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LETTER

Vertebrate range sizes indicate that mountains may be 'higher' in the tropics

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Abstract

In 1967, Daniel Janzen proposed the influential, but largely untested hypothesis, that tropical mountain passes are physiologically higher than temperate mountains. I test his key prediction, the one upon which all the others rely: namely, that elevational range sizes of organisms get larger on mountains at increasing latitudes. My analyses use 170 montane gradients spanning 36.5° S to 48.2° N latitude compiled from over 80 years of research and 16 500 species of rodents, bats, birds, lizards, snakes, salamanders, and frogs. In support of Janzen's prediction, I find that elevational range size increases with increasing latitude for all vertebrate groups except rodents. I document additional lines of evidence for temperature variability as a plausible mechanism for trends in vertebrate range size, including strong effects of thermoregulation and daily temperature variability, and a weak effect of precipitation.

Keywords

Adaptation, AIC, dispersal, elevation, environmental gradient, speciation, temperature.

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INTRODUCTION

In proposing that mountain passes are physiologically higher in the tropics, Janzen (1967) brought together disparate ideas from both ecology and evolution, including climate, physiology, adaptation, and speciation across the combined large-scale gradients of latitude and elevation (Janzen 1967; Huey 1978; Ghalambor *et al.* 2006; Kozak & Wiens 2007). Janzen (1967) insightfully observed and documented that annual temperatures vary little at single sites on tropical mountains, whether at high or low elevation, whereas annual temperatures vary greatly at single sites on temperate mountains (Fig. 1a). For example, large seasonal variation in temperatures in the US Rocky Mountains leads to periods of warm and cold temperatures at both the lowest and highest elevations. On Costa Rican mountains, in contrast, temperature is constant over the year at each site, resulting in almost no overlap in temperature at low and high elevations. Based on this observation, Janzen assumed that species evolve physiological adaptations reflecting the range of environmental variation encountered in their local vicinity. He predicted that species experiencing high variability in temperature – temperate species – would evolve broad temperature tolerances and acclimation abilities, whereas species experiencing low variability in temperature – tropical species – would evolve narrow temperature tolerances and acclimation potentials. Janzen then predicted that tropical species would have smaller elevational range sizes and lower dispersal abilities than temperate species experiencing large seasonal temperature fluctuations (Fig. 1a). Janzen argued that if this were the case, tropical mountains of height equal to that of temperate mountains would present a larger physiological barrier to dispersal of organisms, as species would experience more conditions beyond their adaptive or acclimation capabilities. Tropical montane barriers would present a larger fitness cost of dispersal, thus qualifying as 'higher'.

His ideas have captivated scientific imaginations for decades although most of his main assumptions and predictions have yet to be tested (Ghalambor *et al.* 2006). Huey (1978) was the first to test Janzen's hypothesis by examining the amount of faunal overlap between a high and a low elevation site on nine montane gradients using lizards, snakes, and frogs. In support of Janzen, he found that faunal similarity was greater between high and low elevations on temperate than tropical mountains. Implicit in this test was that range sizes were larger on temperate than tropical mountains, although not directly tested. Several other studies have documented small range sizes on tropical mountains, but have not directly or quantitatively compared ranges from temperate and tropical latitudes (e.g. Heyer 1967; Wake & Lynch 1976; Terborgh 1977; Lieberman *et al.*

