Thermal tolerances to cold do not predict upper elevational limits in New Guinean montane birds

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ABSTRACT

\textbf{Aim} To test predictions of the ‘fundamental physiological niche’ hypothesis that thermal tolerances are tightly correlated with upper elevational limits in New Guinean montane birds.

\textbf{Location} New Guinea.

\textbf{Methods} I combined previously published data describing New Guinean montane birds’ (1) metabolic responses to temperature, (2) elevational distributions and (3) recent upslope shifts, with an empirically measured lapse rate (temperature–elevation regression) to test two predictions of the fundamental physiological niche hypothesis – that species’ thermal tolerances to cold temperatures, measured as lower critical temperatures (LCTs) and thermal conductances, are correlated with their upper elevational limits (n = 24 species), and that species’ thermal mismatches (the difference between the mean temperatures species experience at their upper elevation limits and their LCTs) predict the magnitude of recent warming-associated upslope shifts (n = 11 species).

\textbf{Results} Species’ LCTs and thermal conductances were not correlated with the ambient temperatures they experience at their upper elevational limits (cold range limit), and species’ thermal mismatches were not related to the magnitude of recent upslope shifts at their upper elevational limits.

\textbf{Main Conclusions} My results do not support the fundamental physiological niche hypothesis and suggest New Guinean montane birds’ upper elevational limits are unlikely to be set by the direct influence of temperature on adult birds’ thermal tolerances. I also found no evidence that warming-associated upslope shifts in this avifauna are related to species’ thermal physiology. While this result is based on a small sample size, it is consistent with the hypothesis that recent upslope shifts result from biotic factors indirectly related to temperature.

\textbf{Keywords} biotic interactions, distributional limit, elevational gradient, global warming, thermal mismatch, thermonutral zone.

INTRODUCTION

Tropical mountains harbour some of the most biodiverse floras and faunas on Earth (Myers \textit{et al.}, 2000). Temperature declines predictably with increasing elevation along tropical elevational gradients that span from hot lowlands to cold high-elevation forests and grasslands above treeline (Janzen, 1967). Because most tropical montane species inhabit narrow elevational distributions (Patterson \textit{et al.}, 1998; McCain, 2009) and seasonal temperature variation in the tropics is minimal, tropical montane species typically experience a relatively narrow range of environmental temperatures, particularly within closed-canopy forest (Janzen, 1967). Thus, elevational specialization in tropical montane species may be associated with physiological adaptation to the thermal conditions found within a particular elevational zone (Ghalambor \textit{et al.}, 2006; Deutsch \textit{et al.}, 2008; Bozinovic \textit{et al.}, 2011). Supporting the hypothesis that temperature is a strong influence on the elevational limits of tropical montane species, tropical plants (Feeley \textit{et al.}, 2011; Jump \textit{et al.}, 2012),
ecotherms (Raxworthy et al., 2008; Chen et al., 2009) and endotherms (Forero-Medina et al., 2011; Freeman & Class Freeman, 2014) are shifting upslope at rates significantly associated with local temperature increases due to global warming.

However, the mechanisms by which temperature influences tropical montane species’ elevational limits remain unclear. One possibility is that temperature directly influences species’ elevational limits, a hypothesis termed the ‘fundamental physiological niche’ hypothesis by Jankowski et al. (2012). This scenario hypothesizes that montane species’ physiological adaptations to specific thermal environments limit their elevational distribution (Janzen, 1967; Deutsch et al., 2008; Sinervo et al., 2010). While the fundamental physiological niche hypothesis may especially apply to tropical ectothermic species (Buckley et al., 2008; Deutsch et al., 2008; Tewksbury et al., 2008), tropical endotherms’ distributions may also be directly affected by the temperatures they experience (McCain, 2009; Krockenberger et al., 2012; Khaliq et al., 2014). An alternate perspective is that temperature influences species’ elevational limits through indirect effects. For example, species’ range margins (and their warming-associated upslope shifts) could be controlled primarily by biotic interactions that may themselves ultimately link to temperature (Davis et al., 1998; Tylianakis et al., 2008; Thomas, 2010) or by interactions between direct and indirect influences of temperature (e.g. Helland et al., 2011).

