

Little evidence for Bergmann's rule body size clines in passerines along tropical elevational gradients

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ABSTRACT

Aim To test whether intra- and interspecific patterns in body mass along elevational gradients follow Bergmann's rule for a subset of tropical montane passerines.

Location Tropical elevational gradients in New Guinea, Borneo, Peru and Costa Rica.

Methods I used linear regressions to assess intraspecific patterns in body mass along elevational gradients in common New Guinean passerines (2697 mist-netted individuals of 21 species). I then evaluated interspecific patterns using two data sets. First, I investigated differences in body mass in species pairs of elevational replacements, closely related species with minimal overlap along elevational gradients (species pairs; New Guinea: $n = 45$, Borneo: $n = 22$, Peru: $n = 58$ and Costa Rica: $n = 30$). Second, I used a comparative phylogenetic approach to test whether species' mid-point elevations predicted their masses within entire passerine avifaunas found along single elevational gradients (species; New Guinea: $n = 184$, Peru: $n = 529$ and Costa Rica: $n = 220$).

Results New Guinean passerines exhibited minimal intraspecific variation in mass along elevational gradients. In two species, lower elevation individuals had significantly larger masses than upper elevation conspecifics. In species pairs of elevational replacements, there was no trend for upper elevation species to have larger masses than lower elevation species. Overall, species pairs tended to have positive mass disparities (mass of upper elevation species/mass of lower elevation species). However, contrary to predictions of Bergmann's rule, mass disparity was unrelated to elevational overlap. When considering entire passerine avifaunas along single elevational gradients, species' masses were uncorrelated with their mid-point elevational distributions.

Main conclusions I found little evidence that tropical montane passerines have larger body masses at higher elevations where temperatures are colder. This lack of pattern was consistent across evolutionarily independent avifaunas of different biogeographical regions. These results suggest mean temperature is not a generally important driver of body size evolution in tropical montane passerines.

Keywords

Bergmann's rule, body size, body size clines, comparative phylogenetics, ecogeographic rule, elevational gradient, tropical mountains

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INTRODUCTION

Body size is an ecologically influential trait that varies widely within and among species (LaBarbera, 1989; Brown *et al.*, 2004). Although many abiotic and biotic mechanisms can

drive the evolution of body size (Brown *et al.*, 2004), temperature is one potentially important abiotic factor influencing body size evolution – Bergmann's rule describes the pattern that populations or species of endotherms living in colder environments tend to be larger than related

populations or species living in warmer environments (Bergmann, 1847; James, 1970). The proper formulation of Bergmann's rule remains debated; perhaps most importantly, Bergmann's rule has been considered both a pattern (a negative relationship between body size and temperature) and a process (temperature exerts selection on body size via physiological mechanisms such as thermoregulation; e.g. Watt *et al.*, 2010; Meiri, 2011; Olalla-Tárraga, 2011; Watt & Salewski, 2011). Investigations of Bergmann's rule have traditionally analysed body size clines along latitudinal gradients (e.g. Ashton, 2002; Ashton & Feldman, 2003; Watt *et al.*, 2010; Feldman & Meiri, 2014). However, temperature declines not only with increasing latitude, but also with increasing elevation; thus, studies have also analysed whether Bergmann's rule patterns are found in body size clines along elevational gradients (e.g. Brehm & Fiedler, 2004; Herzog *et al.*, 2013).

Tropical elevational gradients offer an excellent geographical arena to investigate whether body size clines are associated with temperature. Temperatures decline over short distances along tropical mountain slopes, where ambient mean temperature drops *c.* 5–6 °C per 1000 m gain in elevation (Forero-Medina *et al.*, 2011; Freeman & Class Freeman, 2014a). As a consequence, sites on steep slopes may be located just a few kilometres apart but experience very different temperatures. Because temperature variation is typically minimal at particular sites along tropical elevational gradients (e.g. daily temperatures at a given site within the forest understorey vary by *c.* 5 °C, and annual variation is typically minor), sedentary tropical organisms separated by even small (*c.* 750 m) expanses of elevation can experience completely distinct temperatures, at least in the shaded forest interior (Janzen, 1967).

