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BIOTIC AND ABIOTIC INFLUENCES ON THE EVOLUTION OF ELEVATIONAL RANGE LIMTS AND LIFE-HISTORY STRATEGIES OF TROPICAL BIRDS

By

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Biotic and abiotic influences on the evolution of elevational range limits and life-history strategies of tropical birds

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Environmental gradients provide natural forums for understanding how and why species differ. The study of interspecific variation across gradients has provided foundations for our understanding of community ecology, species distributions, life-history evolution and physiological ecology (Janzen 1967; Macarthur 1972; Martin 2015). In this dissertation, I explore questions in these disciplines, using a comparative approach on elevational and latitudinal gradients. My primary focus is understanding the biotic and abiotic processes that limit species distributions and how those same forces scale up to influence the composition of communities on an elevational gradient. I also test a physiological hypothesis for the gradient of life history strategies, the pace-of-life hypothesis, by examining the relationship between metabolic rate and adult mortality probability across a global latitudinal gradient.

I examine these issues in songbird communities on Mt. Kinabalu in Malaysian Borneo (6°N). Kinabalu Park is a large protected area encompassing the largest intact elevational gradient in southeast Asia (400m – 4100m). It is a reserve with tremendous conservation importance; it is a stronghold for more than 90% of Borneo's endemic bird species including several whose mountaintop ranges put them at risk of extinction assuming upward range shifts due to climate change (Colwell et al. 2008). Understanding the mechanisms that underpin elevational distributions in such megadiverse threatened areas is a central goal of ecology and vitally important to conservation locally and globally.

In chapters 1-3 I used experimental and descriptive approaches to assess the importance of interspecific competition and physiology in setting elevational range limits and structuring communities across elevations. We found evidence that interspecific competition may set range limits in some species, but that aggressive interactions with close relatives could not explain range boundaries in other cases. We also found that birds occupying different elevations had similar thermal physiology, suggesting range limits are not directly set by climatic variables like temperature. Using phylogenetic and trait-based approaches, we found evidence that interspecific competition plays a strong role in structuring bird communities at low elevations, while environmental filtering appears to be important at high elevations. Based on clustering of morphological traits, particularly bill shape, we speculate that the influence of climate on prey size and diversity may restrict many species from high elevation communities.

Finally, we tested the ability of metabolic rate to explain variation in average lifespan within and across latitudes. The pace-of-life hypothesis posits that damaging byproducts from cellular metabolism are the primary physiological driver of lifespan, such that long-lived tropical species are expected to have low metabolic rates (Pearl 1928; Hulbert et al. 2007; Wiersma et al. 2007; Williams et al. 2010). We tested this hypothesis by measuring metabolic rates and estimating adult survival probability in songbirds at Kinabalu Park

(6°N) and in Arizona, USA (34°N). We found that metabolic rate explained variation in annual adult survival probability within sites, but that it could not explain the longer lives of tropical birds compared with temperate zone relatives.

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Chapter 1: Phylogenetic structure and functional diversity of avian communities along a tropical elevational gradient

Andy J. Boyce , Subir Shakya, Frederick H. Sheldon, Robert G. Moyle and Thomas E. Martin

ABSTRACT

Understanding how biotic interactions and abiotic constraints influence community assembly and composition is a fundamental issue in community ecology. Addressing this issue is particularly tractable in the context of tropical mountains which have large variation in community diversity, high rates of species turnover and strong gradients in abiotic conditions. Here, we examined elevational patterns of avian community structure in tropical Malaysia to assess changes in the relative strength of biotic interactions and abiotic constraints. We used metrics based on phylogenetic relatedness and functional traits associated with resource acquisition and tolerance of abiotic challenges to identify patterns and causes of elevational differences in community structure. High elevation communities were composed of more phylogenetically and functionally similar species than would be expected by chance (clustered), while middle and low elevation communities showed little structure, with few communities composed of more dissimilar species (overdispersed) than expected by chance. Traits associated with resource acquisition were clustered at high elevations, suggesting low resource and habitat diversity were the primary drivers of clustering in those communities. Traits typically associated with tolerance of cold temperatures and low atmospheric pressure showed no elevational patterns. All traits were neutral or overdispersed at low elevations suggesting an absence of strong abiotic filters or an increased influence of interspecific competition. However, relative bill size, which is important for thermoregulation, was larger in low elevation communities, suggesting abiotic factors were also influential there. Regardless of metric, clustered and neutral communities were far more frequent than overdispersed communities, implying that interspecific competition among close relatives may not be a pervasive driver of elevational distributions

and avian community structure. Overall, our analyses reveal that a diverse set of biotic and abiotic factors underlie elevational variation in community structure and that both biotic and abiotic forces are likely important in structuring communities across elevations.

INTRODUCTION

Understanding the ecological processes that influence community assembly and composition across geographic gradients is a fundamental problem in ecology (Macarthur & Levins 1967; Diamond 1975; Hubbell 1979). Competition among species is the most commonly invoked process underlying community structure (Schoener 1983) and is thought to explain adjacent but generally non-overlapping elevational ranges of congeners (Terborgh & Weske 1975; Remsen Jr. & Graves 1995a; Jankowski, Robinson & Levey 2010; Freeman 2015). Specifically, species that are similar in resource use are thought to compete most intensely and are less likely to coexist (Connell 1961; Macarthur & Levins 1967; Diamond 1975; Gilpin & Diamond 1982). Abiotic conditions are also thought to affect the composition and structure of species assemblages by limiting the species or lineages present in a community to those with the necessary traits to colonize and persist in a given set of abiotic conditions (Grinnell 1917; Connell 1961; Webb 2000; Graham *et al.* 2009). Physiology can limit elevational ranges of congeneric species when they differ in tolerance to abiotic factors such as temperature, moisture, and atmospheric conditions that vary with elevation (Gifford & Kozak 2011; Graham *et al.* 2012). Yet, the relative importance across elevations remains poorly understood.

Theory predicts the relative importance of competition and abiotic factors will vary across environmental gradients. For example, competition is thought to be most important in abiotically benign environments with abiotic factors becoming increasingly important in temperate regions or high elevations in the tropics with harsher or more variable climates (Dobzhansky 1950; Macarthur 1972; Schemske *et al.* 2009; Sexton *et al.* 2009). This shift from biotic to abiotic drivers of community structure along latitudinal gradients has support (Schemske *et al.* 2009), but tests across elevational gradients have produced inconsistent results (Bryant *et al.* 2008; Graham *et al.* 2009; Gifford & Kozak 2011). Temperatures decrease and temporal variation in conditions increases moving from the equator towards the poles or from low to high elevations in temperate regions. However, variation in climate remains extremely low across elevational gradients in the tropics (Janzen 1967; Ghalambor *et al.* 2006). Stable conditions across elevations on tropical mountains may reduce the influence of abiotic factors at high elevation relative to latitude if organisms can adapt to a narrow range of conditions. Thus, factors influencing community composition and structure may differ in elevational versus latitudinal contexts, which underscores the need for additional studies of elevational patterns in phylogenetic and functional community structure.

On the other hand, environmental stability may be less important than absolute levels of climatic conditions. Cold temperatures, low atmospheric pressure, and low primary productivity make high elevation environments physiologically challenging to endotherms. Such harsh abiotic conditions are thought to restrict availability of these habitats to species or clades with traits necessary to cope with these challenges. Conversely, interspecific competition and other biotic interactions are thought to be a dominant force at low elevations due to the general lack of strong abiotic filters (Janzen 1967; Macarthur 1972). Thus, theory predicts that low elevation communities should be structured largely by competition and high elevation communities should be structured largely by abiotic filtering. Studies of hummingbirds and ants both found support for this idea (Graham *et al.* 2009, 2012; Machac *et al.* 2011). However, the opposite pattern has been observed in plants (Bryant *et al.* 2008), and microbial communities appear to be influenced primarily by abiotic conditions at all elevations (Bryant *et al.* 2008), with some evidence for an increasing influence at high elevations (Wang *et al.* 2012). This lack of consensus suggests that different groups of organisms may be responding to different ecological mechanisms or that methods for determining the factors underlying structure may be inappropriate.

The synthesis of community ecology and phylogenetics has provided a quantitative framework to infer the relative importance of biotic and abiotic forces in determining community composition (Webb 2000; Webb *et al.* 2002). The phylogenetic structure of communities is thought to reflect the relative importance of biotic (competition, facilitation) versus abiotic filtering in determining community composition. Such interpretation is based on the assumption that traits important for resource exploitation and tolerance of abiotic conditions are phylogenetically conserved (Webb 2000, Webb et al. 2002, Wiens and Graham 2005, Lovette and Hochachka 2006, Hardy and Senterre 2007, Kraft et al. 2007, but see Gerhold et al. 2015). Specifically, closely related species should compete more strongly due to similar traits related to resource use (Macarthur & Levins 1967; Wiens & Graham 2005). Accordingly, communities where interspecific competition is important in determining community composition should be composed of species that are more distantly related than would be expected by chance (phylogenetic overdispersion). In contrast, communities where harsh abiotic conditions select for a narrow range of adaptive traits should consist of species that are more closely related than expected by chance (phylogenetic clustering) (Losos 1996; Webb 2000; Webb *et al.* 2002; Graham *et al.* 2009).

An alternative way of detecting the influence of abiotic filtering and/or biotic interactions on community structure is via the distribution of functional traits among co-occurring species. Phylogenetic methods use relatedness as a proxy for niche similarity, but we can also directly measure traits that are likely to be important to resource or habitat use and compare the distribution of these traits within and across communities (Ricklefs & Travis 1980; Weiher, Clarke & Keddy 1998). In communities where interspecific competition is a dominant assembly mechanism, functional traits should be distributed such that maximal trait-distance exists between species (overdispersion)(Macarthur & Levins 1967; Hespenheide 1973), reflecting minimal overlap in ecological niches and alleviating competition between similar species. In contrast, if environmental filtering is dominant, traits that confer an advantage in such a community should be similar among species, or clustered relative to a null model of community assembly.

Applying both phylogenetic and trait-based methods simultaneously to the same dataset has multiple advantages. First, if traits that are important to either competition or habitat filtering are not phylogenetically conserved, patterns in phylogenetic structure alone will be uninformative on community assembly processes. In such a case, an absence of phylogenetic community structure is expected even if abiotic filtering or competition are strong drivers of community structure, but trait-based methods will detect either overdispersion or clustering of traits depending on the dominant assembly process (Cavender-Bares *et al.* 2004). Second, the veracity of results of trait-based methods depends on the assumption that measured traits are important for community assembly processes. However, many traits are difficult to measure and integrating numerous complex traits into a framework suitable for analysis is not always straightforward (but see Villéger et al. 2008), so this assumption may be frequently violated. In such cases, as long as the relevant (unmeasured) traits display phylogenetic signal, phylogeny-based methods can reveal patterns in community structure when trait-based methods do not. Despite these potential benefits, relatively few studies have combined phylogenetic and trait-based methods to investigate community assembly mechanisms (Cavender-Bares et al. 2004, Kraft and Ackerly 2010). We not only conducted tests using our own field data, but also a second dataset from the literature for cross-tests.

Here, we examine patterns of phylogenetic community structure and functional trait diversity across two elevational gradients on adjacent tropical mountains at two different taxonomic scales in bird communities to assess how competition and abiotic filtering may influence community assembly across elevations. We also test whether functional morphological traits are phylogenetically conserved as typically assumed.

METHODS

Study System

We sampled bird communities on two mountains within Kinabalu Park in Sabah, Malaysia (6°N). Kinabalu Park is a large (754 km^2), continuous tract of intact tropical forest spanning lowland (450 m) dipterocarp forests in its northern and eastern sectors to stunted montane forest and bare rock at the summit of Mount Kinabalu (4100 m) near its southern border (Fig 2). In between are a large variety of elevationally defined forest types and associated climatic zones spanning a large climatic gradient (Kitayama 1992). Our sampling area covered an elevational gradient of 1480 m – 3680 m on Mt. Kinabalu, and 600 m – 2579 m on Mt. Tambuyukon (Fig 2). Both sampling areas were bounded by the current extent of primary forest on the lower boundary. The upper boundary of our Tambuyukon transect was the summit, while our sampling area was truncated below the summit on Kinabalu to match the upper limit of vegetation.

Community composition (field data)

We sampled bird communities using 10 minute fixed radius point counts with a maximum detection distance of 100m (Hutto, Pletschet & Hendricks 1986). Fixed-radius counts were chosen over unlimited-radius counts to eliminate the possibility of attributing a distant individual to the wrong elevational community in a topographically complex environment. Point count stations were laid out along narrow and infrequently used forest trails such that stations were at least 250m apart based on straight-line distance and each 200m vertical band of forest contained exactly five stations. Distance between stations and elevation were determined with a regularly-calibrated handheld GPS unit (Garmin, Olathe, KS). Birds were detected both visually and aurally and distances were estimated for all detections. All point counts took place between February and June, 2012 – 2015 and were exclusively conducted by AJB. All points on Kinabalu were sampled 2-3 times per season, while Tambuyukon points were surveyed once per season. Point counts below 1400m on Tambuyukon, where species diversity is highest, were recorded so that any unknown vocalizations could be identified later. All bird species detected within a given 200m elevational band were deemed to be present in that community. Additionally, birds were considered present in all elevational bands between their highest and lowest detection points on each gradient (McCain 2004). Despite the documented advantages of using abundance estimates in community structure analyses (Freilich & Connolly 2015), we did not attempt to do so here because of unequal sampling across sites and because estimating detection probability would have been problematic for a large number of rarely encountered species.

Community composition (literature data)

We used elevational distribution data from Harris et al. (2012) for all species of birds known from Kinabalu Park. This dataset is based on multiple data sources including direct sampling by the authors, citizen science projects, the literature, and unpublished data from experienced observers. To improve the quality of this dataset, elevational ranges were broadened where direct observations from our field data fell outside of the published elevational range. Additionally, where elevational ranges included single observations that were more than 200m either above or below all other known observations, we assumed these were misidentifications or represented temporary movements. These records were discarded and the elevational range re-described based on the remaining data.

Phylogenetics

We constructed a phylogenetic tree of 197 species representing most of the resident passerine birds of Borneo (Supplementary Data 1). Of the 197 species, 14 were collected in the Philippines, Sumatra or Vietnam because we did not have Bornean specimens. Two species were aviary birds. The outgroup consisted of three non-passerine species: *Psilogopon eximius* (LSU B51190), *Harpactes oreskios* (LSU B78728) and *Sasia abnormis* (LSU B36374).

DNA sequences of the following genes were collected for comparisons: two mitochondrial loci, NADH dehydrogenase subunit 2 (ND2) and cytochrome B (CYTB); and two nuclear loci, transforming-growth factor, beta 2 (TGFB2) intron 5 and muscle, skeletal, receptor tyrosine kinase (MUSK) intron 13. When they were available, we downloaded sequences from GenBank. To fill gaps in the data, we generated 510 new sequences.