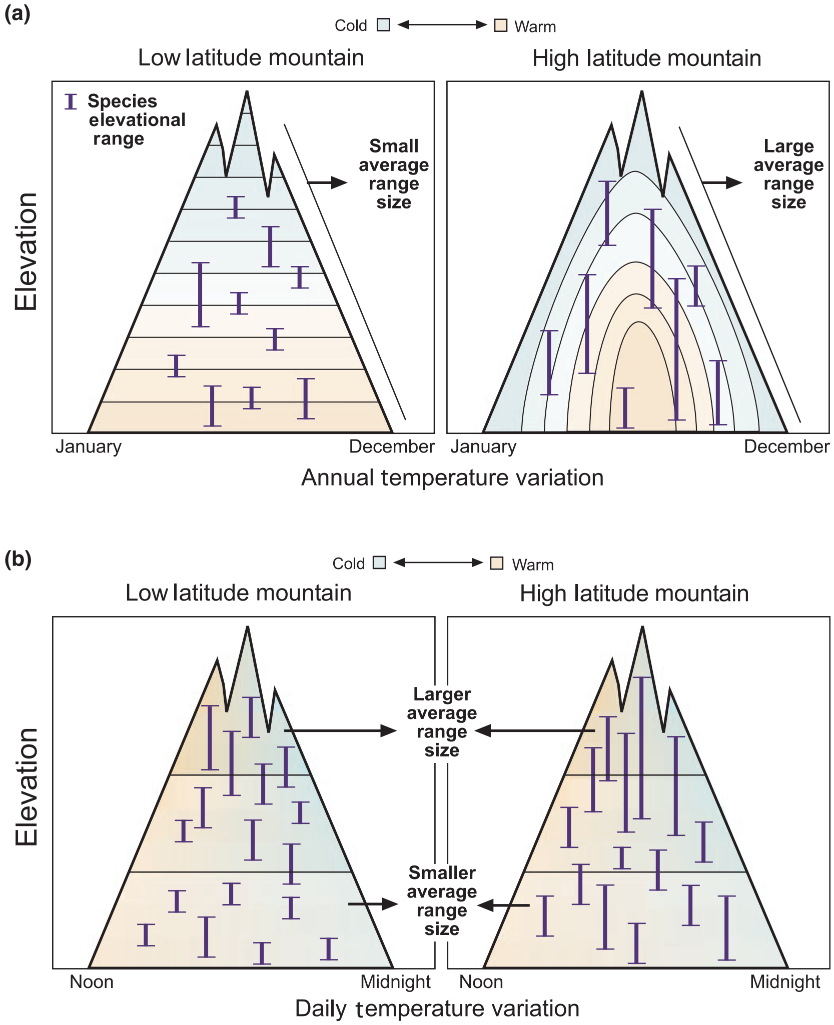

Figure 1 Diagram of Janzen's hypothesis: (a) annual temperature variation at single elevations on tropical mountains is remarkably stable and overlaps little with higher elevations, whereas temperature fluctuates greatly at single elevations on temperate mountains and overlaps substantially with higher elevations. Thus, in response to this variation, Janzen predicted that on average elevational range sizes should be smaller on tropical than temperate mountains. (b) Janzen's predictions can be extended to daily variation in temperature on single mountains where high elevations experience extreme variability in temperature within 24 h, whereas low elevations experience relatively little daily variation in temperature thus, predicting that high elevation assemblages should have larger range sizes than lower elevation assemblages.

1996; Rahbek & Graves 2001). Thus, the basic prediction of smaller range sizes on tropical mountains is still an open question. Scattered support exists for latitudinal differences in breadth of thermal tolerance and acclimation abilities (Kozak & Wiens 2007), but most tests are limited to a few species on one or a few mountains (e.g. Christian *et al.* 1988; Gaston & Chown 1999; Addo-Bediako *et al.* 2000). The lack of thorough testing has not been from lack of interest, but purely from lack of enough appropriate data.

Here I use a large collection of data for 7 vertebrate groups, 170 mountain gradients, and data on elevational range sizes collected over 80 years of study to test whether tropical and temperate species do in fact have detectably divergent elevational range sizes. Such a test is a critical and necessary first step to evaluate the case for Janzen's other assumptions and predictions. I also explore whether Janzen's hypothesis can be extended to explain differences among vertebrate groups owing to the mode of thermoregulation, variation in daily temperature at low and high elevations, and among mountains with different precipitation regimes (e.g. wet vs. arid mountains).

The ideal way to test Janzen's hypothesis is to compare species from mountains of equal height (Janzen 1967; Ghalambor *et al.* 2006). But mountains vary substantially in height across the globe from old, low mountains like the Great Smoky Mountains to precipitously high, relatively young mountains like the Himalayas. This variability can present biases in range size. The maximum potential size of a species' elevational range is equal to the height of the mountain; therefore, the average range size of an assemblage from a mountain of 1800 m will most likely, but not necessarily, be smaller than that of a species assemblage from a 5000 m mountain. Additionally, researchers sample species distributions at different scales (e.g. local transects or regional surveys) and sample various portions of a mountain. In both cases, sampling scale and effort can influence sampled mountain height, and thus influence range sizes. In testing the strength of Janzen's elevational range size predictions, I directly examine and control for differences in mountain height, sampling scale, and sampled height on elevational range sizes.

Temperature is the critical driving force in Janzen's (1967) hypothesis (Huey 1978; Ghalambor *et al.* 2006). If in fact temperature drives latitudinal variation in range sizes as Janzen predicts, then temperature should also explain other differences in range sizes among species assemblages. Here I test two extensions of Janzen's hypothesis with respect to temperature: thermoregulatory effects and the influence of daily temperature variation. First, the sensitivity of ectotherms to variation in temperature should make them more apt to follow Janzen's predictions than endotherms, which control their body temperature (Porter & Gates 1969; Ghalambor *et al.* 2006). I examined this possibility by contrasting endothermic (rodents, bats, and birds) to ectothermic vertebrates (lizards, snakes, frogs, and salamanders). Second, large daily variation in temperatures experienced by high-elevation species, particularly tropical, can be just as pronounced as annual temperature variation experienced by temperate species (Fig. 1b; Ghalambor *et al.* 2006). Thus, high-elevation tropical species should show larger physiological tolerances and acclimation abilities, and thus larger elevational ranges, than low-elevation tropical species. Such a contrast of species ranges on single mountains also might confound our ability to find support for Janzen's main predictions (e.g. Porter *et al.* 2002). Thus, to test whether high-elevation assemblages have larger ranges than lower assemblages, and whether their latitude-range size trends differ, I divide species into assemblages from the lower- and upper-third of the mountains, analyse each separately, and compare their trends.

Finally, I extend the tests of Janzen's predictions to explore precipitation differences (wet vs. arid mountains), which may also influence the effectiveness of a montane barrier (Janzen 1967; Ghalambor *et al.* 2006). Divergent range sizes on humid and dry mountains may be a reflection of species' adaptations to water availability (McCain 2007, 2009), or it may reflect a response to homogeneous vs. heterogeneous distribution of habitats. I test whether precipitation regime influences elevational range size and thus affects our ability to support Janzen's predicted relationship between elevational range size and latitude. If my tests of Janzen's range size and temperature predictions are generally supportive, then his other predictions of reduced dispersal ability, niche breadth, and physiological tolerance may well have validity and beg further detailed examination.