Evidence that tropical and subtropical montane faunas exhibit body size clines consistent with Bergmann's rule along elevational gradients is mixed. Increases in body size in colder high elevation environments within species have been found in some cases (e.g. Rand, 1936; Lu *et al.*, 2006; Vanderwerf, 2012), and in interspecific comparisons in clades of Neotropical frogs (Gouveia *et al.*, 2013) and lizards (Cruz *et al.*, 2005; Zamora-Camacho *et al.*, 2014), but not in clades of Asian frogs (Hu *et al.*, 2011) or Neotropical butterflies (Hawkins & Devries, 1996), moths (Brehm & Fiedler, 2004) or dung beetles (Herzog *et al.*, 2013). Results can be inconsistent within a taxonomic group in a single geographical region. For example, patterns of intraspecific body size variation in Andean birds follow Bergmann's rule in some (Traylor, 1950; Graves, 1991; Bulgarella *et al.*, 2007) but not all (Remsen, 1984, 1993) species, including an example where a species exhibits Bergmann's rule body size clines across latitudinal but not elevational gradients (Gutiérrez-Pinto *et al.*, 2014). This inconsistency holds for analyses at the interspecific level – some clades of tropical birds exhibit Bergmann's rule body size clines while others do not (Blackburn & Ruggiero, 2001).

Thus, it remains unclear whether tropical montane birds generally exhibit larger body masses at higher (colder)

elevations as predicted by Bergmann's rule. I addressed this question by testing how body sizes in the largest group of tropical montane birds – the passerines – are related to their elevational distributions. To assess the generality of any patterns (or lack thereof), I investigate the relationship between body mass and elevational distribution in interspecific comparisons within the evolutionarily distinct avifaunas of the Neotropics, Southeast Asia and Melanesia. I consider Bergmann's rule to simply be a negative relationship between body size and temperature (i.e. a pattern; hereafter 'Bergmann's rule'). As such, Bergmann's rule predicts that (1) within species, individuals at high elevations should tend to be larger than individuals at low elevations, (2) within species pairs of closely related species, upper elevation species should be larger than lower elevation species, with this relationship strongest in species pairs that inhabit non-overlapping elevational distributions (and thus experience more different ambient temperatures relative to species pairs with greater elevational overlap) and (3) when accounting for phylogenetic relationships, elevational distributions should be significantly positively related to body size in large assemblages of species. I tested these predictions using (1) field data for common species of New Guinean understorey passerines captured along two single elevational gradients, (2) relative body masses in species pairs of closely related species that inhabit minimally overlapping elevational distributions along an elevational gradient in four distinct tropical montane regions (the Eastern highlands of New Guinea, Manu National Park in the Peruvian Andes, the Caribbean slope of Costa Rica and the highlands of Malaysian Borneo) and (3) phylogenetic comparative methods to assess whether species' mid-point elevational distributions significantly predicts their body size in the entire passerine avifaunas found in three regions (the Eastern highlands of New Guinea, Manu National Park in the Peruvian Andes and the Caribbean slope of Costa Rica). Taken together, these analyses provide a general test of whether tropical montane passerines conform to Bergmann's rule.

MATERIALS AND METHODS

Intraspecific

Bergmann's rule predicts that, within species, individuals should tend to have larger masses at high elevations. I tested this prediction using field body mass data gathered along two elevational gradients in Papua New Guinea: the YUS Conservation Area, Morobe Province and the north-west ridge of Mt Karimui, Chimbu Province. The YUS Conservation Area (hereafter YUS, approximate coordinates: –6.00, 146.84) is located on the northern scarp of the Saruwaged Range on the Huon Peninsula. Between 2010 and 2012, a team of fieldworkers conducted mist-net surveys in primary forest along a single elevational gradient from 230 to 2940 m in YUS; a total of 18 mist-net surveys were completed along 1-km trails cut along elevational contours at intervals of

120–200 m in elevation (see Freeman *et al.*, 2013, for more information). On the north-west ridge of Mt. Karimui (approximate coordinates: $-6.56, 144.76$), a team of fieldworkers surveyed the understorey bird communities with mist nets along a continuous gradient of primary forest between 1150 m and 2520 in June–July 2012 (see Freeman & Class Freeman, 2014b, for further details). At both sites, captured individuals were weighed using Pesola spring scales (a 30-g scale for smaller species and a 100-g scale for larger species).