Total genomic DNA was extracted from frozen or alcohol preserved tissue or blood samples using DNEasy® Blood and Tissue Kit (Qiagen) and manufacturer protocols. PCR amplifications were performed in 25 µl reactions using Taq DNA Polymerase (New England BioLabs Inc). Various primers were used to amplify the corresponding regions of DNA (Supplementary Table 2). Amplification consisted of 34 cycles of denaturing at 95°C, annealing at temperatures varying according to the primer pair used, and extension at 72°C. An annealing temperature of 50°C was used for MUSK (primer pair 13F and 13R), 54°C for ND2 (primer pair L5215 and HTrpC), 55°C for CYTB (primer pair L14851 and H4A), and 58°C for TGFB2 (primer pair 5F and 6R). A new primer was developed for CYTB to amplify sequences of individuals in which the basic primer pair did not work. PCR products were visualized in 1% agarose gels stained with SYBR® Safe DNA Gel Stain (Invitrogen). They were sequenced by Beckman Coulter Genomics (Danvers, MA).

Sequence contigs were assembled in Geneious 8.0.5 (Biomatters). Sequences were manually checked and trimmed to eliminate errors and to identify ambiguous sites. Sequences were aligned using

MUSCLE (Edgar 2004), implemented in Geneious. The four loci were concatenated into sequences of 3736 bp and placed in a single alignment containing all species. This dataset was divided into eight partitions: mitochondrial genes with three partitions each based on codon position, and nuclear genes with one partition each. Bayesian Information Criterion (BIC), implemented in the program Partition Finder v1.1.1, was used to find the best substitution model for each partition.

Bayesian methods were used to construct trees from the concatenated sequences. A time-calibrated tree was generated using BEAST v2.3 (Drummond *et al.* 2002, 2006) using a relaxed clock, log normal distribution and a birth-death speciation model. The dataset was partitioned based on the best substitution model determined in Partition Finder. Default priors were used for all parameters. Two independent MCMC chains were run for 100 million generations. Tracer v.1.6 (Rambaut *et al.* 2014) was used to check for convergence among runs, and TreeAnnotator was used to generate a maximum clade credibility tree after 25% of trees were discarded as burn-in.

To provide a tree of all birds we used Jetz et al. (2012), built on the Hackett et al. (2008) backbone. We used birdtree.org to prune trees to match our datasets and sampled 1000 trees from the available distribution. Majority-rules consensus trees were then constructed in Mesquite (Maddison & Maddison 2011). These consensus trees were imported into R using the 'ape' package and were used for all phylogenetic analyses except estimation of phylogenetic signal (see below). Constructing a de novo tree for our datasets that included all Bornean bird species would have been ideal. Because this was not possible, however, we included tests using the Jetz et al. (2012) tree. The Jetz et al. tree has the weakness that not all of the included relationships are based on genetic comparisons. Nevertheless, while this shortcoming weakens inferences based on the Jetz et al. tree, it allows for construction of trees that includeall species for which community data were gathered.

Functional traits

We used morphological measurements to describe species resource and substrate use (Miles & Ricklefs 1994). While many authors have applied categorical variables as functional traits to assign species to feeding or foraging guilds, such categorizations would be simplifications of actual resource use, especially for many of the rare or little known species in our dataset. We compiled measurements of 5 morphological characters for species present in our communities: body mass, wing chord, tarsus, bill width and exposed culmen length. These characters were chosen because they are easily measured on both live birds and archived specimens and all are thought to be important in mediating biotic interactions via diet, foraging strategy and foraging substrate (Hespenheide 1973; Miles & Ricklefs 1984, 1994; Pigot, Trisos & Tobias 2016) or facilitating use of abiotically challenging environments. For example, greater body mass and large wings relative to body mass should be advantageous in cold, high elevation environments that favor lower surface to volume ratios to reduce rates of heat loss and increase flight power in thinner air, respectively (Altshuler & Dudley 2006; Graham *et al.* 2012; McNab 2016), while large bills, controlled for body mass, act as thermoregulatory organs and are important for dissipating heat in hot environments (Symonds & Tattersall 2010; Greenberg *et al.* 2012; Tattersall, Arnaout & Symonds 2016; Danner *et al.* 2017).

Data were primarily gathered directly by measuring netted birds at our long-term site at Kinabalu Park (see Martin et al. 2015). When field data were absent, we measured specimens archived at Sabah Parks Museum and LSU Museum of Natural Science. For dimorphic species we used the midpoint values of male and female trait means, whereas in non-dimorphic species all measurements were pooled and population means were used. Only data from adult individuals were included in our analyses. Body mass data were obtained from the literature (Dunning 2007) in cases when it was unrecorded for dry specimens.

Statistical Analyses

Phylogenetic Community Structure – We calculated net-relatedness index (NRI) and nearest-taxon index (NTI) as metrics of phylogenetic community structure for each elevational community (200m elevational bands for directly sampled point count data and 100m bands for literature data). NRI describes the average pairwise phylogenetic distance among all species pairs in a sampled community while NTI describes the average phylogenetic distance between each species and its closest relative within a community. These values are then compared to those from communities generated by a null-model algorithm from a regional pool of species (Webb 2000) to determine if real communities are more overdispersed or clustered than is expected by chance alone. We employed both metrics because NRI is more sensitive to environmental filtering (clustering) while NTI is more sensitive to structuring due to competition among similar species (overdispersion) (Freilich & Connolly 2015). We used the 'independent swap' algorithm (Gotelli 2000; Gotelli & Entsminger 2003) to generate 1000 random communities while holding species richness and occupancy constant. This null model essentially treats elevational range breadth as "rarity", which may not be biologically accurate. However, using this method instead of a 'richness' model, which allows occupancy to vary in null communities, should result in more conservative estimates of standardized effect sizes (NRI & NTI) by minimizing the likelihood of type 1 error (Gotelli 2000). We used all species present across elevations to populate the regional species pool as no geographic barriers exist along this gradient and all species sampled have distributions that extend beyond the study area (Sheldon, Moyle & Kennard 2001), indicating that dispersal ability alone is not constraining elevational distributions. We used independent regional species pools for field and literature community datasets to eliminate the possibility of including species in the regional pool that were simply undetectable by the observer during field sampling. Analyses were done in R (R Core Team 2015) using the 'picante' package (Kembel *et al.* 2010).

Functional Trait Diversity – We used the same metrics (NRI, NTI) to describe the distribution of functional traits in elevational communities. Hereafter we denote the trait-based metrics as NRI_t NTI_t. We used raw measurements to describe bill shape (bill width and culmen length), and residual values from regressions of log-transformed wing chord and tarsus on log-transformed body mass to describe relative wing size and relative tarsus length. Relative bill size values were residual values of a regression of bill surface area [(bill width * culmen length)/2] on log-transformed body mass. Log-transformed body mass was our final functional trait. We then calculated Gower's distance, a metric that integrates multiple traits into an index of dissimilarity for each pairwise combination of species (Gower 1971). These distances were used to populate a distance matrix, analogous to a distance matrix of phylogenetic relatedness. Because abiotic filtering and competition may be acting simultaneously and on different traits (Swenson & Enquist 2009; Graham *et al.* 2012), we also calculated NRI_t for each morphological trait individually using our literature dataset. NRI only detects the presence or absence of clustering, but not whether trait values in clustered communities are higher, lower or intermediate compared to neutral or overdispersed communities. We also calculated mean ± SE trait values for each elevational community to test predictions on how abiotic filters may influence trait distributions at high elevations.

Phylogenetic Signal – We estimated Blomberg's *K* statistic as a measure of phylogenetic signal in our three PCA axes used to determine overall trait diversity patterns, as well as in 4 individual morphological functional traits thought to be important for either mediating competition or utilization of high elevation environments. Blomberg's *K* is a measure of the trait variation among species compared to that expected based on a Brownian motion model of evolution, given shared evolutionary history determined from the phylogeny (Blomberg, Garland & Ives 2003). When $K = 1$, phylogenetic signal is thought to be strong, with trait variation equal to that predicted by a Brownian motion null model. When *K* approaches 0, there is an absence of phylogenetic signal. *K* values were calculated in Picante using the function multiPhylosignal (Kembel *et al.* 2010). This function requires a fully-resolved tree, but our consensus tree contained several polytomies, which, when forcibly resolved using the multi2di function in Picante, can artificially inflate *K* values by creating 0 length branches in unresolved clades (Davies *et al.* 2012). To resolve this problem, we calculated *K* for each of the 1000 fully-resolved trees in the distribution sampled from birdtree.org, and present a mean ± SD *K* values.

Elevational Patterns – To evaluate patterns of phylogenetic and functional trait community structure across elevations, we used two methods. For field data we used linear mixed-effect models with our community structure metrics as response variables, elevation as a fixed effect and site as a random effect. For literature data we used a simple linear model with community structure metrics as response variables and elevation as a fixed effect.

RESULTS

Phylogeny

The phylogenetic tree generated for this study is shown in Figure 1. The tree comprises 36 families of birds, and the relationships among these families and their constituent species are consistent with those observed in recent phylogenetic studies (Johansson, Fjeldså & Bowie 2008; Moyle *et al.* 2016).

Community composition

Point count sampling resulted in detection of 163 species of birds, including 113 passerines and 50 non-passerines along our elevational transects. Our literature search, combined with directly sampled data yielded elevational distribution data for 222 species, including 161 passerines and 61 non-passerines. Phylogenetic and/or trait data were not available for all species, so datasets for community structure analyses were restricted to 139 directly sampled species (100 passerines, 39 non-passerines) for our point-count data, and 189 species for our literature-based dataset. Species richness declined with increasing elevation in passerines ($P < 0.01$) and across all birds ($P < 0.01$) based on field-sampling (Fig 3). Species richness was higher for a given elevation on Mt. Kinabalu than Mt. Tambuyukon ($P < 0.01$) with maximum diversity between 500 and 700 m on Mt. Tambuyukon (68 total, 45 Passerines) and minimum diversity between 3650 and 3850 m on Mt. Kinabalu (2 total, 2 Passerines). Species richness patterns were similar in our literature dataset for Mt. Kinabalu, with maximum diversity between 600 and 700 m (113 species) and minimum diversity between 3800 and 3900 m (1 species), with α diversity decreasing monotonically with elevation ($P < 0.01$; Fig 3).

Phylogenetic signal in functional traits

All measured morphological traits showed significant phylogenetic signal in each of our three datasets (Table 1) indicating that closely related species are more likely to possess similar morphology and thus similar ecological niches. Mass and bill width both showed K values greater than 1 across all three datasets, indicating particularly strong phylogenetic signal in these traits. Culmen length also showed strong phylogenetic signal in datasets including all birds, but weaker signal when considering passerines only (Table 1). Tarsus length showed the opposite pattern, showing stronger signal within passerines than among all birds (Table 1).

Phylogenetic Community Structure

Overall, bird communities exhibited a pattern of neutral community structure over much of the elevational range, but some phylogenetic overdispersion at low and phylogenetic clustering at high elevations (Fig 4A). Clustering increased with elevation in our field-sampled dataset that included all birds based on NRI ($P < 0.01$), but no significant pattern in community structure was detected using NTI ($P = 0.15$). When limiting our dataset to passerines only, phylogenetic clustering increased with increasing elevation based on NRI ($P = 0.05$). Clustering in passerines also increased with elevation based on NTI ($P = 0.01$), but anomalously, the pattern was driven solely by overdispersed communities at low elevations on Mt. Tambuyukon (Fig 4A). More communities were found to be significantly clustered in our directly-sampled datasets based on NRI, while NTI detected similar (all birds) or more (passerines) overdispersion (Fig 4A). In our literature dataset, clustering increased with elevation when using both NRI ($P < 0.01$) and NTI ($P < 0.01$). More communities were significantly clustered than overdispersed according to both metrics, and NRI detected significant overdispersion and clustering more frequently than NTI (Fig 4A).

Functional Trait Diversity

Elevational patterns of community structure based on functional traits were largely consistent with those based on phylogenetic relatedness (Fig 5). This was not surprising given the strong phylogenetic signal in our trait data (Table 1). Overall, functional traits were clustered at high elevations, neutral at middle elevations and overdispersed at low elevations (Fig 4B). Based on NRI_t, the pattern of increased clustering with elevation was consistent across directly sampled gradients including all birds ($P < 0.01$), passerines only ($P = 0.01$), and our literature dataset ($P < 0.01$). Based on NTI_t, clustering increased with elevation for our passerine ($P = 0.05$) and literature datasets ($P < 0.01$), but this pattern was weaker when including all birds ($P = 0.08$). Trait-based metrics detected significantly overdispersed or clustered communities with similar or higher frequency than phylogenetic metrics regardless of metric or dataset (Fig 4).

Analysis of community structure patterns of individual traits revealed variation in patterns among traits. Relative wing size exhibited no elevational pattern in community structure ($P = 0.90$), and body mass showed greater clustering at high elevations ($P = 0.04$), but the pattern was weak compared to other traits(Fig 5). Relative tarsus length (*P* < 0.01), and both measures of bill shape (bill width; *P* < 0.01, culmen length; *P* < 0.01) and relative bill size (*P* < 0.01) showed strong patterns of overdispersion at low elevations and clustering at high elevations (Fig 5). All morphological measures that were clustered at high elevations also showed significant changes in mean trait values across elevations (Fig 6). High elevation communities contained species with lower body mass (*P* < 0.01), longer relative tarsus length (*P* < 0.01), as well as narrower (*P* < 0.01) and shorter (*P* < 0.01) bills, and smaller relative bill size (*P* < 0.01) compared to low elevation bird communities (Fig 6). Initially, we were concerned that the absence of hornbills (Bucerotidae, 4 species) at high elevations, combined with their massive size compared with other bird species, was driving the results presented above. However, removing hornbills had no qualitative effect on any of our results and the data presented here are those with hornbills excluded and are thus conservative.

DISCUSSION

Several studies have found overdispersed communities at low elevations (Machac *et al.* 2011; Graham *et al.* 2014) and clustered communities at high elevations (Bryant *et al.* 2008; Graham *et al.* 2009; Machac *et al.* 2011; Wang *et al.* 2012; Smith, Hallwachs & Janzen 2014). We found a similar pattern but also that clustering was a stronger pattern at high elevation than overdispersion was at low elevations. This pattern suggests that environmental filtering plays a principal role in driving avian community structure at high elevations, while resource competition among species at low elevations is less evident. Indeed, we found far more clustered than overdispersed communities across the entire gradient (Fig 4), matching results in hummingbirds (Graham *et al.* 2009). The rarity of overdispersed communities suggests that interspecific competition may not be the dominant force in avian community assembly as long thought (Terborgh 1971; Terborgh & Weske 1975; Jankowski *et al.* 2010; Freeman 2015).

Although elevational patterns in community structure found here were broadly similar to other studies in birds, we found contrasting results when we examined how individual functional traits varied across elevations. Large relative wing size and large mass are significantly clustered at high, cool locations in hummingbirds (Graham *et al.* 2012), suggesting a strong influence of environmental filtering on high elevation hummingbird communities. However, relative wing size showed no pattern of increased clustering at high elevations in our system (Fig 5). Moreover, body mass distributions were clustered at high elevations as found in hummingbirds, but mean body mass was smaller not larger in high elevation bird communities. Thus, traits subject to filtering in challenging environments may be clade-specific. Specifically, large body size and large wings may be especially important for hummingbirds which are extremely small and thus subject to rapid heat loss, and use flight maneuvers that are particularly aerodynamically demanding at low atmospheric pressures (Segre *et al.* 2016). Alternatively, differences between these two studies could be attributed to topographical differences between sites. Mt. Kinabalu is an isolated massif with a summit elevation of 4095 m, whereas the Ecuadorean Andes where Graham and colleagues (2009, 2012) sampled hummingbird communities reach 6000 m. The more extreme abiotic conditions in the high Andes may exert a stronger abiotic filter than the highest elevations at our study site.