DATA

Janzen (1967) predicted smaller elevational ranges in tropical species and larger elevational ranges in temperate species. His mountain pass hypothesis is broad and encompasses all species living and breeding on mountains. Given that his hypothesis is applicable to a large proportion of species, tests of his hypothesis should include all species in the montane community. For that reason, the fundamental test of his prediction is whether the central tendency of range sizes of all species in a taxonomic group on particular mountains increases with increasing latitude, calculated either as mean or median range size of species on each gradient. Qualitatively, the results were the same for both mean and median measures, so only results of mean range size are shown here. I focus on the seven taxonomic groupings of vertebrates used in published accounts: rodents, bats, birds, snakes, lizards, salamanders, and frogs, which include a large proportion of the world's vertebrate diversity (16 581 species).

Elevational range size for every species on each gradient was compiled in conjunction with meta-analyses of elevational diversity for terrestrial vertebrates (McCain 2005, 2007; McCain, 2009, unpublished data). Elevational range data were taken directly from published articles and appendices, or compiled from regional field guides, surveys, or online distributional databases (e.g. Global Amphibian Assessment 2008; see previous citations for more details). All rare species known only from a single site or with no elevational range were assumed to have a range size of 50 m (e.g. Stotz *et al.* 1996). Most literature reported range sizes calculated with range interpolation, which assumes that a species was present between its highest and lowest reported elevations. For standardization, all additional compilations used the same methodology (but see Colwell & Hurtt 1994; Grytnes & Vetaas 2002).

Montane gradient studies were selected based on several *a priori* sampling criteria, as sampling is highly important in detecting unbiased patterns in comparative analyses (Rickart 2001; McCain 2005, 2007; Rahbek 2005). First, a mountain was included in quantitative analyses only if sampling covered at least 70% of the elevational gradient (or habitable portion of the gradient). Second, sampling effort needed to be substantial and not strongly biased elevationally. Third, gradients with strong elevational trends in wide-scale habitat disturbance were not included. After these restrictions, range sizes for each vertebrate group were included for multiple mountains across a broad span of latitudes (>84°) for rodents (33 mountains), bats (12), birds (28), lizards (16), snakes (16), salamanders (23), and frogs (42) (see Appendix S1 in Supporting Information). These are the best data we have to date and represent more than 80 years of field research efforts by countless individuals. Nonetheless, these data are not perfect: there are more datasets from the western and northern hemispheres than the eastern and southern hemispheres, mountains vary dramatically in height from 851 to 8848 m, and there are sampling and scale biases inherent to all field studies and compilations. Despite these deficiencies, these data should be robust enough to detect a trend if one exists, given application of statistical methods to reduce sampling, scale, and height biases.

METHODS AND ANALYSIS

The portion of the mountain sampled on each gradient differed among studies, mainly because not all studies were undertaken with the express intent to document elevational range sizes. But clearly, range sizes may not be as complete or as accurate without sampling the highest or lowest elevations. Sampling scale was either a local-scale transect study with short-term sampling protocols or a regional-scale compilation from many years of sampling across many localities on a mountain or mountain range. Each sampling scale has its strengths and limitations. For example, regional studies can overestimate range sizes as they are based on sampling across an entire mountain range or region encompassing variation in conditions not encountered on a single slope or transect (e.g. mountains of Peru). At the same time, because sampling is more intensive both at individual elevations and across all available elevations, actual range sizes may be more accurate and more rare species will be included. Local studies, for their part, may include less geographic variation but may under-sample range sizes of many species or miss rare species because of low sampling effort or a less complete survey of elevations. Additionally, local studies vary methodologically in the elevational distance between survey plots, which can also influence the estimation of elevational range sizes. For these reasons, the influences of sampling completeness and sampling scale on the latitudinal trend in elevational range sizes was carefully examined and controlled. Each gradient was assigned a precipitation regime (wet or arid) based on vegetation present at the base of the mountain: arid includes hyper-arid, arid, and semi-arid vegetation types (humidity index < 0.50; UNEP's, 1997, World Atlas of Desertification classification) and wet mountains include various forest vegetation types (humidity index > 0.50).

Range size models for each taxon are constructed for all possible multiple regressions and compared with the Akaike information criterion (AIC). AIC weighs both model fit and parameter complexity, thus determining models that parsimoniously detect the strongest relationships (Burnham & Andersen 2002). Model variables include latitude, mountain height, percentage of height sampled, sampling scale (local vs. regional), precipitation regime, and number of species. Models with the highest AIC weight identify the strongest relationships between measured variables and elevational range sizes (Burnham & Andersen 2002). I use multi-model inference to assess the importance of each variable by summing the Akaike weights across all models, and I use model averaging to provide slope estimates of each variable with strong AIC relationships with range size (Burnham & Andersen 2002).