I compiled field body mass data for 2548 individuals of 21 common understorey passerines from seven families found within YUS (see Appendix S1 in Supporting Information). These species were commonly captured (mean number of weighed individuals = 122, range = 48–327 weighed individuals/species) across a range of elevations (mean elevational breadth per species = 1220 m, range = 520–1810 m). I additionally included field body mass data for 139 individuals from two species from Mt. Karimui ($n = 102$ and 37 weighed individuals; elevational breadth = 800 and 1025 m, respectively; these same two species also appear in the YUS data, see Appendix S1). I then used linear regressions implemented in R (R Core Team, 2014) to test if, for each species at each site, individuals captured at higher elevations tended to be heavier than individuals captured at lower elevations. I included sex as a predictor variable for four species in which males and females differ in plumage [black berrypecker (*Melanocharis nigra*), fan-tailed berrypecker (*Melanocharis versteri*), regent whistler (*Pachycephala schlegelii*) and black fantail (*Rhipidura atra*)], though note that juvenile males have female-like plumage in these species, and applied a Bonferroni correction to account for the influence of multiple tests on statistical significance.

Interspecific: Elevational replacements

Bergmann's rule predicts that, when closely related species inhabit different elevational zones, (1) the upper elevation species should have a larger mass and (2) this difference in mass should be positively correlated with elevational divergence within the species pair (i.e. upper elevation species should have especially larger masses than their lower elevation relatives when species within a species pair inhabit completely distinct elevational zones and thus experience a greater difference in temperatures than species pairs with greater elevational overlap). I tested these predictions by identifying species pairs of closely related species (nearly all congeners, see Appendix S2) that occupied divergent elevational distributions (defined as species pairs with elevational overlap < 50%; most species pairs in this data set had narrow elevational overlaps, with the median elevation overlap = 8.8% and the 75th percentile of elevational overlap = 23.2%). Such species pairs of 'elevational replacements' are prominent in tropical montane faunas (Patterson *et al.*, 1998; Pyrcz & Wojtusiak, 2002; Pasch *et al.*, 2013) and are especially common in birds (Terborgh & Weske, 1975; Jankowski *et al.*, 2010; Freeman & Class Freeman, 2014b). I

used single references to compile species pairs of passerine elevational replacements found along forested elevational gradients in four regions that feature large mountain ranges spanning from lowlands (< 400 m) to above tree line (> 3000 m): the Eastern highlands of New Guinea ($n = 45$ species pairs; Pratt & Beehler, 2014), Manu National Park in the Andes of south-eastern Peru ($n = 58$ species pairs; Walker *et al.*, 2006), the Caribbean slope of Costa Rica ($n = 30$ species pairs; Stiles & Skutch, 1989) and Malaysian Borneo ($n = 22$; Myers, 2009). I quantified body masses for each species using a single reference volume (Dunning, 2007; see Appendix S2). I limited my analysis to forest passerines (hereafter 'passerines'), as the majority of habitat in these regions is forested.