Despite increased clustering at high elevations, estimates of community structure at the highest elevations often approached neutral values (Fig 4). This result could reflect issues related to extremely low species richness in our highest communities. While habitat filtering may be less intense at extremely high elevations, simulations show that the power to detect environmental filtering decreases sharply when species richness is very small relative to the regional species pool (Freilich & Connolly 2015). The decrease in clustering at extremely high elevations was most evident in directly-sampled datasets (Fig 4), where communities had especially low species richness (Fig 3). Additionally, summit communities experience the coldest temperatures and lowest atmospheric air pressures, conditions thought to be physiologically challenging for birds (Altshuler & Dudley 2006; Graham *et al.* 2009; Cheviron & Brumfield 2012), emphasizing the likelihood that these neutral values are a statistical artifact and not ecologically meaningful.

Elevational patterns of community structure appear to differ across clades when we look beyond birds. Ant communities appear to show patterns similar to birds, with clustered high elevation communities and either neutral or overdispersed low elevation assemblages (Machac *et al.* 2011; Smith *et al.* 2014), while microbial communities appear to be phylogenetically clustered regardless of elevation (Bryant *et al.* 2008; Wang *et al.* 2012). Plants are a distinct outlier, with neutral structure at low elevations and overdispersion at high elevations (Bryant *et al.* 2008). However, in some plant taxa, facilitation among closely related species increases with elevation (Callaway *et al.* 2002), which should result in the opposite pattern. The variation in patterns of community structure across elevations suggests that the forces that govern community assembly, and the way in which they change across elevations, may differ among taxonomic groups.

Clustered high-elevation communities have often been attributed to constraints imposed directly by harsh environmental conditions on morphological or physiological traits (Graham *et al.* 2009, 2012). Based on an analysis of morphological traits we find no evidence that abiotic factors such as cold temperatures or low atmospheric pressure are directly driving clustering in high elevation bird communities. Instead, clustered traits are those related to food acquisition. Specifically, species at high elevations are smaller and have short and narrow bills (Fig 5-6). Avian body size and bill shape are correlated with prey size (Schoener 1971; Sam *et al.* 2017) and insect body size declines with increasing elevation (Janzen 1973; Sam *et al.* 2017). Thus, a possible cause for the smaller bills of high elevation species is an absence of large prey. In this case, abiotic factors may not be directly influencing avian community structure, but are doing so indirectly by influencing community structure of organisms on a different trophic level. The argument that insect size distributions may drive patterns avian diversity has been made in the context of latitudinal gradients (Schoener 1971), but our results suggest this may apply to elevational gradients as well.

Studies of community structure suggest that the forces governing community assembly are complex and vary across geographic gradients and among clades (Cavender-Bares, Keen & Miles 2006; Bryant *et al.* 2008; Graham *et al.* 2012). We show that tropical bird communities across a large elevational gradient are clustered due to a lack of resource and habitat complexity at high elevations, and appear to be simultaneously structured by interspecific competition and warm temperatures at low elevations. The rarity of overdispersed communities in this study and others (Graham *et al.* 2009, 2012) provides evidence that interspecific competition may not be the primary driver of avian community structure as previously thought.

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Table 1. Measures of phylogenetic niche conservatism as estimated by Blomberg's *K* for 5 morphological functional traits. *P*-values indicate the estimate is significantly different than zero, with larger numbers indicating stronger phylogenetic conservatism of a given trait. *K* values calculated for literature and all birds datasets have standard errors associated with them because estimates of *K* presented here are mean values from distributions of 1000 trees to avoid artificial inflation of *K* due to the presence of polytomies in a consensus tree. This process was not necessary for our Passerine dataset because the associated tree did not contain polytomies.

	Literature Data		All Birds		Passerines	
Trait	*K*	*P*	*K*	*P*	*K*	*P*
Mass	1.26 ± 0.26	< 0.001	1.13 ± 0.21	< 0.001	1.13	< 0.001
Wing size	0.60 ± 0.14	< 0.001	0.47 ± 0.11	< 0.001	0.89	< 0.001
Tarsus length	0.76 ± 0.13	< 0.001	0.63 ± 0.11	< 0.001	1.06	< 0.001
Bill width	1.19 ± 0.23	< 0.001	1.22 ± 0.24	< 0.001	1.82	< 0.001
Culmen length	1.20 ± 0.25	< 0.001	1.49 ± 0.23	< 0.001	0.66	< 0.001

Figure Legends

Figure 1. Phylogenetic tree of Bornean passerines. Posterior probabilities of each node represented by pie-charts at nodes with uncertainties represented by the proportion of black on the pie-chart (white circle = posterior probability of 1.0).

Figure 2. Topographic map of the study area within Kinabalu Park, including Mt. Kinabalu and Mt. Tambuyukon. Elevational transects along which point counts were conducted are shown as dashed lines. Contour lines are in increments of 200 m.

Figure 3. Changes in community species richness with elevation for our literature dataset spanning all of Kinabalu Park and directly-sampled datasets on Kinabalu and Tambuyukon.

Figure 4. Plots of phylogenetic (**A**)**,** and trait-based (**B**) community structure versus elevation for directly-sampled and literature datasets. Positive values of NRI and NTI indicate clustering, while negative values indicate overdispersion. Point color denotes whether NRI values are statistically different from zero at thresholds of $P < 0.10$ (black) or $P < 0.05$ (dark gray).

Figure 5. Community structure patterns for morphological functional traits across elevations based on our literature dataset. Positive values indicate that traits are more clustered than expected under a null-model distribution. Point color denotes whether NRI values are statistically different from zero at thresholds of $P < 0.10$ (black) or $P < 0.05$ (dark gray).

Figure 6. Changes in mean ± SD trait values for bill width, culmen length and residual tarsus length for avian communities across an elevational gradient based on our literature dataset. Bill width and culmen length are presented as raw values, residual tarsus length is calculated as the residual value from a regression of tarsus length on log-transformed body mass, and body mass is log-transformed.

Figure 1

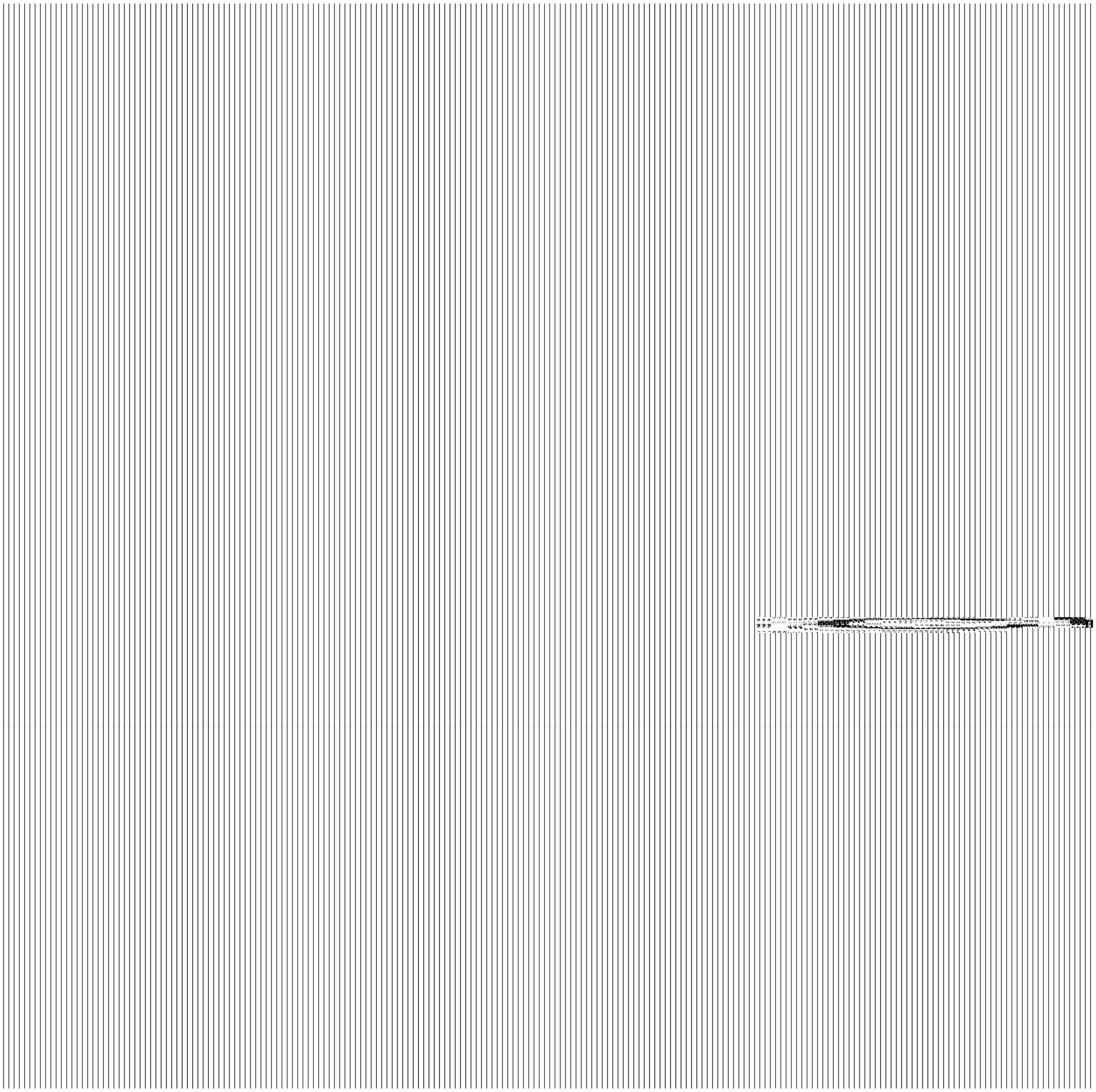


Figure 2

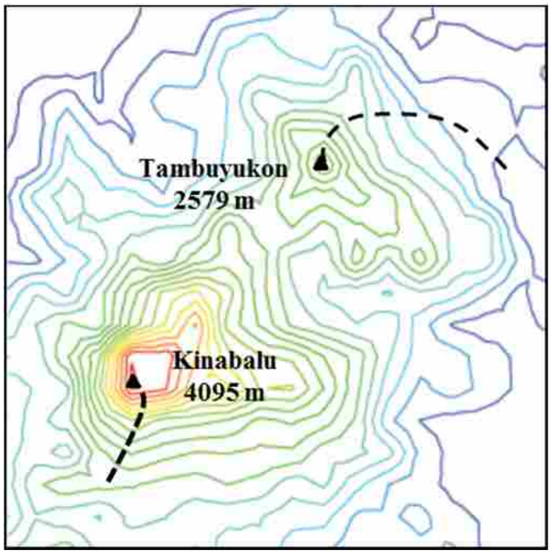


Figure 3

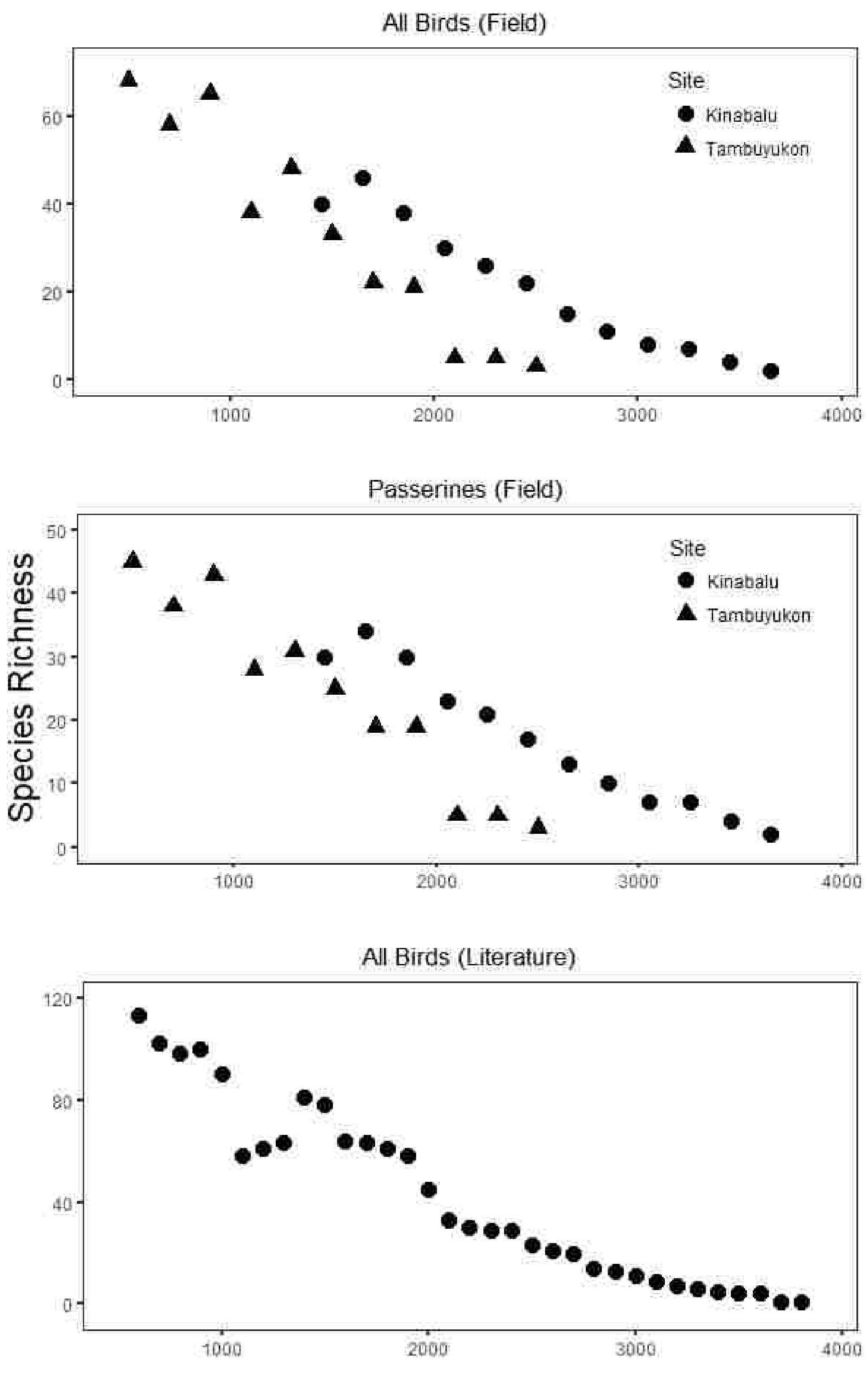

All Birds (Field)
Site
Kinabalu
Tambuyukon
0
20
40
60
1000
2000
3000
4000
Passerines (Field)
Site
Kinabalu
Tambuyukon
Species Richness
0
10
20
30
40
50
1000
2000
3000
4000
All Birds (Literature)
0
40
80
120
1000
2000
3000
4000