Because of the strong influence of mountain height, sampling scale, and percentage, two methods were implemented in order to reduce their influence. The first method was best subset analyses (Appendix S1). Best subsets for each taxon were limited to continental mountains of >2000 m from which 80% or more of the mountain was sampled at a regional scale (unless sample sizes were too small, e.g. bats). Additionally, certain taxon-specific culling was necessary based on biological or sampling issues inherent to a taxon's data. For birds, the best subset included only breeding bird data, owing to a potential bias in elevational range size with seasonal, long-distance migrants (only taxon with such long-distance migrants). For amphibians, I excluded datasets based on compilations from multiple countries encompassing a large latitudinal range (e.g. Global Amphibian Database). Finally for rodents, bats, breeding birds, and frogs, combined diversity in a dataset needed to be greater than 10 species.

The second method to reduce the influence of mountain height was a series of truncated mountain analyses. Each dataset was truncated at a particular height and range sizes within the height compared across latitude. This allowed for comparisons across the same elevational spread for all mountains. Truncation was conducted at three heights chosen to maximize the number of mountains included for each taxonomic group. For instance, as salamander gradients ranged in height from 1900 to 5775 m, three truncation heights were analysed at 1800 m ($n = 22$), 2500 m ($n = 19$), and 3000 m ($n = 13$).

In order to assess the influence of thermoregulatory ability, I used a nonparametric Mann–Whitney U-test to determine if the average fit (r^2 value) to Janzen's predicted range size–latitude relationship is higher among ectotherms than endotherms. I tested whether low and high elevation species varied in elevational range sizes and latitudinal response (Ghalambor *et al.* 2006) by calculating a low and high mean range size for those species occurring in the lower and upper one-third of inhabited mountain height, respectively, for each gradient. A paired t-test was used to examine if elevational range sizes were larger at high vs. low elevations. A nonparametric Mann–Whitney U-test was used to assess if the average fit (r^2 value) for the range size–latitude relationship was higher for the lower one-third than for the upper one-third of elevational assemblages.

RESULTS

Rodents

Contrary to Janzen's prediction, elevational range size either decreased with increasing latitude or showed no discernable relationship with latitude (Table 1 and Fig. 2a). The best models for all and the best subset data found mountain height to be the strongest predictor of elevational range size. With mountain height truncations, latitude and percentage of mountain sampled were the strongest variables, although average summed weights of each were less than 60%.

Table 1 Best multiple regression models based on highest Akaike information criterion (AIC) weight for testing relationship between vertebrate elevational range size and latitude (Lat) with secondary parameters of mountain height (Hgt), number of species (Spp), scale (Scl), percentage of mountain sampled (%Mt), and precipitation (Pre). Slopes of relationships are shown for latitude based on model averaging; other variable slopes are: height is positive (0.04–0.31); scale is negative (−99 .0 to −228.9); % Mt is positive (1.3–1188.6); precipitation is positive (216.6, 125.2); species number is negative (−0.15 to −3.9) except for salamanders, 11.0

Dataset	Best model parameters						R^2	AIC weight	# mountains	# models	Slope latitude
Rodents											
All	Lat*	**Hgt*****	Spp	Scl**	%Mt		0.80	0.19	33	58	−3.4
Best		**Hgt***					0.68	0.52	9	31	
800					**%Mt**		0.08	0.27	9	31	
1400	**Lat**						0.34	0.50	9	31	−3.3
1800	**Lat**						0.26	0.33	7	25	−2.1
Bats											
All	**Lat*****			Scl*			0.75	0.27	12	58	28.2
Best	**Lat****	Hgt					0.89	0.57	8	51	38.6
1300	Lat*			**Scl****			0.90	0.57	8	56	6.7
2100	**Lat*****					Pre*	0.96	0.69	7	41	37.2
2300	**Lat*****						0.98	0.98	5	6	29.2
Birds											
All		**Hgt*****	Spp***	Scl***			0.73	0.47	28	58	
Breeding birds											
Best	Lat	**Hgt*****					0.74	0.45	11	31	8.2
1800	**Lat**						0.37	0.40	11	31	3.3
2000	**Lat**						0.32	0.35	11	31	3.5
2800		**Hgt****	Spp				0.92	0.46	8	30	
Lizards											
All		**Hgt****	Spp				0.46	0.21	16	58	
Best	**Lat*****						0.70	0.70	9	31	24.3
1400	**Lat****						0.58	0.61	9	31	10.5
2000	**Lat****						0.61	0.67	9	31	16.2
2300	**Lat***						0.70	0.66	8	30	16.8
Snakes											
All		**Hgt*****					0.37	0.20	16	58	
Best	**Lat***						0.40	0.41	9	31	19.9
1400					**%Mt**		0.30	0.36	9	31	
2000	**Lat**						0.34	0.36	9	31	12.8
2300	**Lat**						0.45	0.51	8	30	12.2
Salamanders											
All	**Lat*****						0.56	0.28	23	31	26.8
Best	**Lat*****						0.66	0.37	12	31	35.9
1800	**Lat****						0.53	0.43	11	31	17.5
2500	**Lat*****						0.82	0.74	10	31	48.1
3000			**Spp****				0.56	0.76	7	14	
Frogs											
All	**Lat*****	Hgt*	Spp	Scl**	%Mt		0.49	0.12	42	58	14.7
Best	**Lat*****						0.61	0.34	11	31	35.5
1200	**Lat*****						0.57	0.41	11	31	15.8
2000	**Lat*****	Hgt				Pre*	0.90	0.44	11	31	38.8
2500	**Lat*****						0.75	0.64	10	31	38.9

Individual variable weights (sum of Akaike weights): *** >0.9; ** >0.75; *>0.6; **bold** indicates the most explanatory variables.

