groups find positive, linear relationships [~ 80% (Gaston, 1996, 2003)]. This pattern was not quite significant for elevational ranges of tropical rodents in Costa Rica at a local scale, but was significant at the regional scale. Gaston (2003) noted that the strength of the geographic range size–abundance pattern declines with increasing spatial scale and increasing taxonomic diversity, which is the reverse of the pattern found here. The predictive ability of the range size–abundance relationship (30–40%) corresponds to that detailed for previous analyses of geographic ranges, which normally range between 20 and 40% (Gaston, 1996, 2003). The range size–abundance relationships at both spatial scales were robust to substantial levels of error; only the most extreme levels of error produced large differences from the other results.

Most studies reporting a positive range size–abundance pattern are based on data from birds, plants, and insects from the USA, Britain, and Europe (Brown, 1984, 1995; Lacy and Bock, 1986; Blackburn *et al.*, 1997; Gaston *et al.*, 1997a, 1997b; Quinn *et al.*, 1997). However, non-significant relationships exist both at local scales (Thompson *et al.*, 1998, Hunter, 2003) and at regional scales (Thompson *et al.*, 1998; Dennis *et al.*, 2000; Blackburn *et al.*, 2001). Two range–abundance studies on mammals both found significant relationships between geographic range size and abundance, in England (Blackburn *et al.*, 1997) and in Australia (Johnson, 1998). There is some support for lower abundances at lower

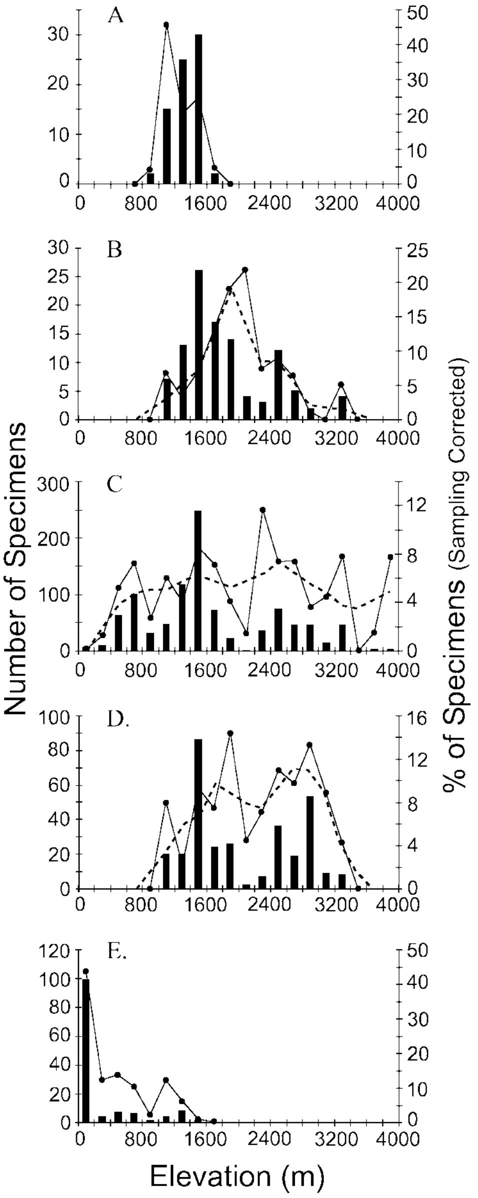

Fig. 5. Abundance patterns of five species across their elevational ranges in Costa Rica measured from specimens in 23 national and international collections (see Acknowledgements). Black bars are actual specimen numbers per elevational band, black lines are sampling-corrected abundance estimates, and dashed lines LOWESS smoothed curves for: (A) *Heteromys* sp., (B) *Oryzomys albigularis*, (C) *Peromyscus nudipes*, (D) *Scotinomys teguina*, and (E) *Proechimys semispinosus*. No LOWESS curves are seen for *Heteromys* sp. (A) or *P. semispinosus* (E) because the curves are identical to the sampling-corrected curves.

latitudes (Gaston, 2003). Lower abundances would lead to less predictive geographic range size–abundance patterns (Johnson, 1998). I saw this in my local analysis in Costa Rica where most rodent species are rare, and it may underlie the non-significant pattern. However, the local analysis had a smaller sample size making the detection of significance less likely (Type II error).