I first used a sign test to ask whether cases where upper elevation species had larger masses than their lower elevation relatives ('high and heavy' species pairs) outnumbered reversed cases ('low and large' species pairs) in each region. This simple analysis does not consider quantitative differences in mass difference. I therefore calculated the mass disparity for each species pair – the mass of the upper elevation species divided by the mass of the lower elevation species, such that positive mass disparities indicate 'high and heavy' cases – and used *t*-tests to assess whether species pairs within regions had significantly positive mass disparities. This analysis, in turn, overlooks differences in the degree to which species within species pairs experience different ambient temperatures. If colder temperatures are associated with larger body masses, as predicted by Bergmann's rule, body mass disparities should be negatively correlated with elevational overlap (greater mass disparities in species pairs that occupy distinct elevational zones that do not overlap). I tested this prediction using a *t*-test to examine whether species pairs with non-overlapping elevational distributions ($n = 63$, a subset of the total data set) had mass disparities significantly greater than zero, and also a linear regression model, with mass disparity as the response variable and elevational overlap and region as predictor variables.

Interspecific: Passerine avifaunas

Bergmann's rule predicts that, in large assemblages of species, species' elevational distributions should be significantly related to their body mass when taking phylogenetic relationships into account. I tested this prediction using the passerine avifaunas found along elevational gradients in three distinct regions, the Eastern highlands of New Guinea, Manu National Park in south-eastern Peru and the Caribbean slope of Costa Rica. I used the same reference volume to quantify body masses for each species in each region (Dunning, 2007) and single sources (New Guinea: Pratt & Beehler, 2014; Costa Rica: Stiles & Skutch, 1989; Peru: Walker *et al.*, 2006) to define passerine species' elevational ranges within regions (New Guinea: $n = 184$ species; Peru: $n = 529$ species; Costa Rica: $n = 220$ species), and used elevational mid-point to characterize species' elevational distributions (see

Appendix S2). Because body mass data were unavailable for many Bornean species, I did not include the passerine avifauna of Malaysian Borneo in this analysis.

I then used comparative phylogenetic methods to test whether species' elevational mid-points were significantly related to their mass while accounting for evolutionary relatedness among species. I transformed both response and predictor variables using log transformations so that residuals conformed to a normal distribution. I used a phylogenetic tree from Jetz *et al.* (2012) that consisted of passerine taxa with genetic information ('Hackett sequenced species'), in combination with phylogenetic generalized least squares (PGLS, Martins & Hansen, 1997), implemented using the packages 'nlme' (Pinheiro *et al.*, 2013) and 'ape' (Paradis *et al.*, 2004) in the R programming environment (R Core Team, 2014). I scaled internal branch lengths according to Pagel's λ model, which estimates the amount of phylogenetic signal present in the evolutionary history of a given character (Pagel, 1999; Blomberg *et al.*, 2003). In this model, the λ parameter varies from 0 (no phylogenetic signal or a star phylogeny) to 1 (phylogenetic signal equal to Brownian motion or branch lengths remain unchanged) and therefore provides a convenient measure of evolutionary lability for the trait in question. I examined residual plots by eye and removed one outlier from the analysis of Costa Rican passerines. Results were very similar with and without this outlier; I present results of the model with the outlier excised. I also investigated using a Ornstein–Uhlenbeck (OU) model of trait evolution to investigate body mass evolution in each region, but OU models failed to converge and were thus unable to be parameterized (Ho & Ané, 2014). I therefore report only results of Pagel's λ models.

RESULTS

Intraspecific

Most species exhibited minimal variation in body mass along New Guinean elevational gradients. Coefficients for species' mass elevation regressions are clustered around 0, and 95% confidence intervals overlap with 0 in nearly all cases, indicating that body size clines along elevation were rare in this sample (Fig. 1, see Table S1 in Appendix S3 for full results). After using a Bonferroni correction to account for multiple tests, only two species (out of 23) showed significant elevational body size clines. Both cases were opposite to that predicted by Bergmann's rule; the little shrikethrush (*Colluricincla megarhyncha*), found in the lowlands and foothills, and the rufous-backed honeyeater (*Ptiloprora guisei*) found at middle and upper elevations, are each *c.* 12% smaller in mass at their high elevation limits in YUS compared to their low elevation limits (see Figure S1 in Appendix S3).