Figure 4A

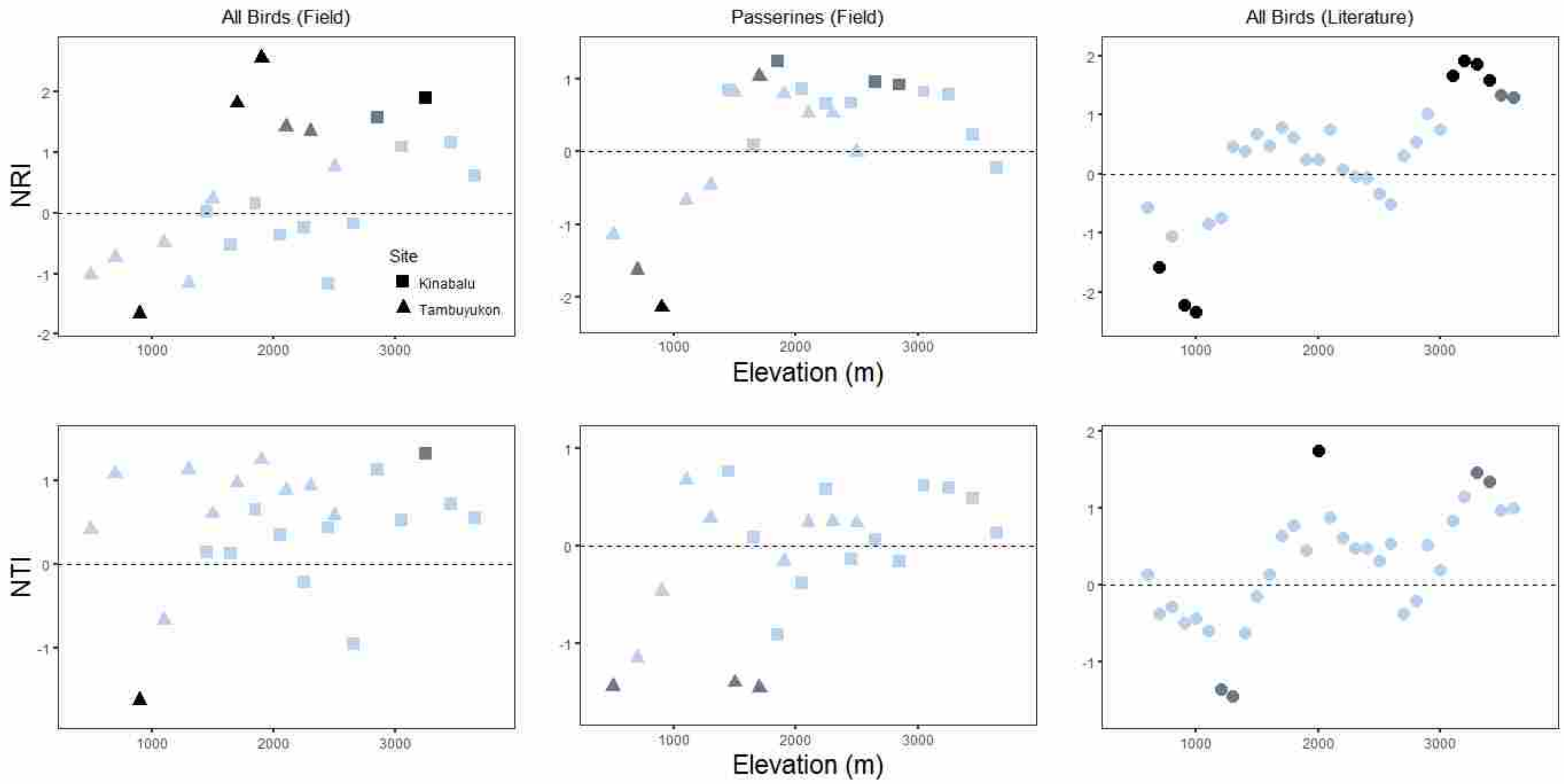

All Birds (Field)
Passerines (Field)
All Birds (Literature)
NRI
NTI
Elevation (m)
Site
■ Kinabalu
▲ Tambuyukon
1000
2000
3000
-2
-1
0
1
2

Figure 4B

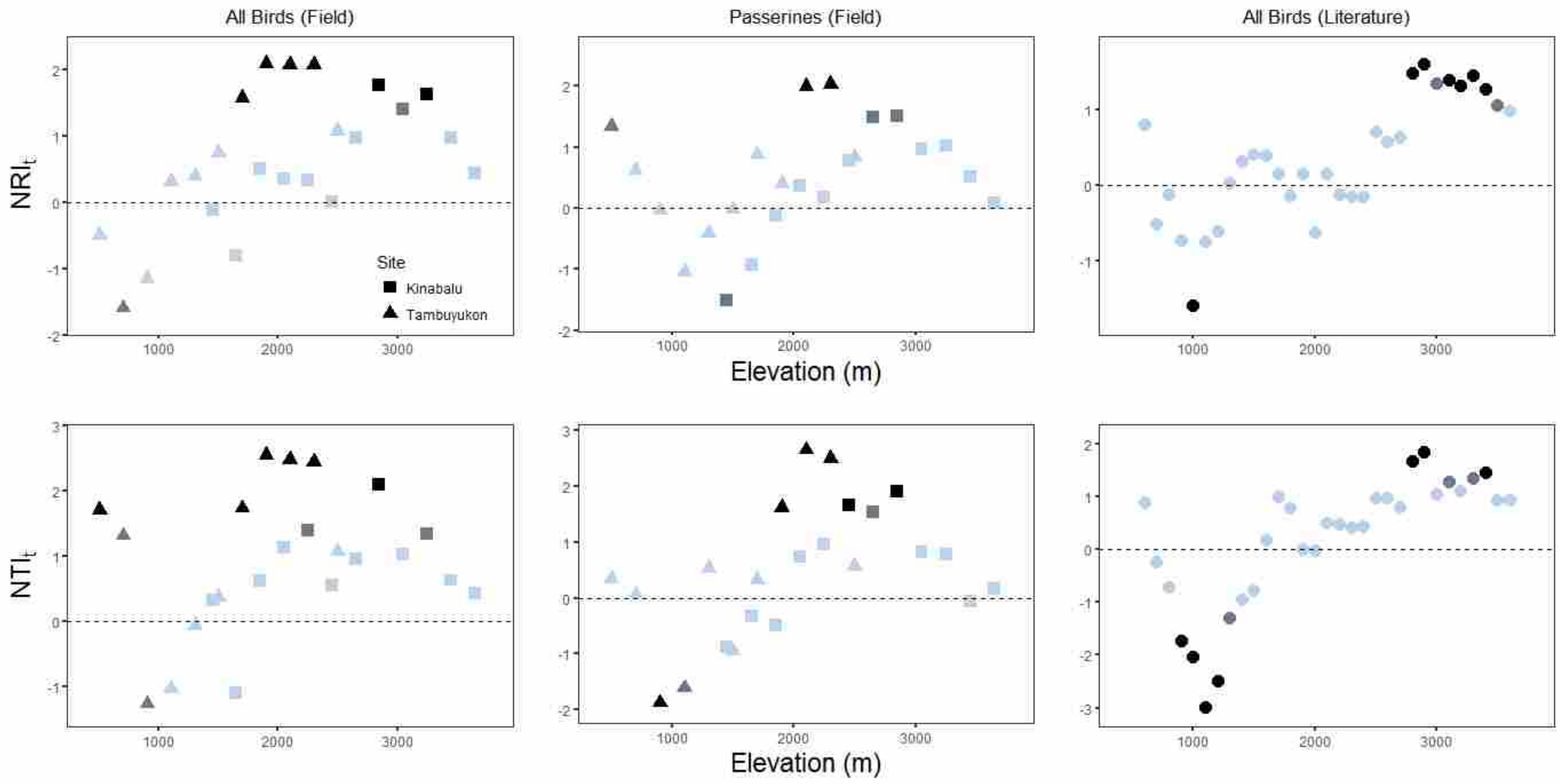

All Birds (Field)
Passerines (Field)
All Birds (Literature)
NRI$_t$
NTI$_t$
Elevation (m)
Elevation (m)
Site
Kinabalu
Tambuyukon
1000
2000
3000
-2
-1
0
1
2
3

Figure 5

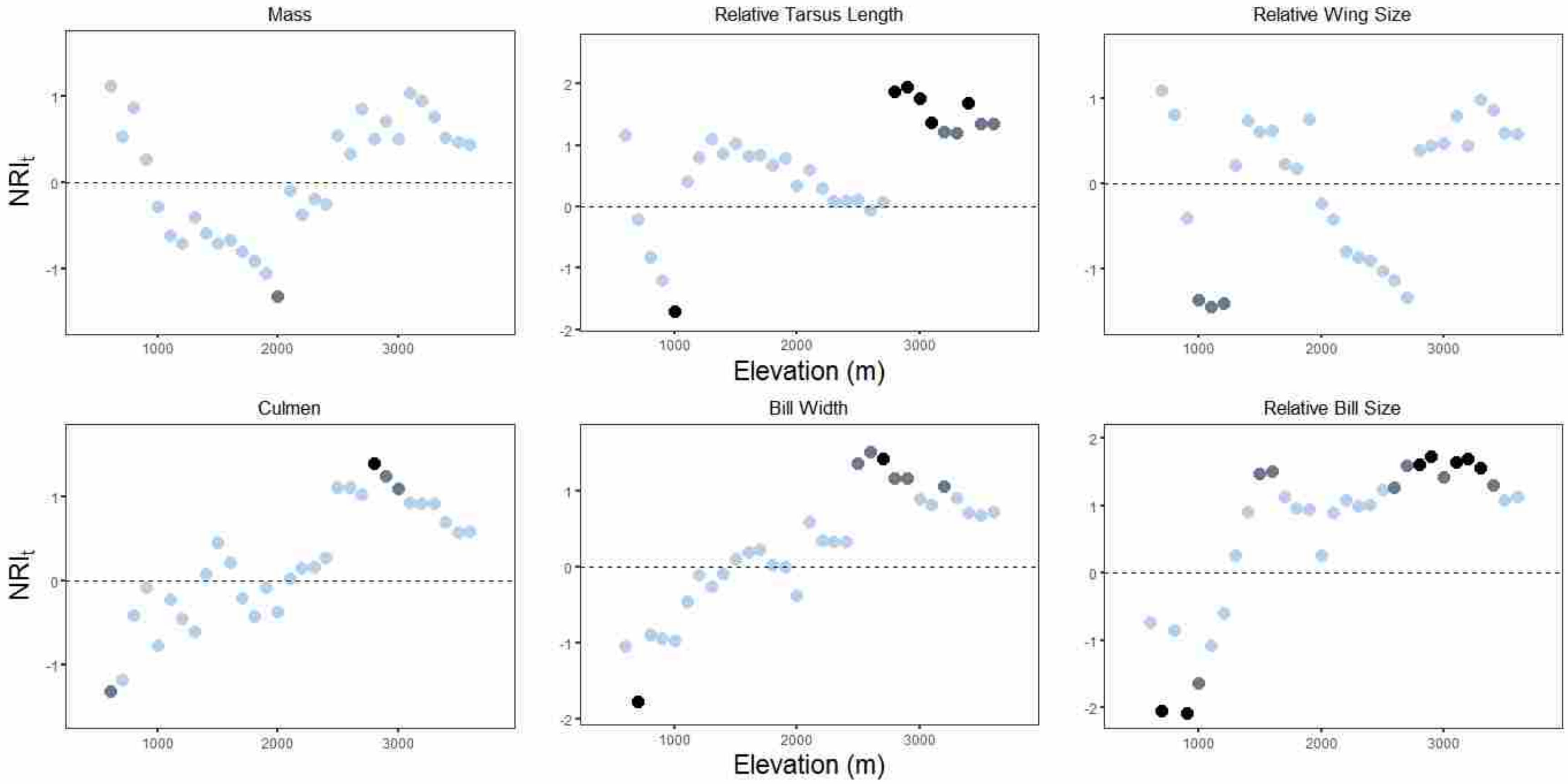
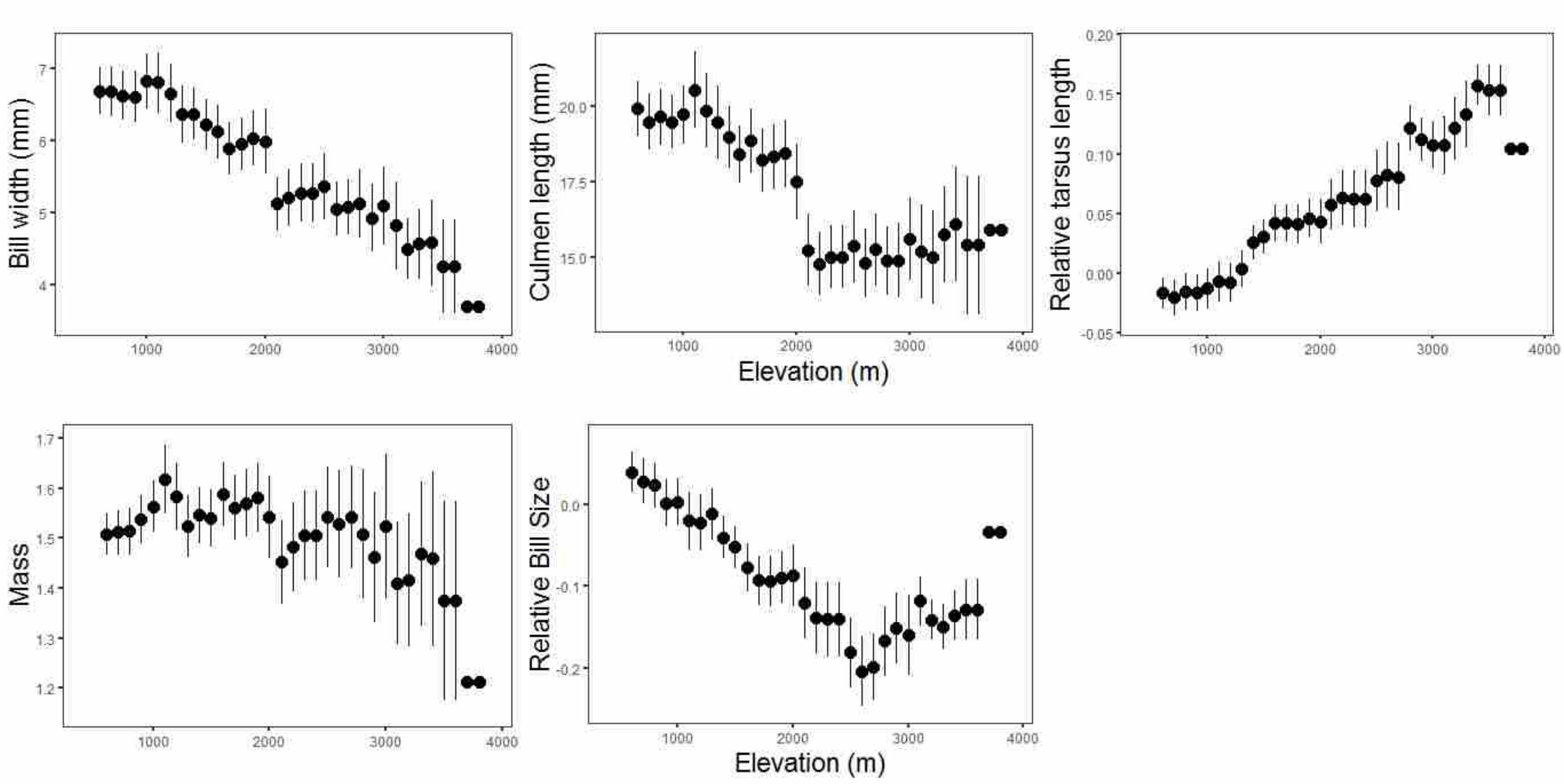

Mass
Relative Tarsus Length
Relative Wing Size
Culmen
Bill Width
Relative Bill Size
NRI_t
NRI_t
Elevation (m)
Elevation (m)
1000
2000
3000
2
1
0
-1
-2

Figure 6



Bill width (mm)
7
6
5
4
1000
2000
3000
4000
Culmen length (mm)
20.0
17.5
15.0
1000
2000
3000
4000
Elevation (m)
Relative tarsus length
0.20
0.15
0.10
0.05
0.00
-0.05
1000
2000
3000
4000
Mass
1.7
1.6
1.5
1.4
1.3
1.2
1000
2000
3000
4000
Relative Bill Size
0.0
-0.1
-0.2
1000
2000
3000
4000
Elevation (m)

Chapter 2: Thermal physiology does not drive elevational range limits in Bornean songbirds.