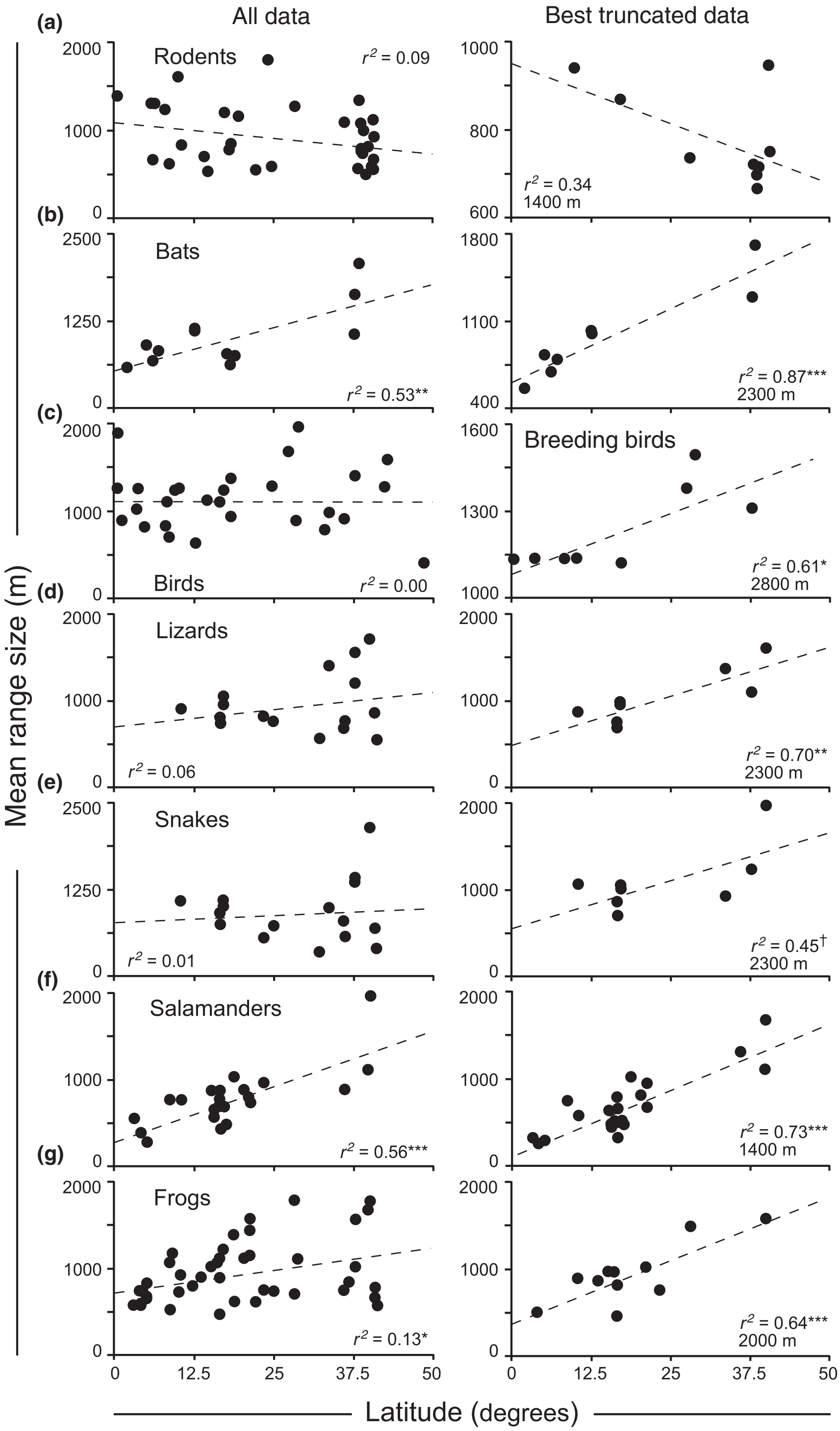

Figure 2 Relationships between elevational range size and latitude for: (a) rodents, (b) bats, (c) birds, (d) lizards, (e) snakes, (f) salamanders, and (g) frogs using all mountains and the best truncated mountain dataset. Linear regression *P*-values for elevational range size and latitude: $^{\dagger}< 0.07$; $^{*}< 0.05$; $^{**}< 0.01$; $^{***}< 0.005$; see Table 1 for details on best Akaike information criterion, multiple regression models.

Bats

In accordance with Janzen's prediction, elevational range size increased strongly with increasing latitude (Table 1 and Fig. 2b). Latitude was consistently the strongest variable in all analyses (summed weights averaged 89%), except for the 1300 m truncation analysis where sampling scale was stronger.