Interspecific

In each region, 'high and heavy' cases (where the upper elevation species had a larger mass) were not significantly more

frequent than 'low and large' cases (where the lower elevation species had a larger mass; *P*-values from sign tests = 0.20–1, Table 1). However, the difference in masses within a species pair tended to be greater in 'high and heavy' cases compared to 'low and large' cases (Fig. 2a) – mass disparities were significantly positive in Peru (95% confidence interval for mass disparity = 0.0057–0.16; $t = 2.16$, d.f. = 57, $P = 0.035$) and positive in each of the other three regions (New Guinea: 95% confidence interval for mass disparity = -0.037 to 0.17; d.f. = 44, $t = 1.28$, $P = 0.21$; Costa Rica: 95% confidence interval for mass disparity = -0.015 to 0.17; d.f. = 29, $t = 1.70$, $P = 0.099$; Borneo: 95% confidence interval for mass disparity = -0.075 to 0.27; d.f. = 15,

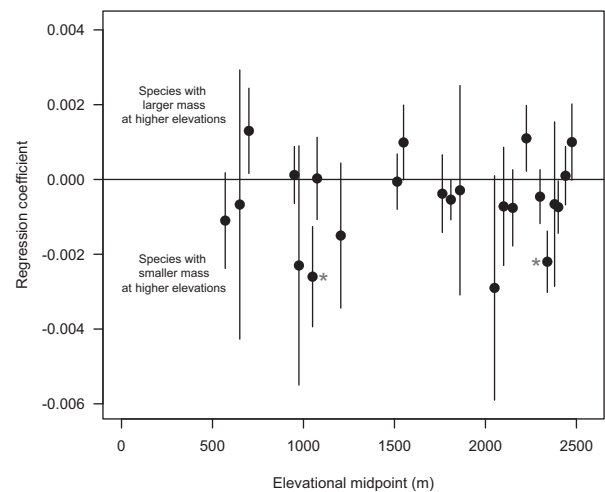


Figure 1 Intraspecific elevational patterns in body mass in 21 species of New Guinean passerines found along two elevational gradients. Each species' coefficient and 95% confidence interval from a mass elevation regression is plotted; points above the zero line indicate species that tended to have larger masses at higher elevations. Asterisks denote two species with significant intraspecific body size clines ($P < 0.05$) following Bonferroni correction (see Fig. S1).

Table 1 Regional patterns of body mass variation in elevational replacements of tropical montane passerines. Species pairs were classified as 'high and heavy' when the upper elevation species had a larger mass and 'low and large' when the lower elevation species had a larger mass. *P*-values give results from sign tests within regions. Two species pairs from Peru had identical body masses and body masses were unavailable for six species pairs from Borneo.

Region	'High and heavy' species pairs	'Low and large' species pairs	<i>P</i> -value
New Guinea (Eastern Highlands)	23	22	1
Peru (Manu National Park)	28	28	1
Costa Rica (Caribbean slope)	19	11	0.20
Borneo (Sabah)	6	10	0.45