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ABSTRACT

The climatic variability hypothesis posits that stable abiotic conditions in the tropics cause narrow physiological tolerances and inhibit dispersal along abiotic gradients. This phenomenon is thought to explain the narrow elevational ranges of organisms on tropical mountains including ‘parapatric’ pairs of closely-related species with abutting but non-overlapping ranges. To test whether divergent physiological tolerances limit elevational ranges of tropical birds, we measured resting metabolic rate (RMR), lower critical temperature (LCT) and metabolic sensitivity to temperature (S_T) in 28 species of songbirds from mid (1450m) and high elevation (3200m) communities including two species pairs with parapatric distributions. RMR was similar for mid and high elevation species, but was correlated with lower elevational range boundary. LCT and S_T were similar between species sampled at mid and high elevation sites and were not correlated with any aspect of elevational range. Additionally, there were no consistent differences in thermal physiology in elevationally parapatric species pairs. Our results suggest that abiotic conditions do not set elevational range limits in tropical birds.

INTRODUCTION

Understanding the ecological and physiological mechanisms that limit species distributions is a fundamental goal of ecology and biogeography (Darwin 1859; Macarthur 1972; Lomolino, Riddle & Brown 2006). Furthermore, determining the role of abiotic conditions in limiting distributions is critical to predicting range dynamics in response to rapid climate change (Parmesan 2006; Deutsch *et al.* 2008). Biotic and abiotic factors can both limit distributions in specific contexts, but the relative importance of these two factors across environmental gradients is not well understood (Sexton *et al.* 2009; Jankowski *et al.* 2012). Species inhabiting tropical mountains often have narrow elevational ranges with closely-related taxa occupying adjacent elevational zones (Terborgh 1971; Stotz *et al.* 1996; McCain 2009). This pattern leads to rapid species turnover along mountainsides (Huey 1978) and drives exceptional biodiversity and endemism on tropical mountains (Cadena *et al.* 2011; Merckx *et al.* 2015). Yet, the factors limiting elevational ranges of tropical species are not well understood (Jankowski *et al.* 2012).

Abiotic factors are thought to be particularly important in setting elevational range limits in the tropics. The *climatic variability hypothesis* posits that stable abiotic conditions at low latitudes allow species to develop narrow physiological tolerances (Dobzhansky 1950). On tropical mountains, temporal stability in climate combined with dramatic changes in conditions across elevations may inhibit elevational dispersal (Janzen 1967) and explain the small elevational ranges of tropical species and parapatric (abutting, non-overlapping) distributions of closely-related species (Ghalambor *et al.* 2006). Upward range shifts in conjunction with rising temperatures suggest that physiological tolerances can be important in setting elevational range limits (Parmesan 2006; Moritz *et al.* 2008; Chen *et al.* 2009; Tingley *et al.* 2009; Harris *et al.* 2012; Freeman & Class 2014). Moreover, tropical species tend to have narrower elevational ranges and narrower thermal tolerances than temperate counterparts (Stevens 1992; Ghalambor *et al.* 2006; Deutsch *et al.* 2008; Sunday, Bates & Dulvy 2011; Gill *et al.* 2016), as predicted by the climatic variability hypothesis. However, while evidence for narrower thermal niches in the tropics than the temperate zone exists for ectotherms, this pattern is debated for endotherms (Khaliq *et al.* 2014; but see Wolf *et al.* 2017). Thermoregulatory abilities buffer endotherms from the direct impacts of climate and may weaken the influence of abiotic conditions on the evolution of thermal tolerances and range limits (Ghalambor *et al.* 2006). Moreover, elevational range-shifts in endotherms are sometimes linked to the absence of a putative competitor (Terborgh & Weske 1975; Remsen Jr. & Graves 1995a; b; Martin & Martin 2001; Gifford & Kozak 2011, but see Cadena & Loiselle 2007), or to changes in habitat or land use (Rowe, Finarelli & Rickart 2010; Jankowski *et al.* 2013). Such patterns suggest that elevational range limits may be more strongly influenced by habitat associations or interspecific competition than climate.

Songbirds (Passeriformes) are a tractable system in which to examine possible abiotic or physiological drivers of elevational range limits in endotherms. In the tropics, many avian clades have parapatric distributions with congeners "stacked" on top of each other in narrow elevational bands (Terborgh 1971; Diamond 1973; Remsen Jr. & Graves 1995a; b; Stotz *et al.* 1996). The ability of physiological traits to explain elevation patterns in songbirds is still unclear. Increased metabolic rate (BMR/RMR) is thought to be beneficial in cold environments, including high elevations, to facilitate greater thermogenic capacity (McKechnie & Swanson 2010). Birds inhabiting high-elevation habitats had higher BMR in New Guinea (McNab 2005, 2013), but BMR was similar across elevations in the Andes (Londoño *et al.* 2017). High elevation species may also incur lower metabolic costs of thermoregulation in cold environments via increased mass or biochemical adaptations to increase cold-tolerance (Pörtner 2002; Fangue, Richards & Schulte 2009; Jankowski *et al.* 2012). On the other hand, tropical songbirds do not appear to increase in mass at high elevation (Freeman 2017) and mass-independent differences in cold-tolerance may be subtle (Londoño *et al.* 2017) or absent (McNab 2013; Freeman 2016a) across elevations. Yet, previous studies included critical assumptions that raise questions about their conclusions. In particular, measures of thermal physiology were mathematically dependent on measures of body temperature and assumed physical properties alone influence thermoregulatory costs at low temperatures (McNab 1980, 2013; Londoño *et al.* 2017). Such assumptions ignore physiological adaptations that may decrease energetic costs of thermoregulation are ignored (McNab 1980). Furthermore, measurements of internal body temperature are highly variable within species and among measurement methodologies (Bouwknecht, Olivier & Paylor 2007; Nord *et al.* 2016). Consequently, the role of evolved differences in thermal physiology in limiting elevational ranges in tropical birds remains unclear. To improve our understanding of elevational variation in thermal physiology and the potential ability of this variation to limit elevational ranges, direct measurements of metabolism as a function of temperature are required.

To test whether physiological tolerance to temperature limits elevational ranges in tropical endotherms, we measured resting metabolic rate (RMR), lower critical temperature (LCT; the temperature below which RMR increases for thermoregulation) and metabolic sensitivity to temperature (S_T; the rate of increase in metabolism below LCT) in free-living songbirds inhabiting mid and high elevation habitats on a tropical mountain. We used phylogenetically-informed methods to test for differences in physiological traits between mid and high elevation communities and compare traits in two pairs of closely-related species with parapatric elevational distributions. We also tested for relationships between physiological traits and upper and lower elevational range limits to assess if thermal physiology is more important at lower (warmer) or upper (colder) elevational range boundaries.

METHODS

Study system

All data were collected at Kinabalu Park, Sabah, MY (6°N, 116°E), a large tract of tropical forest spanning 400 – 4100m on the island of Borneo. Metabolic measurements were performed in mid-elevation submontane cloud-forest at Park HQ (1560m) and high-elevation “Ceja” forest at Laban Rata (3270m) (Rafiqpoor & Nieder 2006). The two sites are connected by continuous, undisturbed forest bounded below by the park boundary at ~1450m, and above by a zone of bare granite from ~3800m to Low’s Peak at 4095m. All fieldwork was conducted from February – June, 2012-2016.

Climate measurements

We characterized climatic conditions across elevations on Mt. Kinabalu (1500 – 3500m) using Thermochron® Ibutton temperature loggers (Maxim Integrated Products, Sunnyvale, CA, USA). Dataloggers were fixed to 25cm metal stakes and placed in undisturbed vegetation every 100 vertical meters along narrow, rarely-used trails. Loggers were placed such that they were at least 15cm above ground and to avoid direct sunlight. All data loggers were set to record temperature values every 10 min.

Elevational ranges

To describe elevational distributions at our study site and to identify species pairs with parapatric distributions we conducted repeated point count surveys along a continuous transect from 1450m – 3800m on Mt. Kinabalu (Boyce *et al.* 2018a). Points were placed at least 200m straight-line distance apart, at a density of 5 points per 200 vertical meters. Counts were 10 minutes in duration, during which we recorded all individuals detected visually or aurally. Counts were conducted between civil twilight and 08:00 with a maximum of 5 counts per morning. All counts were conducted by AJB. The entire transect was sampled either two (2014-2015) or three (2012-2013) times per season. The order in which each cluster of points was sampled was reversed after each transect to avoid sampling bias related to time of day. The park boundary limited the low-elevation extent of our point counts at ~1450m, obscuring variation in lower range boundary for many species. To address this, we characterized the full extent of species elevational ranges in the park using elevational distribution data from Harris et al. (2012). This dataset is based on multiple data sources including direct sampling by the authors, citizen science projects, the literature, and unpublished data from experienced observers. To improve data quality, elevational ranges were broadened where direct observations from our field data fell outside of the published elevational range. Furthermore, where elevational ranges included single observations that were more than 200m either above or below all other known observations, we assumed these were misidentifications or represented temporary movements. These records were discarded and the elevational ranges described based on the remaining data.

Metabolic Measurements

Birds were captured for metabolic measurements by both passive and targeted mist-netting. Breeding females (based on presence of a brood patch) were excluded to minimize disruption of nesting and because the extreme vascularization of the avian brood patch is likely to alter RMR. Birds were transported to the lab and held for 1-2 hrs, depending on mass, to insure they were post-absorptive during measurements. Birds were watered before and after measurements and returned to the location of capture upon completion of metabolic measurements.

We used an open-flow respirometry system (described in Gerson et al. 2015) to characterize resting metabolic rate (RMR) as a function of temperature. We used 2L and 5L transparent plastic containers (Rubbermaid, Atlanta, GA, USA) as metabolic chambers, depending on the size of the study species. These containers were modified to include incurrent and excurrent air ports, with wire mesh platforms and plastic perches to allow subjects to rest comfortably. The bottom of the chamber contained a 2cm layer of mineral oil to trap moisture and gas associated with feces. Containers were placed inside a large cooler modified to hold an integral peltier device (model AC-162, TE Technology, Traverse City, MI), mated to a custom temperature control system (Gerson *et al.* 2015). Incurrent air was supplied by a high capacity vacuum pump (model DAA-V515-ED, Gast Manufacturing, Benton Harbor, MI, USA), and was routed through a coil of copper tubing prior to entering the inner chamber to facilitate rapid temperature equilibration. Air flow rates were regulated by mass-flow controllers (Alicat Scientific, Tucson, AZ). Flow rates were set between 2-15 L/min depending on mass of study species. Incurrent and excurrent air were subsampled at rates between 250 and 500 ml/min. CO_2 and H_2O were measured once per second using a portable gas-analyzer (LI-COR model LI-840a, Lincoln, NE, USA) and recorded using Expedata (Sable Systems, Las Vegas, NV, USA). We corrected mass flow rates of humid air, and calculated CO_2 and H_20 production using equations in Lighton (2008). Metabolic rate (W) was calculated as in Walsberg and Wolf (1995). CO_2 production was converted to metabolic energy used a respiratory quotient (RQ) value of 0.71, as suggested for post-absorptive, non-granivorous birds (Gessaman & Nagy 1988).

Humidity of incurrent air was regulated using a dew-point generator constructed of three Nalgene bottles connected in series. Air was bubbled through water in the first two bottles, and the third was empty and served as a water trap. The entire device was then submerged in a water bath kept at approximately 10°C by the addition of small ice-packs. This device buffered rapid fluctuations in humidity and prevented condensation occurring in the system. By adjusting water bath temperature and incurrent air pressure, we maintained relative humidity between 50 and 70%, which is within the range of normal conditions at both sites during the breeding season.

Metabolic measurements began within or near the thermoneutral zone (24- 33°C) (McKechnie & Wolf 2004; McNab 2009) to minimize stress and facilitate acclimation to the chamber. Subject activity was monitored in real-time via an infrared security camera connected with an external LCD screen. For each temperature, we subsetted data for analysis by selecting the longest continuous period of resting behavior after chamber temperature had reached equilibrium for at least 30 minutes. If no period of complete rest greater than two minutes was observed, no data were analyzed for that temperature. After each measurement, ambient temperature was decreased in 3°C increments and the process repeated. Time constraints or other logistical issues occasionally forced measurements at temperatures slightly above or below those at target intervals. Total measurement time was limited to 3 hours, which determined the number of temperatures sampled for each individual.

Statistical Analyses

Within species, metabolic rates vary strongly with mass (Kleiber 1932) and show large variation among individuals after accounting for mass (Auer *et al.* 2017b). To account for both issues when estimating LCT and S_T, we log-transformed RMR and body mass and calculated standardized residuals from a regression of metabolic rate on body mass. We then modeled these residuals (residual metabolic rate) as a function of temperature using segmented mixed-effects models, with individual as a random effect, to obtain initial maximum-likelihood estimates of LCT (Muggeo *et al.* 2014; Muggeo 2016). We selected all metabolic measurements at temperatures below LCT and fit linear-mixed effects models to determine S_t. We estimated RMR for each species by selecting the lowest measurement for each individual at temperatures above the estimated LCT and below 33°C. Final values of LCT were defined as the temperature at which metabolic rate as a function of temperature (S_T) intersected RMR (Fig 1).

We tested for variation in body mass, RMR, LCT and S_T between species at high and mid-elevation sites, and with respect to high and low elevational range boundaries for each species. We used phylogenetic generalized least-squares regression (PGLS), implemented in the package ‘ape’ (Paradis *et* *al.* 2004; Popescu *et al.* 2012), to control for the non-independence of species-level data points associated with phylogenetic relatedness (Felsenstein 1985). We fit three models for each analysis, assuming no phylogenetic signal ($\lambda = 0$), Brownian motion ($\lambda = 1$) and an Ornstein–Uhlenbeck model of trait evolution assuming stabilizing selection (Martins, Hansen & Url 1997). Final models were selected for each trait based on AIC_C values. Phylogenetic trees were acquired from birdtree.org (Jetz *et al.* 2012) using the Hackett backbone (Hackett *et al.* 2008). We sampled a distribution of 1000 trees for each analysis and produced majority-rules consensus trees in Mesquite (Maddison & Maddison 2011). Implementing PGLS for relatively small numbers of species can be problematic (Garamszegi 2014), so we also present raw results for all phylogenetic analyses. RMR, S_T and LCT are correlated with mass at broad scales (Kleiber 1932; Gillooly *et al.* 2001; Fristoe *et al.* 2015), but relationships are less clear for S_T and LCT within passerine birds (Londoño *et al.* 2017). Thus, body mass was included as a covariate in all models. All analyses were performed in R (R Core Team 2015).