It is important to recognize that, in reality, there is not a dichotomy between whether temperature directly or indirectly influences distributions, but rather a gradient between the relative effects of abiotic and biotic pressures, and their interaction, on species’ distributional limits. Nevertheless, situations where temperature is a strong direct influence on distributional limits make qualitatively different predictions regarding the relationship between species’ thermal tolerances and their environmental distributions than situations where temperature exerts a weak direct influence on distributional limits. Thus, it is useful to consider the predictions of the fundamental physiological niche hypothesis.

The thermoneutral zone is the range of ambient temperatures over which a species is able to maintain its basal metabolic rate (Hill et al., 2012). The thermoneutral zone thus describes a ‘comfort zone’ for endotherms, which must respond to ambient temperatures outside their thermoneutral zone [below and above their lower (LCTs) and upper critical temperatures (UCTs), respectively] by increasing their metabolic rate and incurring an energetic cost (Hill et al., 2012). Given that species vary in their lower critical temperatures (LCTs; Araújo et al., 2013; Khaliq et al., 2014), a clear prediction is that species inhabiting colder environments should have lower LCTs than related species inhabiting warmer environments (Kellermann et al., 2009; Sunday et al., 2012; Khaliq et al., 2014). In addition, the rate at which species increase their metabolic rate when exposed to temperatures below their LCT – their thermal conductance – may also reflect physiological adaptation to environmental conditions. Specifically, species in colder environments may be able to increase their metabolic rate when exposed to sub-LCT temperatures at a lower rate than species from warmer environments (McNab, 2002). Finally, the degree to which species’ LCTs match their environments can be quantified as their thermal mismatch, with negative values for species that live in environments where temperatures are colder than their LCT. If thermal tolerances are an important factor directly setting montane species’ distributions, most species should have relatively small positive thermal mismatches, and the degree of thermal mismatch can serve as a proxy for sensitivity to temperature (e.g. when examining warming-associated upslope shifts).

I investigated the relationship between species’ thermal tolerances to cold and their upper elevational limits by studying New Guinean montane birds that are shifting upslope at both warm and cold range limits (Freeman & Class Freeman, 2014). I combined documented warming-associated shifts with a dataset of species’ metabolic responses to temperature (McNab, 2013) and an empirically derived temperature-elevation regression (lapse rate) to assess two predictions of the fundamental physiological niche hypothesis; (1) montane species that experience lower mean ambient temperatures at their upper elevational limit (cold range limit) should have lower LCTs and lower thermal conductances, and (2) montane species with smaller thermal mismatches at their LCTs should undergo larger warming-associated upslope shifts than species with larger thermal mismatches.

METHODS

Thermal physiology

McNab (2013) measured metabolic responses to temperature in wild New Guinean montane birds at two sites in the Central Range of Papua New Guinea – Ambua Lodge (2100 m; Southern Highlands Province) and Kumul Lodge (2860 m; Enga Province). Briefly, McNab captured wild adult birds using mist nets in the late afternoon and measured rates of oxygen consumption of resting birds over a range of temperatures at night (detailed methods in McNab, 2013) to calculate species’ LCTs and minimal thermal conductances (hereafter ‘thermal conductance’). When McNab (2013) reported multiple values of thermal conductances for a species, I used averaged values of thermal conductance for analysis.
Measured thermoneutral zones did not appear to vary for seven species that were measured at both sites (McNab, 2013), although the higher elevation site had markedly colder temperatures (estimated mean ambient temperatures 10.9 °C vs. 14.8 °C, see below for details on the elevation–temperature relationship). This suggests intraspecific variation in thermal tolerances within New Guinea’s Central Range may be small for adult montane birds, although additional data would be necessary to rigorously test this possibility. If populations exhibit local adaptation to different thermal environments, species with large elevational distributions (e.g. elevational breadths > 2000 m) may exhibit differences in their thermal tolerances at the extremes of their elevational distributions. To minimize this possible effect, I limited my analysis to species that occupied largely montane distributions (mostly found above 1000 m), using data for 24 species from 17 families (5.5 ± 3.4 individuals measured per species) for which McNab (2013) reported LCTs and thermal conductances (Appendix S1 in Supporting Information).