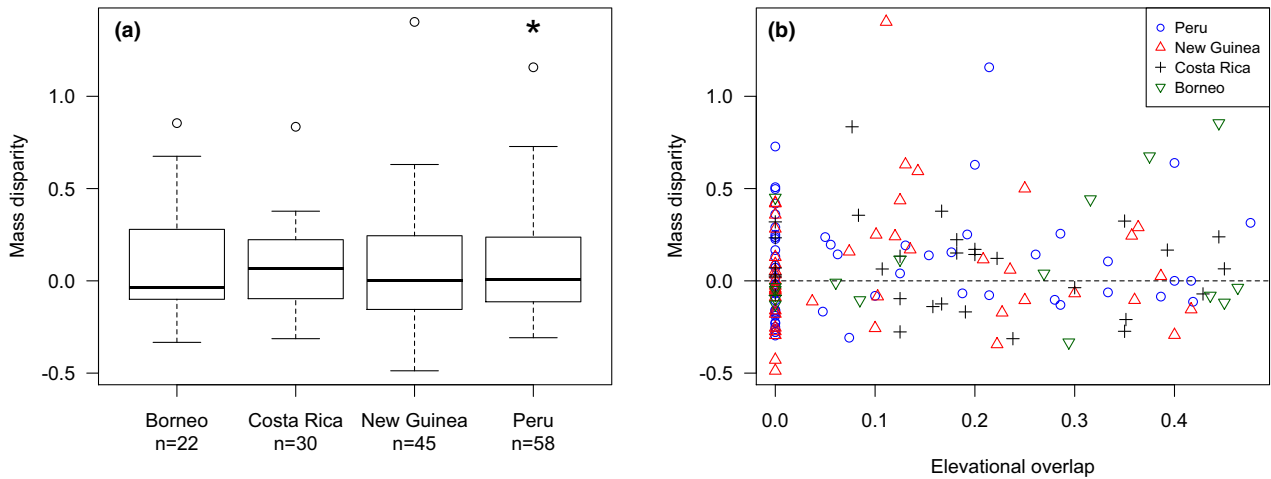


Figure 2 Interspecific elevational patterns in body mass in species pairs of elevational replacements found in four regions: (a) boxplots illustrate mass disparities for species pairs in each region. The median is denoted with a horizontal black bar, boxes demarcate first and third quartiles and points and dotted lines illustrate minimum and maximum values. Median values are close to zero, indicating similar numbers of cases with positive (upper elevation species has larger mass) and negative mass disparities (lower elevation species has larger mass), but mean mass disparity is positive in each region, and significantly so in Peru ($P < 0.05$, denoted by an asterisk). (b) Elevational overlap is unrelated to mass disparity within species pairs of elevational replacements in four regions, indicating that species pairs that experience more divergent temperatures do not tend to have greater mass disparities. The dashed horizontal line at mass disparity = 0 serves to distinguish species pairs with positive and negative mass disparities.

$t = 1.21$, $P = 0.24$). However, mass disparities were not larger in species pairs with less elevational overlap (Fig. 2b). When considering the subset of species pairs with non-overlapping elevational distributions, mass disparities were not significantly different from zero ($n = 63$ species pairs; 95% confidence interval = -0.039 to 0.089 , $t = 0.79$, d.f. = 61, $P = 0.43$, see points at elevational overlap = 0 in Fig. 2b). In addition, parameter estimates for elevational overlap were not significantly different from zero in a linear regression model predicting mass disparity (Fig. 2b, Table S2 in Appendix S3).

Phylogenetic generalized least square models for each region had lambda values very near 1, indicating relatively high phylogenetic signal in passerine body mass (Fig. 3, Table S3 in Appendix S3). Parameter estimates for log mid-point elevation in each model were not significantly different

from zero, indicating that log mid-point elevation does not predict log body mass at the large phylogenetic scale of entire passerine avifaunas found along an elevational gradient.

DISCUSSION

Tropical montane passerines vary widely in body mass (Dunning, 2007). However, I found little evidence that this variation in body mass is related to species' elevational distributions, which serve as a convenient proxy for the ambient temperatures experienced by a species. At the intraspecific level, a sample of New Guinean passerines exhibited minimal variation in body mass along single elevational gradients (Fig. 1), with two case examples wherein species showed significant decreases in body mass with elevation. At the interspecific level, species' body masses were