RESULTS

Temperature declined monotonically with increasing elevation (Fig 2) at a rate of 4.1°C/1000m. Our low elevation sampling site (Park HQ) experienced temperatures with an average daily minimum and maximum of 15.83 ± 0.75°C to 19.73 ± 1.18°C. The high elevation sampling site (Laban Rata) experienced temperatures with an average daily minimum and maximum of 8.20 ± 0.37°C to 10.32 ± 0.54°C.

We measured resting metabolic rate in 208 individuals of 27 species, 21 at mid-elevation and 6 at high elevation (Table 1). RMR did not show a phylogenetic signal and mass explained the vast majority of variation in RMR among species with a scaling exponent of 0.65 ($P < 0.01$, $\lambda = 0$, Fig 3). The allometric scaling exponent was 0.65, which is consistent with known values for birds (Bennett & Harvey 1987; McKechnie & Wolf 2004). RMR did not differ between mid and high elevation species after accounting for mass and phylogenetic relationships ($P = 0.16$). RMR was not correlated with upper elevational range boundary (*P* = 0.42), but was positively correlated with lower range boundary (*P* = 0.03).

Body mass showed a strong phylogenetic signal (λ = 0.75) and did not differ between high and mid-elevation sites (*P* = 0.98). Body mass was not correlated with either upper (*P* = 0.81) or lower (*P* = 0.92) elevational range boundaries.

We were able to estimate LCT and S_T for 18 species, 12 at mid-elevation and 6 at high elevation (Fig 4, Table 1). We sampled an average of 10 individuals per species (range: 4-20, Table 1). S_T scaled allometrically and had a strong phylogenetic signal (*P* = 0.03, λ = 1.00). S_T was similar at high and mid elevation sites and was not correlated with lower (*P* = 0.21) or upper elevational boundary (*P* = 0.51).

LCT was unrelated to mass (*P* = 0.23) and showed a strong phylogenetic signal (λ = 1.00). Species sampled at mid-elevation had colder LCTs compared to high elevation relatives, but the relationship was only marginally significant (*P* = 0.07). LCT was not correlated with lower elevational range boundary (*P* = 0.14) but were warmer with increasing upper range boundary (*P* = 0.03).

We did not find consistent differences in the two paired congeners. Among bulbuls (*Pycnonotidae*), the high elevation species (*P. leucops*) had lower residual RMR, lower S_T, and a warmer LCT than its mid-elevation relative (*A. ochraceus*) (Fig 5A). Among white-eyes (*Zosteropidae*), the high-elevation species (*C. emeliae*) had lower residual RMR, lower S_T, and a colder LCT compared with its mid-elevation relative (*Z. atricapilla*) (Fig 5B).

DISCUSSION

Here we show that songbirds occupying mid and high elevations, including species pairs with parapatric distributions, have similar thermal physiology. The inability of physiological traits to explain elevational range limits in birds appears to be consistent across tropical regions (Freeman 2016a; Londoño *et al.* 2017). This result contradicts predictions of the *climate variability hypothesis* and suggests that factors other than thermal physiology may set range limits and drive rapid turnover of tropical endotherms across elevational gradients. Furthermore, if abiotic conditions are not direct drivers of range limits in tropical endotherms, the use of climate-envelope models in predicting future distributions in the context of climate change may be inappropriate.

Thermal tolerances estimated for resting organisms may be grossly different than in those in active, free-living individuals. Activity leads to increased endogenous heat production such that field metabolic rate is typically more than double RMR in birds (Drent & Daan 1980; Nagy 1987). The large quantities of heat produced as a consequence of activity contribute to thermoregulation such that the LCT is substantially colder in active birds (Zerba & Walsberg 1992; Zerba, Dana & Lucia 1999; Humphries & Careau 2011). The consequences of thermoregulatory substitution for thermal tolerances may be particularly significant in birds due to their energetically-intense nature of flight. Indeed, temperatures that correspond to the thermoneutral zone at rest can result in hyperthermia in flying passerines (Torre-Bueno 1976; Hudson & Bernstein 1981) and observations of starlings in flight suggest that optimal temperatures for flight are 10-14°C, whereas RMR is substantially elevated at these temperatures (Torre-Bueno 1976; Torre-Bueno & Larochelle 1978). Clearly, temperatures that represent challenges or optima in resting birds are unlikely to resemble challenging or optimal conditions in active individuals. At the same time, birds are not constantly active, and typically experience the coldest temperatures at night, when they are at rest. Many species use facultative hypothermia or torpor to reduce energetic costs of thermoregulation when exposed to cold temperatures and there is substantial variation in these strategies across species (McKechnie & Lovegrove 2002; Schleucher 2004). Therefore, comparative studies seeking to determine the role of abiotic conditions in setting range limits of endotherms should take a holistic approach integrating measures of thermal physiology during both resting and active phases.

We found that RMR was correlated with lower elevational range boundary, suggesting that minimizing heat loading in warm, humid environments may be more important than maximizing thermogenic capacity in cold high-elevation environments (Weathers 1997). However, this hypothesis is difficult to justify because body temperature in songbirds is generally upwards of 40°C (Prinzinger, Preßmar & Schleucher 1991), whereas ambient temperature in lowland rainforest in Borneo rarely exceeds 30°C (Kitayama 1992). This differential provides a large thermal gradient to facilitate passive heat loss, so thermal challenges from hot temperatures seem unlikely. Furthermore, the hottest temperatures experienced by forest birds are well within the thermoneutral zone of all passerines measured here, suggesting reduced RMR in species occupying low elevations may be unrelated to thermal ecology.

Our finding that birds occupying divergent elevational ranges do not have consistently divergent thermal physiology provides evidence that elevational range shifts in birds are unlikely to be directly driven by changing abiotic conditions. This idea is supported by observations that elevational range shifts in birds have often been absent, heterogeneous, or smaller than projected by abiotic models (Devictor *et al.* 2008; Forero-Medina *et al.* 2011; Harris *et al.* 2012). Plants and ectotherms are expected to be more sensitive to changing climate than endotherms (Huey *et al.* 2012). Indeed, on Mt. Kinabalu, insects show large and consistent upward elevational range shifts in response to rising temperatures (Chen *et al.* 2009), but range shifts are inconsistent in birds (Harris *et al.* 2012). Because plants and small ectotherms are key components of habitat for songbirds, narrow elevational ranges and range shifts may be driven primarily by associations with habitat and prey rather than with an abiotic niche. If true, mountain passes may indeed be "higher" in the tropics for endotherms, but elevational dispersal may be constrained by biotic not abiotic zonation (Janzen 1967).

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Table 1. Mean values (± SE) for physiological traits and elevational ranges for species sampled in this study. Sample size (n) refers to number of individuals sampled for physiological traits. Site indicates whether a species was sampled at mid (Park HQ, 1560m) or high (Laban Rata, 3270) elevation sites. Elevational ranges include data from all of Kinabalu Park.

							Elevational Range Boundary (m)	
Species	Mass (g)	S_T (W/°C)	RMR (W)	LCT (°C)	n	Site	Low	High
Turdus poliocephalus	75.49 ± 1.16	0.017	1.114 ± 0.044	24.71	6	High	2,700	3600
Zoothera citrina	68.00	-	0.95	-	1	Mid	1400	2000
Myophonus borneensis	123.13 ± 3.87	-	1.393 ± 0.063	-	8	Mid	800	2700
Brachypteryx montana	19.80 ± 0.28	0.014	0.438 ± 0.023	21.32	4	Mid	1400	2900
Enicurus borneensis	39.00 ± 1.14	-	0.634 ± 0.026	-	7	Mid	800	1800
Ficedula hyperythra	8.33 ± 0.13	0.009	0.218 ± 0.014	24.35	9	Mid	1200	2900
Rhinomyias gularis	25.46 ± 0.32	0.009	0.460 ± 0.025	21.73	11	Mid	1400	1900
Eumyias indigo	16.96 ± 0.43	-	0.300 ± 0.004	-	2	Mid	1400	2400
Dicrurus leucophaeus	44.69	-	0.53	-	1	Mid	1000	2200
Pachycephala hypoxantha	22.80 ± 0.30	0.020	0.406 ± 0.007	21.67	12	Mid	1200	2500
Rhipidura albicollis	12.12 ± 0.18	0.013	0.307 ± 0.016	28.05	10	Mid	900	3200
Cissa thalassina	113.00 ± 3.00	-	1.237 ± 0.057	-	2	Mid	900	3200
Aethopyga temminckii	6.01 ± 0.77	-	0.176 ± 0.019	-	2	Mid	800	2000
Alophoixus ochraceous	49.01 ± 0.82	0.027	0.769 ± 0.021	19.50	20	Mid	900	1700
Rhinocichla treacheri	65.49	-	0.74	-	1	Mid	1000	3400
Phylloscopus trivirgatus	9.28 ± 0.10	0.011	0.210 ± 0.012	22.94	12	High	1300	3200
Stachyris nigriceps	15.60 ± 0.28	0.016	0.340 ± 0.011	28.85	17	Mid	1400	2400
Yuhina everetti	13.81 ± 0.23	-	0.359 ± 0.008	-	2	Mid	500	2100
Chlorocharis emeliae	15.34 ± 0.45	0.023	0.391 ± 0.031	26.11	9	High	1500	3800
Zosterops atricapilla	8.64 ± 0.16	0.019	0.250 ± 0.016	24.39	10	Mid	1300	2100
Napothera crassa	28.40 ± 0.72	0.023	0.471 ± 0.028	25.94	9	Mid	1400	2700
Pellorneum pyrrogenys	19.05 ± 0.24	0.016	0.372 ± 0.008	26.99	12	Mid	900	1800

Phyllergates cuculatus	6.99 ± 0.12	0.009	0.217 ± 0.009	25.89	8	Mid	1300	2000
Cettia vulcania	9.59 ± 0.35	0.011	0.249 ± 0.017	27.50	9	High	1400	3600
Urosphena whiteheadi	10.26 ± 0.10	0.012	0. 262 ± 0.015	23.84	12	Mid	1400	2400
Pycnonotus flavescens	29.84 ± 1.05	0.022	0.515 ± 0.014	25.45	7	High	1700	3300
Bradypterus accentor	18.16 ± 0.39	0.013	0.467 ± 0.013	26.03	5	High	1900	3600

Figure Legends

Figure 1. Conceptual figure of metabolic rate as a function of temperature, and associated physiological parameters for endotherms, following Scholander et al. (1950). Lower critical temperature (LCT) is the temperature at which metabolic rate is elevated above basal to maintain body temperature. Resting metabolic rate (RMR) is the rate of energy production for a post-absorptive organism at rest, within the thermoneutral zone. Metabolic sensitivity to temperature (S_T) is defined here as the rate of increase in metabolic rate with decreasing temperature below LCT.

Figure 2. Mean (grey), average daily maximum (±SD) and average daily minimum (±SD) temperature variation across elevations on Mt. Kinabalu from February – September, 2012-2014.

Figure 3. Resting metabolic rate (W) as a function of temperature for 18 species of songbirds (Passeriformes). Each point represents the mean RMR value for a given temperature, error bars are ± SE. Individual points represent temperatures at which only one measurement was taken. Dotted lines characterize resting metabolic rate, LCT and S_T based on segmented mixed-effects models. Associated data including sample sizes are presented in Table 1.

Figure 4. The allometric relationship between resting metabolic rate (RMR) and body mass for species measured at mid and high elevation sites.

Figure 5. Thermal physiology and elevational ranges of two parapatrically distributed species pairs; **A)** bulbuls (*Pycnonotidae*) and **B)** white-eyes (*Zosteropidae*) at Kinabalu Park. Axes for high and low elevation species are scaled similarly for visual comparison of LCT and $S_{T.}$ Dotted lines represent allometric predictions for RMR based on our data (Table 1).

Figure 1

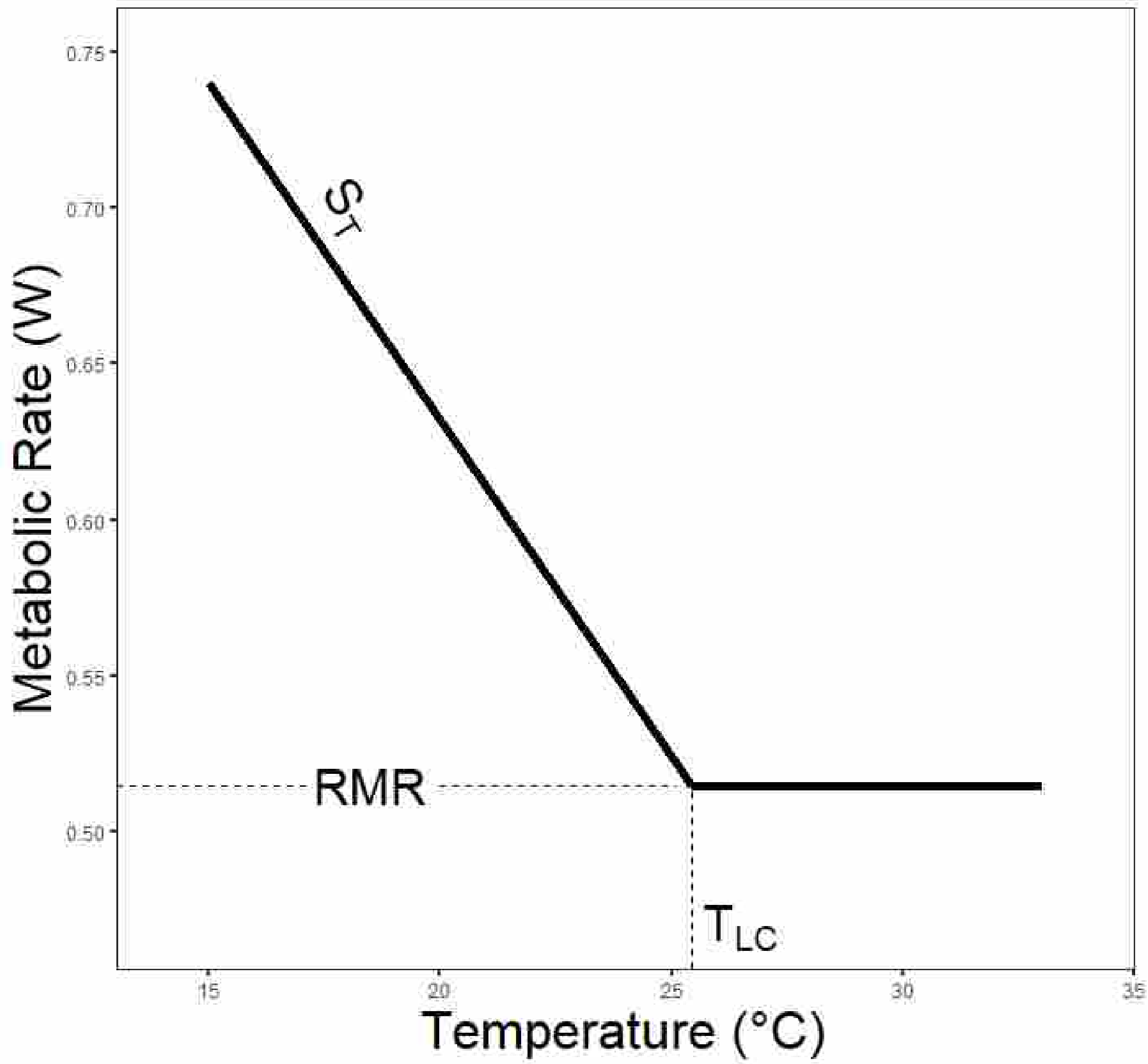

0.75
0.70
0.65
0.60
0.55
0.50
Metabolic Rate (W)
S_T
RMR
T_{LC}
15
20
25
30
35
Temperature (°C)