Only one other range size–abundance study has focused on elevational ranges. Brown (1984) re-analysed Whittaker's North American plant and insect data along elevational gradients (Whittaker, 1956, 1960) and found significant relationships between elevational range size and abundance. Thus, there have been no previous studies of range size–abundance patterns along elevational gradients in the tropics even though abundance and diversity data have been collected along many tropical gradients (e.g. Heaney, 2001 and references therein; Md. Nor, 2001; Li *et al.*, 2003; McCain, 2005). Also, some examinations of Rapoport's rule have been applied to elevation (Ruggiero and Lawton, 1998 and references therein; Stevens, 1992). Thus, it appears that rodents in tropical Costa Rica generally support the positive range size–abundance relationship at the local and regional scales, but the relationships may be weakened by a preponderance of species with low abundances. The few species that are relatively abundant (*Heteromys desmarestianus*, *Liomys salvini*, *Melanomys caliginosus*, *Peromyscus nudipes*, *Scotinomys teguina*, *S. xerampelinus* and *Sigmodon hirsutus*) vary in elevational and geographical range size. The only consistent factor among them may be resilience to habitat disturbance.

Studies of body size find linear trends, a triangular relationship, or no pattern with geographic range size and abundance (Brown, 1995; Brown *et al.*, 1996; Gaston and Blackburn, 1996, 2000; Gaston, 2003 and references therein). Since the Costa Rican rodents considered in this analysis do not include the large end of the mammalian body size spectrum, a positive linear relationship between body size and abundance would be expected if mammals as a group display a triangular relationship. However, at the local scale, Costa Rican rodents did not exhibit any relationship between log body size and log abundance (Fig. 3A). And at the regional scale, there was an insignificant negative linear trend between log body size and log abundance (Fig. 3B).

Based on geographical patterns, I expected that body size and range size would show a triangular pattern – that is, species of all body sizes might have large ranges, but the minimum range size would increase with body size (Gaston, 2003). Neither scale of analysis for Costa Rican rodents displayed this triangular pattern (Fig. 3C, D). Similarly, low minimum and high maximum values occurred across all body sizes. Additionally, neither scale supported a significant linear trend between body size and range size. Other recent studies looking for this relationship have also failed to find it [e.g. mammals in Australia (Johnson, 1998); birds in Finland (Solonen, 1994)].

Costa Rican rodent abundances were often higher at some point in the middle of the species' elevational ranges at both scales. But these trends were obscured by the high variation in abundances across species ranges. The majority of patterns were better described by the 'peak-and-tail' pattern, which encompasses the variability in abundance estimates across the range (McGill and Collins, 2003). Only a few species displayed a pattern resembling a normal curve (e.g. *O. albigularis*; Fig. 5B). Lowland species had decreasing abundance with increasing elevation (e.g. *Proechimys semispinosus*; Fig. 5E). The hypothesis most commonly proposed to explain the centred abundance pattern is that species are most common at the optimum biological conditions and decrease in abundance gradually towards their niche limits (Brown, 1984). From an elevational perspective, if the species most common in the lowlands are also best adapted for them, then Brown's hypothesis would lead not to a centred abundance pattern, but to exactly the one I detected.

Since mountains and elevational clines are important aspects of global geography and are often associated with areas of high biodiversity, an accurate understanding of the basic trends in elevational ranges would be useful. Currently, we have no idea whether sizes and locations of elevational ranges vary predictably with slope, aspect, or latitude. There may be striking differences in range sizes and range size trends with scale, especially given variability in mountain height. Smaller mountains may only encompass portions of elevational ranges of certain species, while the largest mountains could encompass entire range extents of all local species.

Diamond (1978) showed that differences in range sizes at local scales may also be influenced by competition. He noted that for three species of congeneric parrots occurring on mountains of New Guinea and surrounding islands, the presence or absence of a competitor led to reduced or expanded elevational ranges. I found little evidence of congeners limiting elevational ranges along the local Costa Rican transect. Of the four genera with multiple species, only one congeneric pair did not have overlapping ranges (*Oligoryzomys*; Appendix 1) but both species were quite rare throughout their ranges. Nonetheless, competition could lead to local range size variation that is fundamental to understanding elevational diversity and distribution patterns (Diamond, 1978; Terborgh, 1971, 1977, 1985; Terborgh and Weske, 1975).