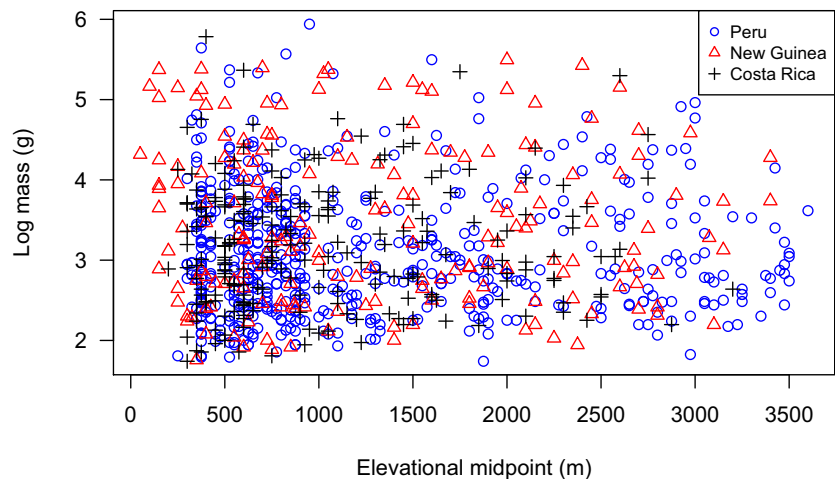


Figure 3 Log elevational mid-point is unrelated to log mass in the passerine avifaunas of three regions. Parameter estimates for elevational mid-point in phylogenetic generalized least squares models were not significantly different from zero (see Table S3).

weakly related to their elevational distributions at a shallow phylogenetic scale (when considering species pairs of elevational replacements, closely related species pairs that inhabit different elevational zones; Table 1, Fig. 2), and unrelated to their body masses at deeper phylogenetic scales (considering entire passerine avifaunas; Fig. 3). Given that the tropical montane passerines in this study did not demonstrate body size clines consistent with Bergmann's rule, the mechanistic processes of physiological adaptation hypothesized to underlie Bergmann's rule seem unlikely to generally apply to tropical montane birds.

These results contrast with previous published studies investigating body mass variation in birds that have often found geographical patterns of body size clines consistent with Bergmann's rule. For example, global analyses of intraspecific variation in avian body mass have found the strong pattern that populations in colder environments are typically larger than those found in warmer environments (Ashton, 2002; Meiri & Dayan, 2003). However, these studies included few tropical species and primarily considered body mass patterns along latitudinal gradients, where differences in temperature covary with many additional abiotic (e.g. temperature seasonality) and biotic (e.g. species richness, resource seasonality) factors that could also influence body size evolution. Intraspecific patterns in tropical birds along elevational gradients are sometimes consistent with Bergmann's rule (e.g. Traylor, 1950; Vanderwerf, 2012), but most New Guinean passerines (21 out of 23 comparisons) in this study did not vary in mass over an elevational gradient, and the two exceptions were in the opposite direction to that predicted by Bergmann's rule. These results conflict with a previous analysis of New Guinean birds that reported body size increases (using wing length as the metric of body size) with elevation in a wide variety of species in the mountains of southeast New Guinea, including several species included in the current analysis (Rand, 1936). This discrepancy could reflect different patterns of body size variation in different montane regions within New Guinea or different methodologies (measuring body mass vs. wing length). However, it seems more likely that the patterns described by Rand (1936) may be artefacts of the small sample sizes of museum specimens then available for analysis (mean = *c.* 10–25 individuals/species in Rand's analysis vs. mean = 122 individuals/species in the current analysis). Nevertheless, further studies are necessary to test the possibility that intraspecific body size clines consistent with Bergmann's rule are present in tropical montane passerines in species omitted in my analysis (e.g. canopy species that are poorly sampled with mist nets), in other regions in New Guinea, or more generally in other tropical regions.

When comparing closely related species that inhabit different elevational distributions within each of four regions, I found equal proportions of cases where the upper elevation species had a larger mass ('high and heavy') and where the lower elevation species had a larger mass ('low and large'; Table 1). While the proportion of 'high and heavy' and 'low and large' cases was similar, 'high and heavy' examples tended

to have a greater difference in mass (mass disparity), and this relationship was significantly positive in one region (Peru). These results provide some support for a positive relationship between body size and elevation. However, the key prediction of the Bergmann's rule pattern, applied to species pairs of elevational replacements, is that mass disparities are largest in species pairs that experience very different temperatures (i.e. species pairs that inhabit non-overlapping elevational distributions). I found no evidence that this was the case in any region (Fig. 2b). Additionally, species' elevational mid-points were not related to their body mass in a comparative phylogenetic analysis of entire passerine avifaunas (Fig. 3).