Because most species in this dataset have relatively narrow elevational distributions (mean elevational breadth ~ 1400 m within the New Guinean Central Range), my analysis may be robust to intraspecific variation along the elevational gradient. I did not include in my analysis an additional nine montane species whose LCTs were measured to be below ~ 12 °C but were not quantified more precisely (McNab, 2013; see Discussion for further consideration of this issue). Finally, McNab (2013) measured UCTs (which are relevant for species’ warm range margins/lower elevational limits) for only a small number of the species he studied; thus, I restrict my analysis to species’ LCTs and upper elevation limits.

**Elevational distributions, upslope shifts and the temperature–elevation relationship**

I used a single authoritative source (Pratt & Beehler, 2014) to define lower and upper elevational limits for each bird species (Appendix S1). Tropical montane species may inhabit different elevational zones in different geographic regions (e.g. Terborgh & Weske, 1975; Diamond, 1986). Therefore, when species exhibited regional variation in the elevational distributions they occupied, I used species’ elevational limits reported for the Central Range of New Guinea, the same biogeographic region where physiological measurements and warming-associated upslope shifts were taken. Regional scale field guide data typically includes extreme records and thus tend to overestimate species’ elevational distributions. To address this issue, I used species’ ‘typical’ elevational distributions presented by Pratt & Beehler (2014), which represent the elevational zones where species are mostly found. Another potential difficulty in assigning elevational distributions is elevational migration. Several species of New Guinean frugivores (e.g. fruit-doves) and nectarivores (e.g. lorikeets) roam widely in search of food and are known to exhibit predictable elevational migrations (Pratt & Beehler, 2014). However, this is unlikely to bias my analysis, as nearly all species in my dataset are insectivores that are not known to undertake elevational migrations. Finally, I used data from a recent resurvey of bird species’ elevational limits along a single elevational gradient on Mt. Karimui, also located in the Central Range, to quantify species’ warming-associated upslope shifts at cold range limits (Freeman & Class Freeman, 2014).

Temperature is relatively invariant at a single site over the annual cycle in the tropics, but declines predictably with increasing elevation (Janzen, 1967). Thus, a montane species’ lower elevation limit is its warm range limit, and upper elevation limit is its cold range limit. The negative relationship between elevation and temperature is quantified as the lapse rate, which typically ranges in tropical mountains between 0.5 and 0.6 °C decline per 100 m increase in elevation (Terborgh & Weske, 1975; Chen et al., 2009; Forero-Medina et al., 2011). For this study, I used a lapse rate of 0.51 °C per 100 m to relate bird species’ elevational limits to mean temperatures. I empirically measured this lapse rate using data from iButton temperature loggers placed at eight locations (at elevational intervals of approximately 150 m) between 1250 and 2175 m along an elevational gradient on Mt. Karimui, Chimbu Province, during fieldwork in June–July 2012 (Freeman & Class Freeman, 2014). Temperature loggers were placed in closed-canopy forest, both on the forest floor and 2 m above the ground. Height above ground did not appear to influence estimation of mean daily temperatures, which dropped from 19.5 °C at 1250 m to 14.7 °C at 2175 m.

Patterns of diurnal temperature variation (e.g. maximum and minimum temperatures) across elevation in the iButton data were similar to the pattern described above for mean temperature; I therefore used mean temperature to characterize thermal environments across the elevational gradient in New Guinea, while recognizing that local temperatures may vary substantially due to differences in microclimate such as exposure to direct sun and wind. While my iButton data described temperatures in Mt. Karimui closed-canopy forest for a relatively short time period (~ 40 days), daily variation in temperature at single sites during this time was minimal, with the temperature profile for 1250 m (extremes: 17–22.75 °C) barely overlapping that of 2175 m (extremes: 12.25–18 °C). Mt. Karimui is located roughly 150 km from the sites (Ambua and Kumul Lodges) where McNab’s (2013) physiological measurements were taken. The temperature–elevation relationship measured on Mt. Karimui was statistically robust (mean temperature regression on elevation, $r^2 = 0.95$) and similar to lapse rates measured on other tropical mountains. Therefore, I applied the Mt. Karimui lapse rate to estimate the mean ambient temperatures montane species experience at their elevational limits in New Guinea’s Central Ranges (Appendix S1).