Lastly, the relationship between geographic range size and elevational extent is little studied. It would be very useful to our understanding of diversity and distributional patterns to determine if there is a predictable relationship. For instance, we could find that geographically widespread species are not necessarily found across a large elevational span, but that geographically constrained species or mid-ranged species may have larger elevational ranges. Elevational diversity studies have become more common, but I would urge researchers to examine also the trends in elevational range sizes, abundance, and scale.

ACKNOWLEDGEMENTS

I thank the curators and collection managers at the following collections who generously provided specimen data from Costa Rica: Royal Ontario Museum, University of Kansas Natural History Museum, Natural History Museum of Los Angeles County, Museum of Vertebrate Zoology at UC Berkeley, Dickey Collection at UCLA, United States National Museum, Florida Museum of Natural History, Field Museum, Museum of Natural Science at LSU, University of Michigan Museum of Zoology, Museum of Southwestern Biology, Carnegie Museum of Natural History, Texas Cooperative Wildlife Collection, Museum of Texas Tech University, Harvard Museum of Comparative Zoology, Denver Museum of Natural History, Burke Museum, San Diego Natural History Museum, Peabody Museum of Natural History, Cornell University Vertebrate Collection, James Ford Bell Museum of Natural History, Michigan State University, and University of Illinois Natural History Survey. Rafael Bolaños, director of Reserva Biológica Bosque Nuboso Monteverde, and the Tropical Science Center made my work at Monteverde productive, and Javier Guevara Sequeira and SINAC-Ministerio del Ambiente y Energía, San José, provided permits for my research. I thank T. Blackburn, B. Foster, T. Holmes, S.K. Lyons, N.A. Slade, R.M. Timm, and two anonymous reviewers for helpful editorial suggestions, and W. Langford for advice on testing error effects. M. Rosenzweig also provided insightful comments that improved the quality of the manuscript. I am indebted to my two field assistants, Arturo Cruz and Lance Arvidson, for their hard work. This work was supported by grants from the Tinker Foundation, Organization of Tropical Studies, M. and L. Self Graduate Fellowship, generous donations of N. and J. Pease, and from various funding sources at the University of Kansas: E.R. Hall Fund, Ida H. Hyde Foundation for Women in Science, Panorama Society, Rudkin Fund, and the University of Kansas Natural History Museum.

REFERENCES

Anderson, R.P. and Timm, R.M. 2006. A new montane species of spiny pocket mouse (Rodentia: Heteromyidae: *Heteromys*) from northwestern Costa Rica. *Am. Mus. Novitates*, **3509**: 1–38.

Anderson, S.D. 1982. Comparative population ecology of *Peromyscus mexicanus* in a Costa Rican wet forest. Unpublished PhD dissertation, University of Southern California.

Blackburn, T.M. and Ruggiero, A. 2001. Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecol. Biogeogr.*, **10**: 245–259.

Blackburn, T.M., Gaston, K.J., Quinn, R.M., Arnold, H. and Gregory, R.D. 1997. Of mice and wrens: the relation between abundance and geographic range size in British mammals and birds. *Phil. Trans. R. Soc. Lond. B*, **352**: 419–427.

Blackburn, T.M., Gaston, K.J. and Duncan, R.P. 2001. Population density and geographical range size in the introduced and native passerine faunas of New Zealand. *Diversity and Distributions*, **7**: 209–221.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *Am. Nat.*, **124**: 255–279.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Brown, J.H., Mehlman, D.W. and Stevens, G.C. 1995. Spatial variation in abundance. *Ecology*, **76**: 2028–2043.

Brown, J.H., Stevens, G.C. and Kaufman, D.M. 1996. The geographic range: size, shape, boundaries, and internal structure. *Annu. Rev. Ecol. Syst.*, **27**: 597–623.

Carleton, M.D. and Musser, G.G. 1995. Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegatus* (Bangs, 1902). *Proc. Bio. Soc. Wash.*, **108**: 338–369.

Channell, R. and Lomolino, M.V. 2000a. Dynamic biogeography and conservation of endangered species. *Nature*, **403**: 84–86.