Birds

Elevational range size did not increase with latitude for all birds, but did increase with latitude for breeding birds in the best subset and the first two truncation datasets (Table 1 and Fig. 2c). Despite attempts to remove the influence of mountain height, it remained the strongest predictor of elevational range size in the best subset and 2300 m truncation dataset. In best AIC models in which latitude was included, the average summed weight was only 56%, despite being the only variable of importance in the 1800 and 2000 m truncation datasets.

Lizards

In accordance with Janzen's prediction, elevational range size increased with increasing latitude (Table 1 and Fig. 2d). Once the influence of mountain height was reduced, all analyses found only latitude to be the best predictor of elevational range size with an average summed weight of 80%.

Snakes

In accordance with Janzen's prediction, elevational range size increased with latitude (Table 1 and Fig. 2e). Once the influence of mountain height was reduced, all analyses except the 1400 m truncation found only latitude to be the best predictor of elevational range size. But the trend was weaker than that of lizards: for best models including latitude, the average summed weight was only 56%.

Salamanders

In accordance with Janzen's prediction, elevational range size increased strongly with latitude (Table 1 and Fig. 2f). All the best models found latitude to be the only strong predictor of elevational range size with an average of 95% summed AIC weights. The exception was the 3000 m truncation model, as all mountains of this height occurred in tropical latitudes.

Frogs

In accordance with Janzen's prediction, elevational range size increased with latitude in all models (Table 1 and Fig. 2g). Latitude was also the strongest predictor of elevational range size in all the best models with an average of 96% summed AIC weights.

Secondary predictions

Ectotherm taxa showed a stronger increase in elevational range size with increasing latitude than did endotherm taxa, as bats were the only endotherms to show a consistently strong signal in AIC best models (Fig. 2). Ectotherms had statistically higher r^2 values than endotherms when examining the simple linear regressions of elevational range size and latitude (Mann–Whitney *U*-test: first truncated $Z = -1.77$, *P*-value = 0.04; second truncated $Z = -1.77$, *P*-value = 0.04; and best subset $Z = -1.41$, *P*-value = 0.08).

Elevational ranges sizes were indeed larger among the species occurring in the upper vs. the lower one-third of the elevational gradients for all taxa except salamanders (Table S1; paired *t*-tests: rodent $t = -2.29$, $P = 0.01$, $n = 33$; bat $t = -4.48$, $P < 0.001$, $n = 12$; breeding bird $t = -3.87$, $P < 0.001$, $n = 17$; lizard $t = -3.56$, $P = 0.001$, $n = 16$; snake $t = -6.40$, $P < 0.001$, $n = 16$; salamander $t = -0.42$, $P = 0.34$, $n = 23$; frog $t = -6.41$, $P < 0.001$, $n = 42$; best subset data showed the same relationships). Janzen's trend of increasing range size with increasing latitude was stronger for the lower than the upper elevation assemblages for all vertebrate taxa except frogs (Fig. 3; Table S1; Mann–Whitney *U*-test: all data $Z = -1.73$, *P*-value = 0.04; best subset $Z = -2.36$, *P*-value = 0.01).

Evidence for a precipitation effect was minimal (Table 1). Only two models found a strong effect of precipitation: bats with the 2100 m truncation dataset (summed weight = 70%) and frogs with the 2000 m truncation dataset (summed weight = 63%). In both cases, elevational range sizes were smaller on arid than on wet gradients.

DISCUSSION

Vertebrates do indeed have smaller elevational range sizes in the tropics (Figs 2 and 3). The results confirm the fundamental range size prediction of Janzen's (1967) hypothesis that mountains may be physiologically higher in the tropics. Salamanders, bats, and frogs showed the strongest latitudinal trend in elevational range size, followed by lizards, snakes, and breeding birds (Figs 2 and 3; Table 1). Rodents were the exception (Fig. 2a). Of the six variables in the vertebrate models, latitude was the strongest both in terms of inclusion and in its predictive strength (Table 1).

Mountain height, scale, and sampling strongly influenced elevational range size trends (Table 1). Effects of scale and sampling percentage were largely removed by focusing on the best subset of data: regional scale studies from mountains ≥2000 m height with at least 80% of height sampled. Best subsets revealed a latitudinal trend in range size for breeding birds, lizards, and snakes, and the strength of the latitude-range size trend increased dramatically for bats, salamanders, and frogs (Table 1; Figs 2 and 3). Even with the best subset data, mountain height was still a strong predictive variable, particularly for endotherms (Table 1). Height effects were mostly reduced with truncated data. In these final models, latitude was the single best predictor of elevational range sizes for vertebrates. Occasionally other variables were included in truncated height models, but rarely were they strong or consistent (Table 1). The three levels of analyses highlighted the necessity of evaluating sampling and mountain height differences when testing Janzen's predictions, and may be why some studies have