**Data analysis**

I used linear regression models to test the predictions that species’ LCTs and thermal conductances predict the ambient temperatures at montane species’ upper elevational limits...
(n = 24 species). Species’ traits may be influenced by their shared evolutionary history, complicating comparative analyses of trait evolution (Felsenstein, 1985). To test whether shared evolutionary history influenced trait evolution in my dataset, I used a posterior set of pruned trees from Jetz et al. (2012), in combination with phylogenetic generalized least-squares (PGLS; Martins & Hansen, 1997), to run phylogenetically controlled regressions using the packages nlme (Pinheiro et al., 2013) and ape (Paradis et al., 2004) in the R programming environment (R Development Core Team, 2014). Internal branch lengths were scaled 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). The λ parameter varies from 0 (no phylogenetic signal) to 1 (phylogenetic signal equal to Brownian motion) in this model and therefore indicates the evolutionary lability of the trait in question. Pagel’s λ was estimated to be negative for both the LCT and thermal conductance PGLS models (−0.11 and −0.19, respectively), indicating that thermal trait values were slightly negatively correlated with evolutionary relatedness in my dataset. Thus, I report results from regression models instead of PGLS models.

The dataset I used contains three species represented by a single individual in McNab’s (2013) data. To test whether results were driven by the inclusion of these three species, I also ran analyses omitting these taxa. Again, Pagel’s λ was estimated to be negative for both the LCT and thermal conductance PGLS models (−0.13 and −0.15, respectively). I therefore report values from regression models for the reduced dataset as well.

Last, I tested whether warming-associated upslope shifts at upper elevation limits (cold range limits) in New Guinean montane birds are larger in species with relatively small thermal mismatches at their LCT (n = 11 species). I calculated species’ thermal mismatches at their cold range limit as the difference between a species’ LCT (°C) and the ambient temperature it experiences at its upper elevational limit. I then used linear regression models to test whether, at cold range limits, species with smaller (or negative) thermal mismatches – those species most likely to be limited by cold temperatures – have undertaken larger upslope shifts than species with larger, positive thermal mismatches.

RESULTS

Montane species’ LCTs did not predict the mean temperatures estimated to occur at their cold range limit (t22 = 0.45, P = 0.66, adj. r² = −0.035, see Fig. 1). Similarly, species thermal conductance values did not predict the mean temperatures estimated to occur at their cold range limit (t22 = −0.19, P = 0.85, adj. r² = −0.044, Fig. 2). I found similar results when using the reduced dataset, indicating that this lack of pattern was not driven by including species where thermal traits were measured for a single individual (reduced dataset – for LCT; t19 = 0.47, P = 0.64, adj. r² = −0.041, for thermal conductance; t19 = 0.09, P = 0.93, adj. r² = −0.052). These results echo previous studies indicating that basal metabolic rate is unrelated to elevation within tropical montane birds (McNab, 2013; Londoño et al., 2014).

The majority of tested species (88%) experience a thermal mismatch at their cold range margin (thermal safety margins at cold limit = −7.0 ± 4.6 °C, Fig. 3; negative thermal safety margins indicate thermal mismatches), with most species experiencing a thermal mismatch (mean ambient temperatures colder than their LCT) at the site where they were captured and measured. Thermal microclimates and behaviour may minimize the degree to which birds at high elevations actually experience temperatures below their LCT. Taken at face value, however, these data suggest that montane New Guinean birds regularly occur at elevations up to 1000 m higher than predicted if their upper elevational limits were strictly set by their LCT. If temperature directly influences warming-associated upslope shifts via impacts mediated by thermal physiology, then species with large negative thermal mismatches (i.e. species that are experiencing the most sub-optimal thermal environments) are predicted to exhibit stronger upslope shifts than species with small negative or positive thermal mismatches. However, species’ thermal mismatches were not related to the magnitude of their upslope shift on Mt. Karimui at their cold range limit (t9 = 1.48, P = 0.17; Fig. 4), although this analysis is based on a small sample size and should be viewed as preliminary.