Channell, R. and Lomolino, M.V. 2000b. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. *J. Biogeogr.*, **27**: 169–179.

Dennis, R.L.H., Donato, B., Sparks, T.H. and Pollard, E. 2000. Ecological correlates of island incidence and geographic range among British butterflies. *Biodivers. Conserv.*, **9**: 343–359.

Diamond, J.M. 1978. Niche shifts and the rediscovery of interspecific competition. *Am. Sci.*, **66**: 322–331.

Fleming, T. 1974. The population ecology of two species of Costa Rican heteromyid rodents. *Ecology*, **55**: 493–510.

Gaston, K.J. 1990. Patterns in the geographical ranges of species. *Biol. Rev.*, **65**: 105–129.

Gaston, K.J. 1996. Species richness: measure and measurement. In *Biodiversity: A Biology of Numbers and Difference* (K.J. Gaston, ed.), pp. 77–113. Oxford: Blackwell Science.

Gaston, K.J. 2003. *The Structure and Dynamics of Geographic Ranges*. Oxford: Oxford University Press.

Gaston, K.J. and Blackburn, T.M. 1996. Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *J. Anim. Ecol.*, **65**: 701–714.

Gaston, K.J. and Blackburn, T.M. 2000. *Pattern and Process in Macroecology*. Oxford: Blackwell Science.

Gaston, K.J., Blackburn, T.M. and Gregory, R.D. 1997a. Interspecific abundance–range size relationships: range position and phylogeny. *Ecography*, **20**: 390–399.

Gaston, K.J., Blackburn, T.M. and Gregory, R.D. 1997b. Abundance–range size relationships of breeding and wintering birds in Britain: a comparative analysis. *Ecography*, **20**: 569–579.

Grinnell, J. 1917. Field tests of theories concerning distributional control. *Am. Nat.*, **51**: 115–128.

Hall, E.R. 1981. *The Mammals of North America*, 2nd edn. New York: Wiley.

Heaney, L.R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global Ecol. Biogeogr.*, **10**: 15–39.

Hengeveld, R. and Haeck, J. 1982. The distribution of abundance. I. Measurements. *J. Biogeogr.*, **9**: 303–316.

Hunter, J.T. 2003. Factors affecting range size differences for plant species on rock outcrops in eastern Australia. *Diversity and Distributions*, **9**: 211–220.

Johnson, C.N. 1998. Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *J. Anim. Ecol.*, **67**: 689–698.

Lacy, R.C. and Bock, C.E. 1986. The correlation between range size and local abundance of some North American birds. *Ecology*, **67**: 258–260.

Li, J.S., Song, Y.L. and Zeng, Z.G. 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecol. Biogeogr.*, **12**: 449–460.

McCain, C.M. 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *J. Biogeogr.*, **31**: 19–31.

McCain, C.M. 2005. Elevational gradients in diversity of small mammals. *Ecology*, **86**: 366–372.

McGill, B. and Collins, C. 2003. A unified theory of macroecology based on spatial patterns of abundance. *Evol. Ecol. Res.*, **5**: 469–492.

Md. Nor, S. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Malaysia. *Global Ecol. Biogeogr.*, **10**: 41–62.

Nichols, J.D. and Conroy, M.J. 1996. Estimation of species richness. In *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals* (D.E. Wilson, F.R. Cole, J.D. Nichols, R. Rudran and M.S. Foster, eds.), pp. 226–234. Washington, DC: Smithsonian Institution Press.

Pielou, E.C. 1979. *Biogeography*. New York: Wiley.

Quinn, R.M., Gaston, K.J., Blackburn, T.M. and Eversham, B.C. 1997. Abundance–range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. *Ecol. Entomol.*, **22**: 453–461.

Reid, F.A. 1997. *A Field Guide to the Mammals of Central America and Southeast Mexico*. New York: Oxford University Press.

Rexstad, E. and Burnham, K.P. 1991. *User's Guide for Interactive Program CAPTURE: Abundance Estimation of Closed Animal Populations*. Fort Collins, CO: Colorado Cooperative Fish and Wildlife Research Unit.

Ruggiero, A. and Lawton, J.H. 1998. Are there latitudinal and altitudinal Rapoport effects in the geographic ranges of Andean passerine birds? *Biol. J. Linn. Soc.*, **63**: 283–304.