Figure 2

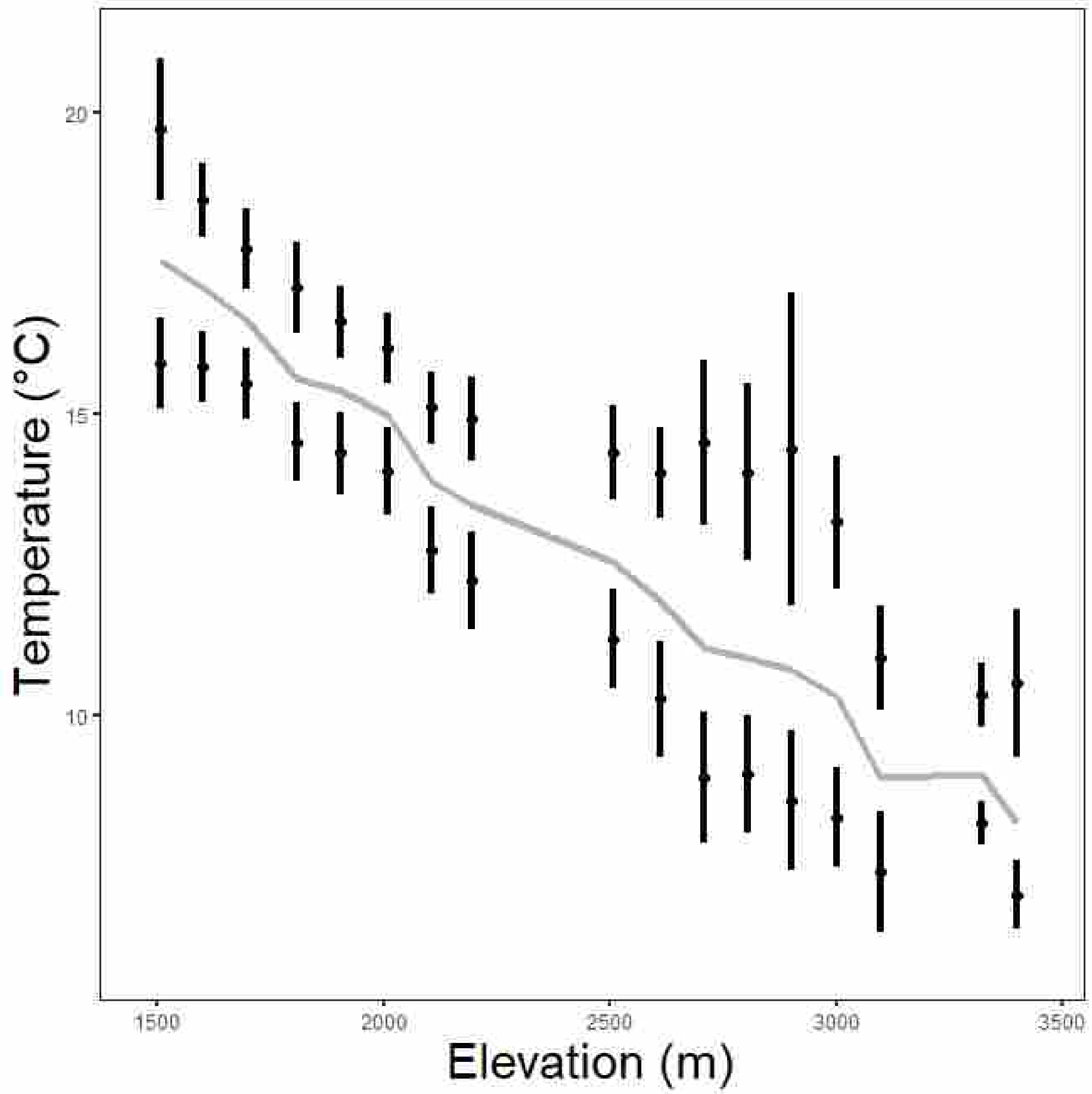


Figure 3

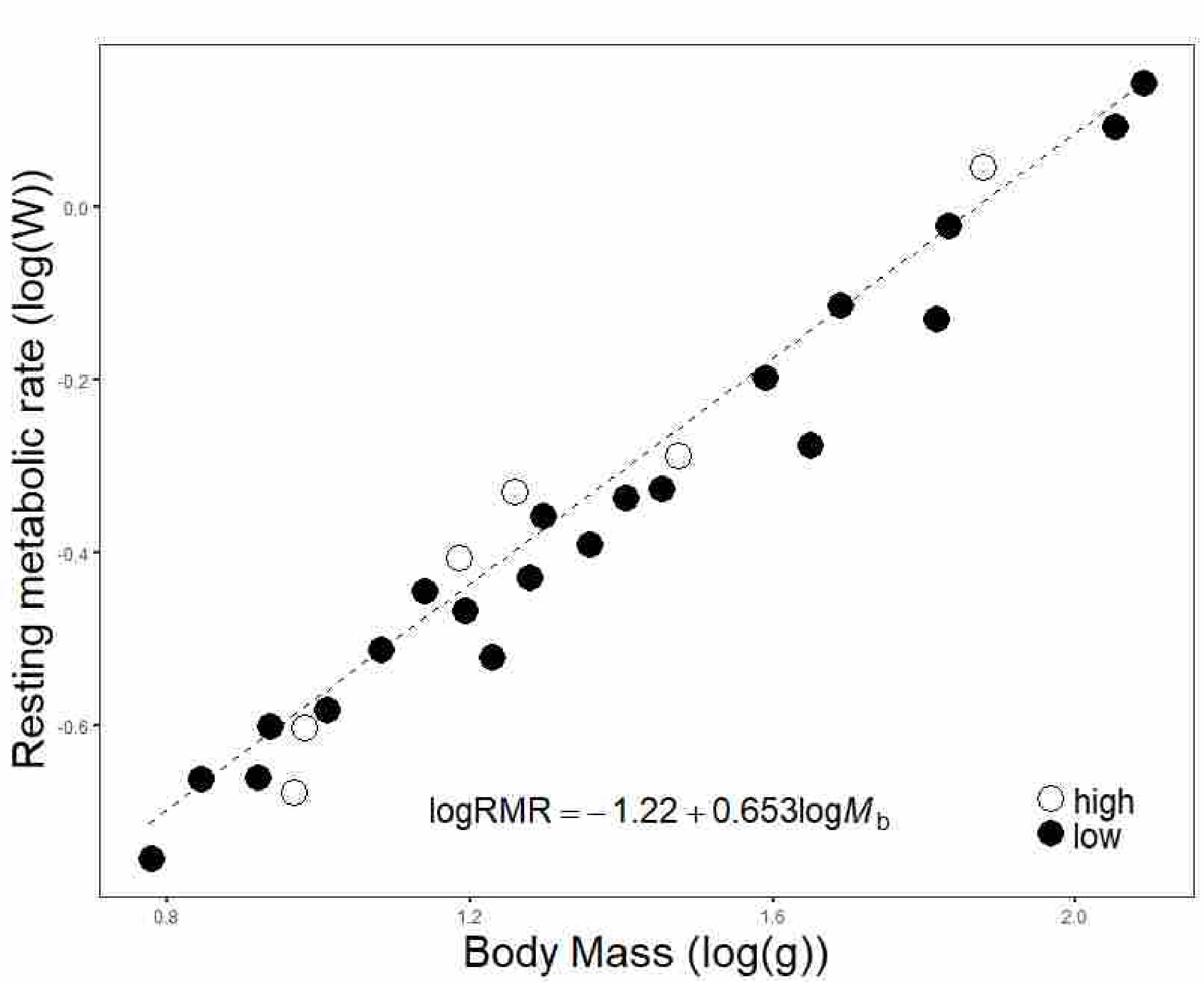

Resting metabolic rate (log(W))
0.0
-0.2
-0.4
-0.6
0.8
1.2
1.6
2.0
Body Mass (log(g))
logRMR = −1.22 + 0.653logM_b
○ high
● low

Figure 4

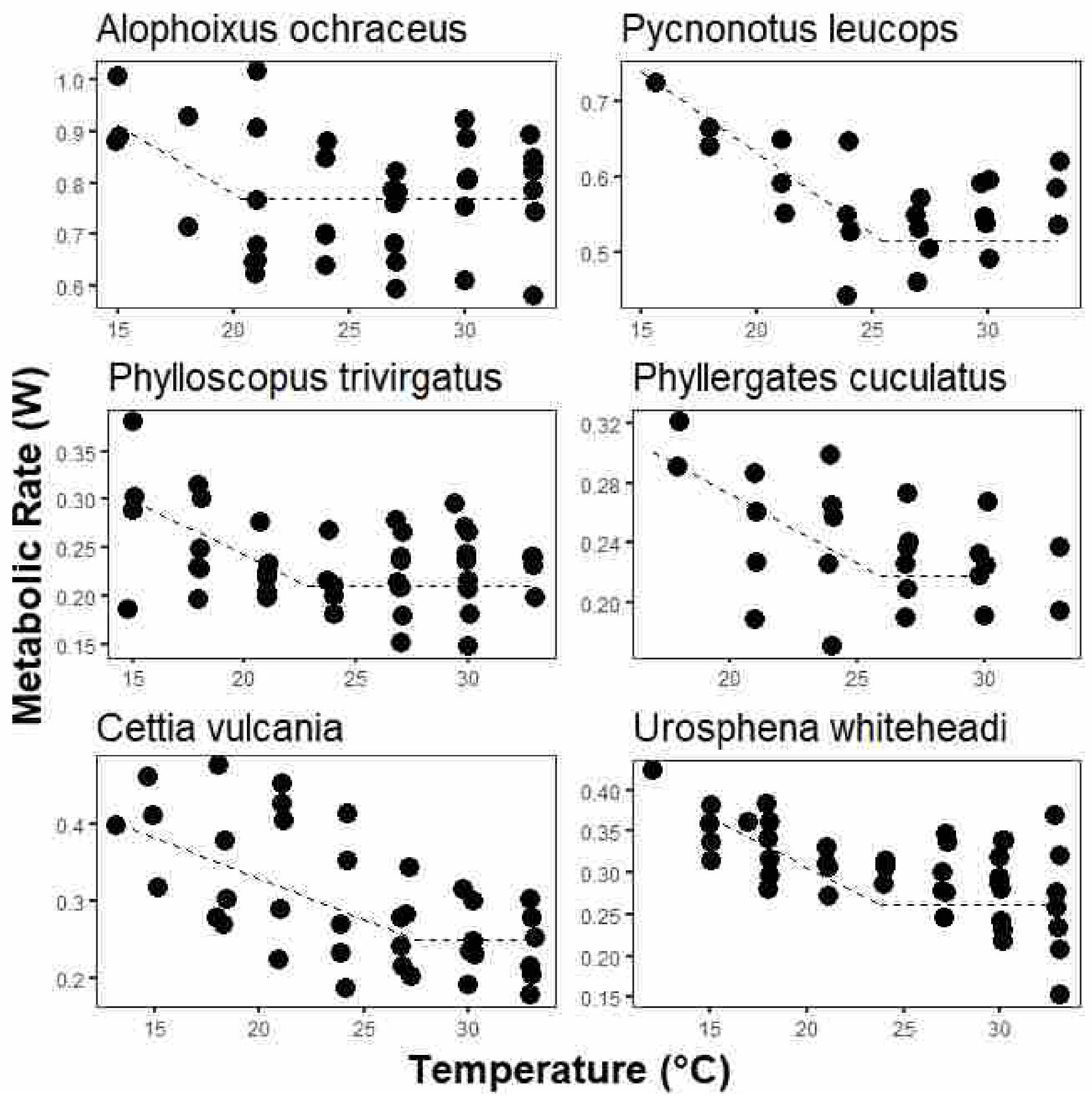
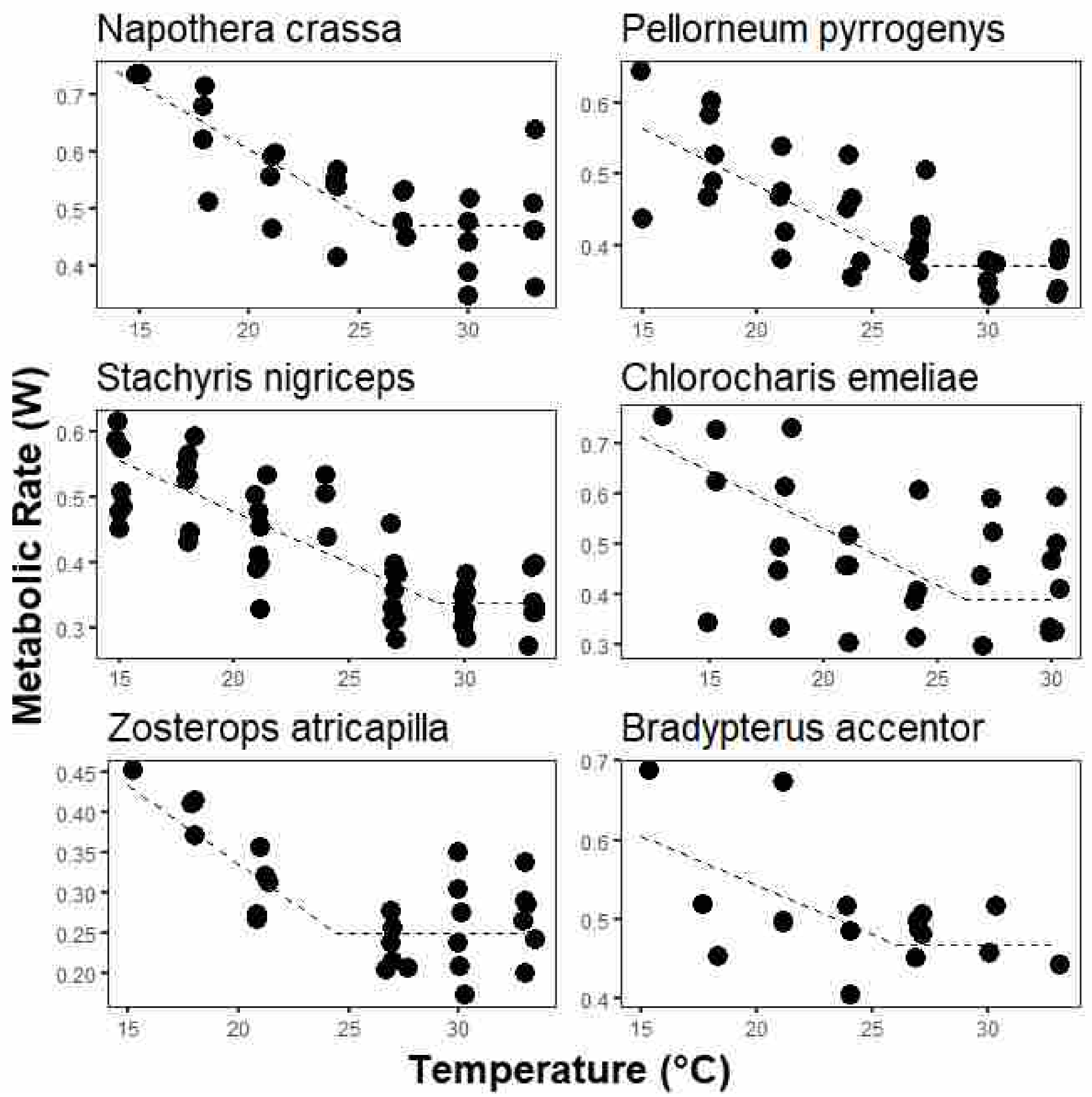