DISCUSSION

New Guinean montane birds have shifted their distributions upslope by around 100 m at both warm (low elevation) and
cold (upper elevation) range limits in the past half century (Freeman & Class Freeman, 2014). These shifts are significantly associated with recent local temperature increases (Freeman & Class Freeman, 2014), indicating that temperature is an important factor that directly or indirectly influences elevational limits in this avifauna. The fundamental physiological niche hypothesis predicts that montane species' elevational distributions are tightly linked to their thermal tolerances. However, I found that species' LCTs and thermal conductances were not correlated with the mean ambient temperatures species experience at their upper elevational limit. In addition, species' thermal mismatches were unrelated to the magnitude of their upslope shifts at their cold range limit (albeit with a small sample size). These results do not support the fundamental physiological niche hypothesis in New Guinean montane birds (applied to their upper elevational limits) and suggest that species' thermal tolerances do not greatly influence species' upper elevational limits in this avifauna.

These results could be influenced by the coarse way I characterized species' thermal environments. For example, the mean temperatures I estimated to occur at species' upper elevational limits might not represent the actual temperatures birds experience due to microclimatic variation, exposure, vegetation structure and other factors. However, most species in this dataset are found in the understorey or midstorey of closed-canopy forest, where temperature fluctuations are minimal compared with more exposed microhabitats, suggesting that the mean temperatures I used to characterize thermal environments are appropriate for this analysis.

These results also depend on the underlying data used for analysis. For example, the conclusion that species' thermal mismatches at their cold range limit were unrelated to the magnitude of upslope shifts is based on a small sample of species (n = 11) and should therefore be considered a preliminary result (although the apparent trend within this small sample is opposite that predicted by the fundamental niche hypothesis). In addition, while results were robust to the inclusion of species for which thermal trait data was measured in a single individual, adding further species to the
dataset could potentially alter conclusions. For example, McNab (2013) did not calculate LCT values for nine montane species with low (< 12 °C) LCTs, and these species could therefore not be included in my analyses. If these omitted species with especially low (but unmeasured) LCTs tended to have particularly high upper elevational limits, the resulting analysis could be biased against finding a relationship between LCTs and upper elevation limits. However, there were three examples where omitted species had congeners present in the dataset that both occupied higher elevation (colder) environments and had higher (> 12 °C) LCTs. Thus, in these three cases, the congener present at higher (colder) elevations had a higher LCT, contrary to the predictions of the fundamental physiological niche hypothesis and suggesting that the omitted species are unlikely to bias the conclusions of this study. Finally, this study concerns variation in thermal tolerances within montane species of New Guinean birds only, and cannot address other important questions, such as whether species’ elevational limits are influenced by their thermal performance curves, whether montane and lowland species consistently differ in their thermal physiology, or the degree to which thermal traits are plastic and reflect acclimation to the thermal environments experienced by adult birds.

Understanding how species’ thermal tolerances are linked to their distributional limits at warm and cold range margins is an important goal of climate change ecology. In endotherms, a global analysis found little variation in heat tolerance in interspecific comparisons inhabiting different thermal environments but wide variation in cold tolerance, suggesting greater potential for evolutionary responsiveness to cold than heat across taxa (Araújo et al., 2013). Species in my analysis also showed variation in their tolerance to cold, with species’ LCTs measured by McNab (2013) at the same site in the New Guinean Central Range ranging from 11 to 22 °C. However, I found that this variation in species’ cold tolerances was not linked to the ambient temperatures they experience. This result is broadly consistent with global analyses that show the correlation between species’ thermal limits and the ambient temperatures they experience tends to be weak in endotherms (birds and mammals; Araújo et al., 2013; the same relationship is strong in ectotherms; Sunday et al., 2012; Araújo et al., 2013; Sunday et al., 2014).