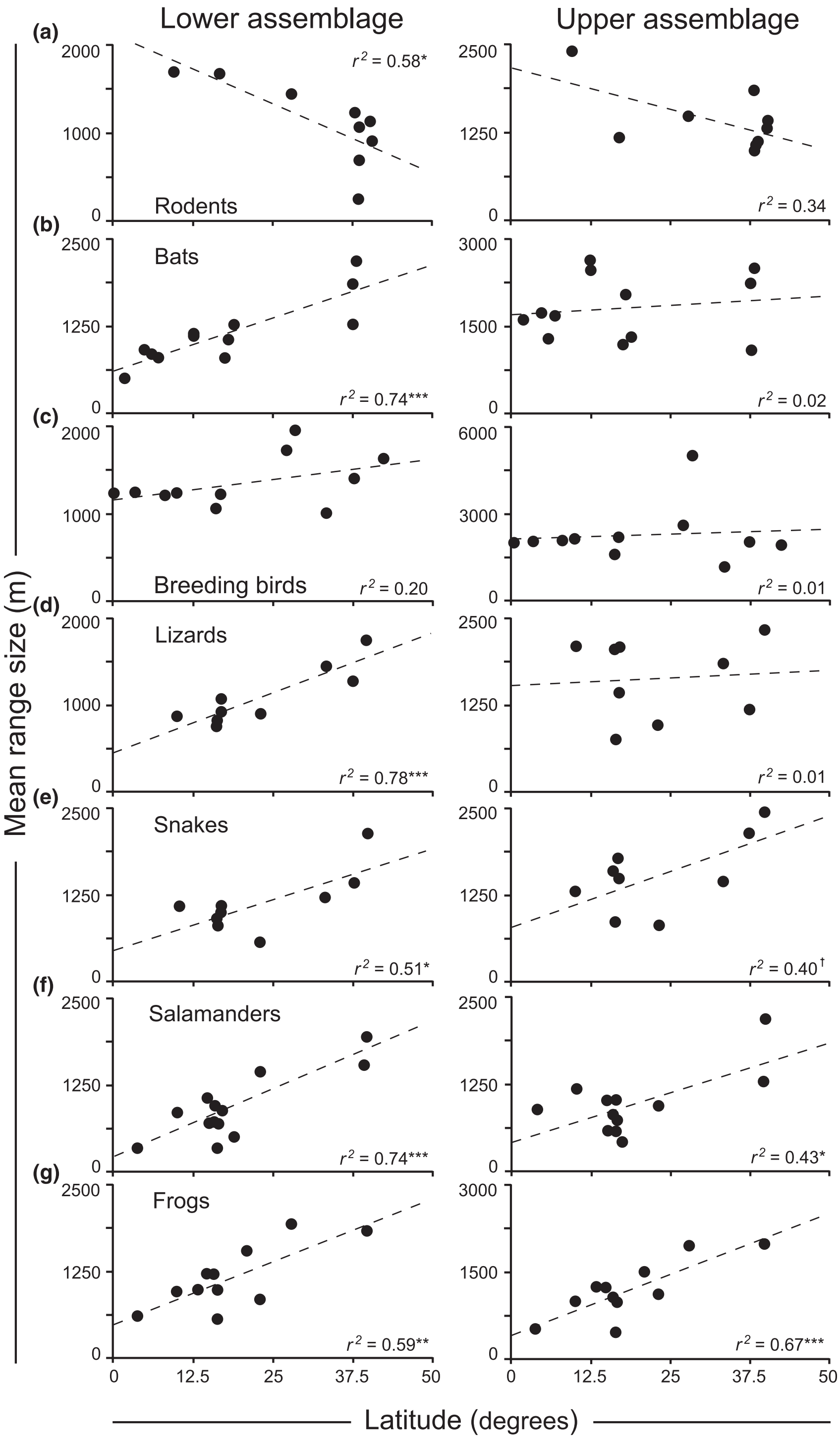

Figure 3 Relationships between elevational range size and latitude for the species assemblages at the lower and upper third of the mountains for: (a) rodents, (b) bats, (c) birds, (d) lizards, (e) snakes, (f) salamanders, and (g) frogs using the best subset dataset. Linear regression *P*-values: $^{\dagger}< 0.07$; $^{*}< 0.05$; $^{**}< 0.01$; $^{***}< 0.005$.

shown a lack of support for range size differences (e.g. Kozak & Wiens 2007).

Ambient temperature is the mechanistic basis of Janzen's hypothesis: the less overlap in temperature among elevationally separated sites, the more pronounced the montane dispersal barrier (Janzen 1967; Huey 1978; Ghalambor *et al.* 2006; Kozak & Wiens 2007). Two additional lines of evidence, mode of thermoregulation, and daily temperature variability, provide support for a temperature mechanism underlying vertebrate range size trends. Ectotherms are limited by temperature and sunlight as their body temperature is a reflection of the surrounding environment, whereas endotherms can be active during a broader array of temperature conditions as they internally maintain their body temperature (Porter & Gates 1969). Because of these thermoregulatory constraints, ectotherms should show stronger effects of temperature than endotherms. This difference was confirmed. More ectotherm taxa increase elevational range size with increasing latitude than do endotherm taxa (Fig. 2) and the strength of the trend was stronger than endotherms. Bats show a stronger trend than expected. Bats may be most sensitive to temperature, among vertebrate endotherms, because of thermoregulatory constraints on mammalian adaptations to flight at cold temperatures (McNab 1969; Graham 1983; Vaughan 1985; Patterson *et al.* 1996; and references therein). For instance, bats do not occur in arctic regions where rodents and birds are numerous (Vaughan 1985). Moreover, upper limits of bats on mountains are generally lower than limits for birds and rodents (data herein; McCain 2005, 2007; McCain, 2009). Rodents do not follow the expected trend; this exception also may be associated with thermoregulation. Rodents may be the most adapted, among vertebrates, in modifying their external thermal environment by burrowing deep into the soil and under snow (Porter & Gates 1969). Such behavioural manipulation of experienced temperature may lead to a decoupling of temperature, elevational range sizes, and latitude. A negative trend with latitude is harder to explain with thermoregulation, and may be a result of sampling, as few datasets on rodents have been collected on tall mountains in the tropics (e.g. Andes; Appendix S1).