Solonen, T. 1994. Finnish bird fauna: species dynamics and adaptive constraints. *Ornis Fenn.*, **71**: 81–94.

Stevens, G.C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *Am. Nat.*, **140**: 893–911.

SYSTAT. 1998. *SYSTAT*, Version 9. Port Richmond, CA: SYSTAT Software, Inc.

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.

Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology*, **58**: 1007–1019.

Terborgh, J. 1985. The role of ecotones in the distribution of Andean birds. *Ecology*, **66**: 1237–1246.

Terborgh, J. and Weske, J.S. 1975. The role of competition in the distribution of Andean birds. *Ecology*, **56**: 562–576.

Thompson, K., Hodgson, J.G. and Gaston, K.J. 1998. Abundance–range size relationships in the herbaceous flora of central England. *J. Ecol.*, **86**: 439–448.

Whittaker, R.H. 1952. A study of summer foliage insect communities in the Great Smoky Mountains. *Ecol. Monogr.*, **22**: 1–44.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. *Ecol. Monogr.*, **26**: 1–80.

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.*, **30**: 279–338.

Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biol. Rev.*, **42**: 207–264.

Whittaker, R.H. and Niering, W.A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. *Ecology*, **46**: 429–452.

APPENDIX

Elevational extents (m), range sizes, and abundances of rodent species from Costa Rica from several spatial scales: local scale documented along an elevational transect in the Tilarán Mountains, and regional scale of all elevational relief in Costa Rica, geographic range coverage in Costa Rica, and latitudinal range size (degrees) of each species

	Local			Regional			
Species	Range	Range size	Abundance (seasonal average)	Range	Range size	Abundance	Latitudinal range
Heteromys desmarestianus				0–2850	2850	459	15
H. new sp.	750–1840	1090	242 (81)	800–1800	1000	183	1.5
H. oresterus				1860–3110	1250	27	1
Hoplomys gymnurus				0–280	280	8	17
Liomys salvini				0–1220	1200	286	8.5
Melanomys caliginosus				0–1600	1600	306	21
Nyctomys sumichrasti	400–1300	900	6 (2)	0–1700	1700	54	12
Oecomys trinitatis				0–1300	1300	5	24.5
Oligoryzomys fulvecens				0–1700	1700	159	26
O. vegatus	800–1050	250	2 (1)	840–3400	2500	77	2
Oryzomys albigularis	750–1840	1090	176 (59)	100–3340	3250	111	15.5
O. alfaroi	900–1500	600	5 (2)	500–2300	1800	81	25
O. bolivaris	750–800	50	44 (15)	0–1400	1400	18	16
O. couesi				0–600	600	67	62.5
O. talamancae				0–525	525	13	4
Ototylomys phyllotis				0–1300	1300	21	9.75

APPENDIX—*Continued*

Species	Local			Regional			Latitudinal range
	Range	Range size	Abundance (seasonal average)	Range	Range size	Abundance	
Peromyscus nudipes	700–1840	1140	859 (287)	150–3950	3800	990	14
Proechimys semispinosus				0–1425	1425	129	21
Reithrodontomys brevirostris				500–2590	2100	8	3.75
R. creper				1400–3670	2300	193	1.5
R. gracilis	800–1550	750	10 (4)	100–2750	2650	33	11.5
R. mexicanus				860–3110	2260	145	15
R. sp.	1500–1840	340	17 (6)	1500–1840	340	15*	1
R. paradoxus				50–1000	1000	2	2.1
R. rodriguezi				1500–3440	1940	8	1
R. sumichrasti				1200–3733	2550	193	11.5
Rheomys raptor				1400–1750	350	8	3
R. underwoodi				2000–2150	150	4	1.75
Scotinomys teguina	1000–1840	840	191 (64)	1100–3400	2300	312	10.5
S. xerampylinus				2350–3700	1400	281	1.5
Sigmodon hirsutus				0–1500	1500	504	8
Sigmodontomys alfari				0–1350	1350	13	8.5
S. aphrastus	1200–1300	100	1 (< 1)	1200–1550	350	3	2
Tylomys watsoni	500–1840	1340	5 (2)	0–2100	2100	18	3.75
Zygodontomys brevicauda				0–1250	1250	92	9

* Approximately (new species to be described).