The prevalence of thermal mismatches in my dataset demonstrates that many New Guinean montane birds are likely paying an energetic cost to live at high elevations. This conclusion applies to adult birds – the thermal tolerances of developing eggs and nestlings of New Guinean montane birds are unknown. If thermoneutral zones of eggs and nestlings are assumed to be similar to or more restricted than those of adults (Webb, 1987), then this conclusion would extend to individuals regardless of life stage. Presumably, food resources are sufficiently plentiful within New Guinean montane forests (and possibly benign thermal microclimates sufficiently common) that montane bird species at high elevations can meet their elevated energy requirements. Recent warming in New Guinea has presumably lessened this energetic cost, at least for individuals within the historic elevational distribution occupied by a species. However, the large majority of species are moving upslope at a rate that roughly tracks local temperature increases (Freeman & Class Freeman, 2014), such that populations as whole are likely experiencing similar thermal pressures through time. While physiological adaptation to abiotic factors undoubtedly impacts distributions of tropical montane birds in some cases (e.g. DuBay & Witt, 2014; see also adaptation to hypoxia at very high elevations; e.g. Cheviron & Brumfield, 2009; McCracken et al., 2009), I did not find support for the fundamental physiological niche hypothesis as applied to cold range limits of New Guinean montane birds.

This result suggests that biotic factors may be important in setting elevational limits of New Guinean montane birds. Limiting biotic factors could include resource availability (Ferger et al., 2014), habitat structure (Diamond, 1972; Ferger et al., 2014) and the presence of competitors (Terborgh & Weske, 1975; Diamond, 1986; Tingley et al., 2014), natural enemies (Ricklefs, 2010) and mutualists (Callaway et al., 2002; Afkhami et al., 2014). To explain why species are shifting upslope in concordance with recent local warming, these biotic factors would have to link to temperature. For example, temperature may have a strong effect on habitat structure (e.g. affecting the lower elevation limit of cloud forest habitat) which in turn influences bird species’ elevational distributions (Diamond, 1972). Ectotherms’ distributions tend to be tightly correlated with temperature (Sunday et al., 2012; Araújo et al., 2013; Sunday et al., 2014) – if warming directly impact distributions and abundances of ectotherms that are important food resources (Ferger et al., 2014), disease vectors (Van Riper et al., 1986) or nest predators (Jankowski et al., 2012), birds’ distributions may change as a result. Finally, the outcomes of species interactions that influence distributional limits may themselves vary depending on ambient temperatures (Davis et al., 1998; Tylianakis et al., 2008; Hellard et al., 2011).

In conclusion, I show that species’ thermal tolerances to cold in a group of tropical endotherms (New Guinean montane birds) are not correlated with their upper elevational limits and appear not to explain why some species are rapidly moving upslope at their cold range margin in association with recent local warming while others are not. These results do not support the fundamental physiological niche hypothesis, at least when using species’ LCTs and thermal conductances to quantify species’ thermal physiologies. Further studies should test whether similar patterns occur in other montane avifaunas, and in other taxonomic groups, ideally directly measuring energy expenditure across a range of biologically relevant temperatures. Finally, the apparently limited influence of temperature to setting elevational limits in New Guinean birds is consistent with the hypothesis that biotic factors indirectly linked to temperature may regulate elevational limits in this avifauna. Tropical mountains are the most biodiverse terrestrial ecosystems on Earth (Myers
et al., 2000), and preliminary evidence suggests tropical montane species are disproportionately sensitive to temperature increases (Colwell et al., 2008; McCain & Colwell, 2011; Freeman & Class Freeman, 2014). Thus, research investigating the biotic factors that limit elevational distributions in New Guinean montane birds and other tropical montane biotas is urgently needed to conserve tropical montane hyperdiversity in the face of global warming and other environmental change.

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REFERENCES


SUPPORTING INFORMATION

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

Appendix S1 Dataset of thermal tolerances, warming-associated shifts and elevational distributions of species used in this study.

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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