On the surface, these results contradict a previous study of Andean passerines that found correlations between species' body masses and elevational mid-points (Blackburn & Ruggiero, 2001). These contradictory results could be due to differences in spatial scale between analyses – instead of the entire avifauna found within a region (i.e. all Andean passerines), I used only the set of species found along a single elevational gradient in south-eastern Peru in my analysis. However, in the regional analysis, mid-point elevation explained only 2% of variation in body mass, and many clades did not follow Bergmann's rule (Blackburn & Ruggiero, 2001). Thus, Blackburn & Ruggiero's (2001) analysis, while supporting the existence of a weak Bergmann's rule pattern in Andean passerines, also suggests that tropical montane passerines do not consistently show body size clines concordant with Bergmann's rule. This view accords with previous studies that found body size patterns in other tropical montane faunas do not conform to Bergmann's rule (Hawkins & Devries, 1996; Brehm & Fiedler, 2004; Herzog *et al.*, 2013).

These results have implications for the relationship between elevational distribution and competitive dominance in birds, where behavioural dominance in interspecific contests is typically associated with body size (Robinson & Terborgh, 1995; Freshwater *et al.*, 2014; but see Martin & Ghalambor, 2014). Recent field experiments have supported the long-standing hypothesis (Terborgh & Weske, 1975) that asymmetric interspecific aggression can influence the elevational distributions of pairs of tropical elevational replacements (Jankowski *et al.*, 2010; Pasch *et al.*, 2013). Many tropical montane passerines are shifting their distributions upslope associated with recent warming (Forero-Medina *et al.*, 2011; Freeman & Class Freeman, 2014a), and it has been hypothesized that asymmetric interspecific aggression between tropical elevational replacements may influence their rates of warming-associated upslope shifts (Jankowski *et al.*, 2010; Freeman *et al.* 2016). I found no consistent pattern in relative body mass between upper and lower elevation species pairs of elevational replacements. Thus, though speculative, if body mass is associated with behavioural dominance in tropical avian elevational replacements, relative elevational distribution alone is unlikely to predict interspecific aggression in these taxa. It is therefore likely that field studies will demonstrate both instances where lower elevation species are larger and behaviourally dominant (and could potentially 'push' their upper elevation replacement upslope with

continued warming; e.g. *Catharus* thrushes in Jankowski *et al.*, 2010 and songbirds in Freeman *et al.* in press; also see Freeman & Montgomery, 2016 for a possible temperate zone example) and also cases where upper elevation species are larger and behaviourally dominant (and may be able to maintain their distributions in the face of continued warming as 'kings of the mountain'; e.g. *Scotinomys* singing mice in Pasch *et al.*, 2013).

In conclusion, I found little evidence that tropical montane passerines conform to Bergmann's rule – in several analyses, the body masses of tropical montane passerines were unrelated to the elevational zones they inhabit. I found this lack of pattern in both intraspecific (New Guinean birds) and interspecific analyses (passerine avifaunas in multiple largely evolutionarily independent biogeographical regions). Because body size clines in tropical montane passerines do not conform to the pattern predicted by Bergmann's rule, the hypothesized process of colder mean temperatures selecting for larger body sizes due to physiological factors is unlikely to generally apply to tropical montane passerines. Thus, mean temperature appears to exert a minimal (or idiosyncratic) influence on body size in tropical montane passerines. In this view, biotic factors (e.g. social selection, resource availability and species interactions), and the interplay between abiotic and biotic factors, may be more important drivers of body mass evolution in tropical montane birds.

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SUPPORTING INFORMATION

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

Appendix S1 Raw data of New Guinean species' masses from mist-net captures.

Appendix S2 Database of species pairs of elevational replacements and all species included in comparative phylogenetic analysis.

Appendix S3 Additional figures and tables.

BIOSKETCH

Benjamin Freeman studies the ecological and evolutionary processes that generate the distributional patterns we observe in modern biotas. His research uses tropical montane avifaunas as a model system to test theories of biodiversity and understand species' responses to environmental change.

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