Second, if temperature variability is the mechanism driving range size trends, then effects of daily temperature variation should also be as detectable as seasonal temperature effects (Ghalambor *et al.* 2006). Upper elevation communities in the tropics and temperate regions experience a daily high variation in temperature with pronounced daytime radiant heat and cold nights that can be of a similar magnitude to temperate annual variability. If temperature is a consistent mechanistic driver of range sizes, then upper elevation species assemblages should have larger ranges than low elevation assemblages. This difference was confirmed. Species occurring in the upper one-third of mountains had larger elevational ranges than low elevation species (except salamanders; Table S1). Also, when analysed separately, the lower assemblages had stronger latitudinal increases in elevational range size than high elevation assemblages (except frogs; Fig. 3 and Table S1). Together, thermoregulatory and daily temperature effects provide additional support for Janzen's prediction that temperature variability is a central component in determining species range sizes on mountains (Ghalambor *et al.* 2006).

Precipitation lacked a strong relationship with elevational range sizes. It was only a strong variable in two truncated models, one for bats and one for frogs (Table 1). In general, elevational range sizes are smaller on arid than on wet gradients. This may reflect species range restrictions to either the lower arid habitats or the higher forested habitats on these gradients, which individually are shorter than completely forested habitats on mountains in wet regions. Among vertebrates, frogs may be the most dependent on water for reproduction (Porter & Gates 1969; Pough *et al.* 2004), which would lead to a strong precipitation effect. Also, recent analyses have shown that in arid montane climates, bats are particularly sensitive to water as compared with the wet, tropical gradients (McCain 2007). But the lack of a consistent precipitation signal across multiple bat and frog analyses suggests that this effect is minor (Table 1).

Are there other reasons that elevational range sizes might increase with latitude besides Janzen's hypothesis? One possibility is the influence of glaciations and re-colonization of high latitude mountain ranges leading to greater elevational range sizes on temperate mountains (Martin & McKay 2004; Ghalambor *et al.* 2006). But low latitudes also experienced large vegetative shifts elevationally owing to climate change similar to the temperate zone, which may have led to similar increases in range sizes (Vuilleumier 1971; Coates 1997; Colinvaux 1997). Another possibility is the influence of larger geographic range sizes at high latitudes, and a coupling between geographic and elevational range sizes. From the testing of Rapoport's (1982) rule (Stevens 1989), we know that some vertebrate groups do have larger geographic ranges at higher latitudes (Stevens 1989; Lyons & Willig 1997; Gaston *et al.* 1998; Arita *et al.* 2005). It is currently unknown if there is a strong correlation between latitudinal and elevational range sizes. Huey (1978) and MacArthur (1972) raised the possibility that greater competition may lead to smaller ranges and/or smaller niche breadth in the tropics than in the temperate region. Other possible explanations include several biogeographic patterns of mountains. For instance, tropical latitudes simply may encompass a greater concentration of mountains, or physically higher mountains, or mountains with a larger spatial extent, all of which could influence speciation, endemism, and range sizes. To my knowledge, none of these factors has been examined in a geographic-latitudinal context, but each presents interesting avenues for future research.

In conclusion, latitudinal trends in elevational range size of vertebrates are consistent with the Janzen's prediction that tropical mountains present a higher physiological barrier. Thermoregulatory differences, daily temperature effects, and lack of a strong relationship with precipitation provide additional lines of evidence for a temperature mechanism influencing vertebrate range sizes. Examination of other groups (e.g. insect and plants), particularly those contrasting key elements of Janzen's hypothesis – sensitivity to temperature, dispersal ability, and diversity patterns – will provide an important comparison and potential additional confirmation of vertebrate trends. Finer scale examinations in vertebrates of reduced dispersal ability, niche breadth, and physiological tolerance predicted by Janzen invite further detailed examination, particularly for groups with the strongest latitude-range size trends – bats, salamanders, frogs, and lizards. There may be other geographic, evolutionary, or biotic factors underlying elevational range size-latitude trends, but these hypotheses are less appealing than Janzen's hypothesis. Nonetheless, many of these possibilities are plausible and are yet unexplored. Finally, latitudinal dynamics of montane range sizes have strong conservation implications and may indicate differential impacts of climate change (Ghalambor *et al.* 2006; Colwell *et al.* 2008). Tropical mountains harbour a considerable portion of the world's diversity and rare species (Orme *et al.* 2005, 2006; Rahbek *et al.* 2007); if these species are less adapted to move upward in response to climate change as Janzen (1967) predicts, then this signals higher extinction risks from climate change and habitat modification.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Statistics examining relationship between elevational range size and latitude for species assemblages at high and low elevation.

Appendix S1 Detailed information on the elevational gradients used to test range size predictions.

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