Alophoixus ochraceus
Pycnonotus leucops
Phylloscopus trivirgatus
Phyllergates cuculatus
Cettia vulcania
Urosphena whiteheadi
Metabolic Rate (W)
Temperature (°C)
1.0
0.9
0.8
0.7
0.6
0.7
0.6
0.5
0.35
0.30
0.25
0.20
0.15
0.32
0.28
0.24
0.20
0.4
0.3
0.2
0.40
0.35
0.30
0.25
0.20
0.15
15
20
25
30

Figure 4



Napothera crassa
Pellorneum pyrrogenys
Stachyris nigriceps
Chlorocharis emeliae
Zosterops atricapilla
Bradypterus accentor
Metabolic Rate (W)
Temperature (°C)
0.7
0.6
0.5
0.4
0.3
0.45
0.40
0.35
0.30
0.25
0.20
15
20
25
30

Figure 4

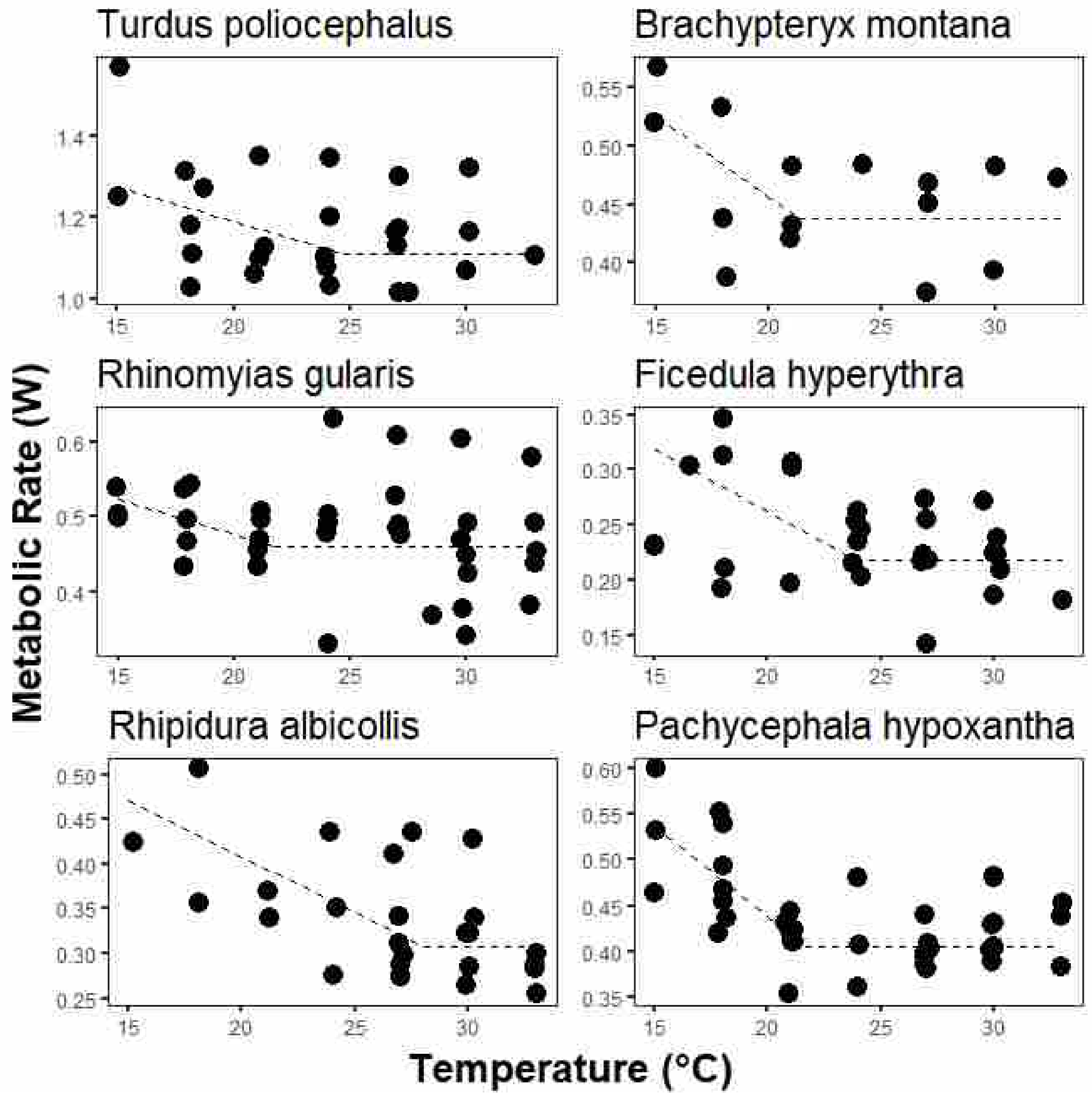

Turdus poliocephalus
Brachypteryx montana
Rhinomyias gularis
Ficedula hyperythra
Rhipidura albicollis
Pachycephala hypoxantha
Metabolic Rate (W)
Temperature (°C)
1.0
1.2
1.4
0.40
0.45
0.50
0.55
0.4
0.5
0.6
0.15
0.20
0.25
0.30
0.35
0.25
0.30
0.35
0.40
0.45
0.50
0.35
0.40
0.45
0.50
0.55
0.60
15
20
25
30

Figure 5A

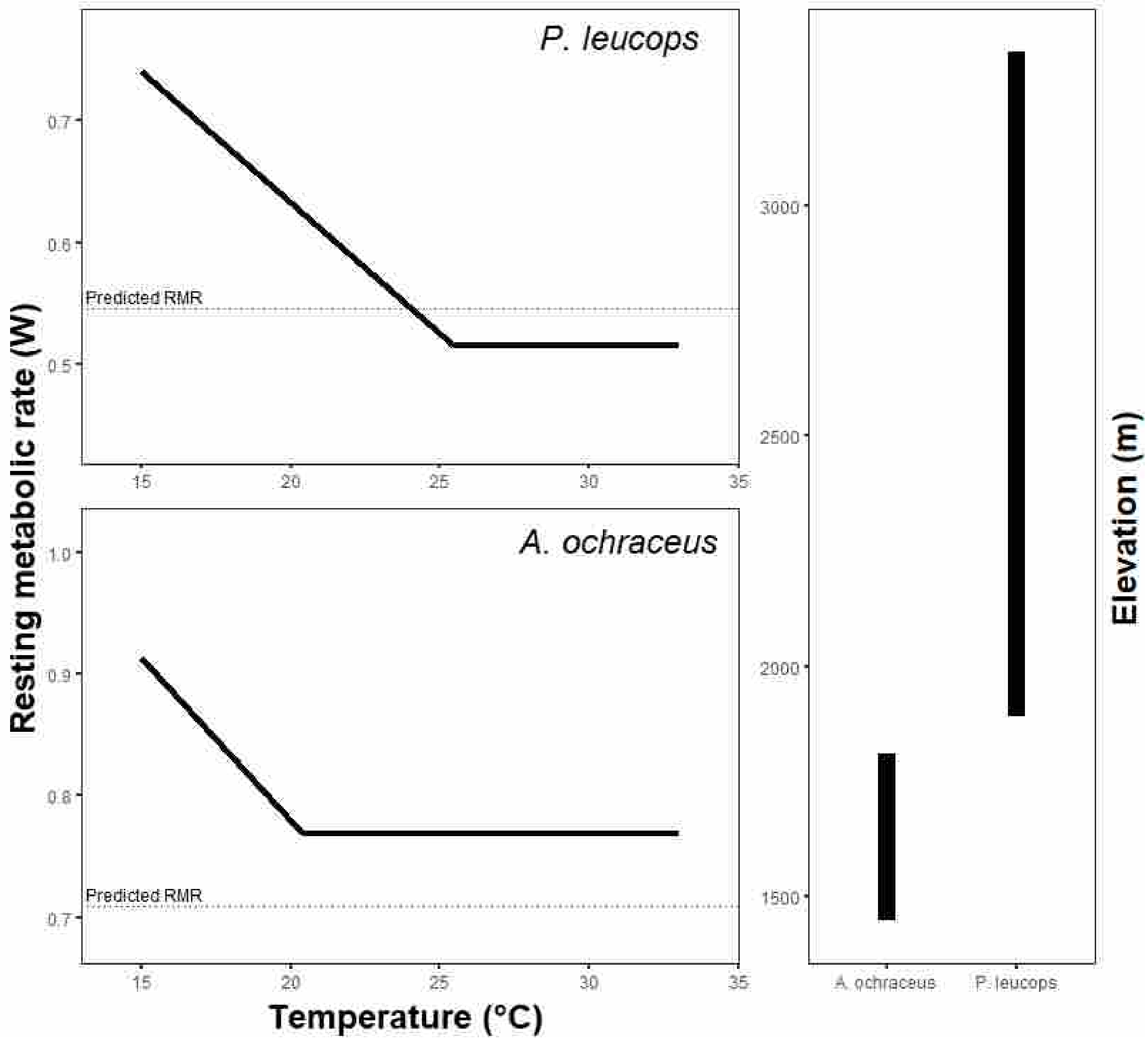
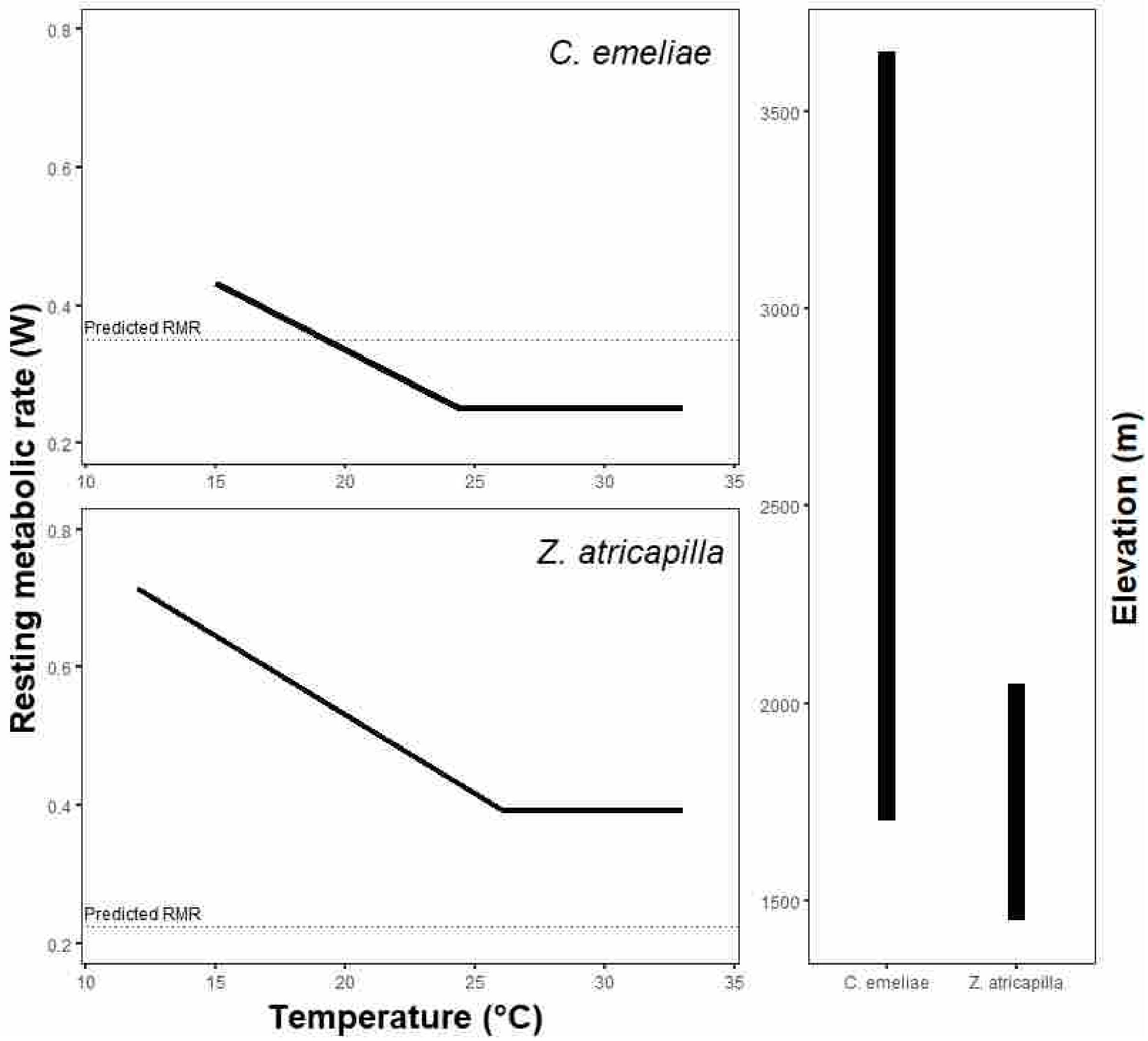

P. leucops
A. ochraceus
Predicted RMR
Predicted RMR
Resting metabolic rate (W)
0.7
0.6
0.5
1.0
0.9
0.8
0.7
15
20
25
30
35
Temperature (°C)
3000
2500
2000
1500
Elevation (m)
A. ochraceus
P. leucops

Figure 5B


C. emeliae
Z. atricapilla
Predicted RMR
Predicted RMR
Resting metabolic rate (W)
0.2
0.4
0.6
0.8
10
15
20
25
30
35
Temperature (°C)
Elevation (m)
1500
2000
2500
3000
3500
C. emeliae
Z. atricapilla

Chapter 3: Interspecific aggression among parapatric and sympatric songbirds on a tropical elevational gradient

Andy J. Boyce and Thomas E. Martin

ABSTRACT

Interspecific competition is hypothesized to be a strong force that set species range limits and is thought to drive parapatric distributions of closely related species on tropical mountains. Yet, experimental evidence that competition drives spatial segregation of closely related species on elevational gradients is lacking. To test whether competition limits elevational ranges of tropical songbirds, we conducted reciprocal playback experiments on two pairs of species with adjacent but non-overlapping distributions and one pair of sympatric species. We found asymmetric interspecific aggression in one parapatric pair *(Pycnonotidae)* and a complete absence of interspecific aggression in the other *(Zosteropidae)*. We also found asymmetric interspecies aggression in two pairs of sympatric flycatchers *(Muscicapidae)*. Our results suggest that interspecific aggression may set range limits in some cases, but it is not a prerequisite for parapatry. Furthermore, the presence of interspecific aggression between co-occurring relatives suggests that while competition may play a role in limiting species distributions, interspecific aggression alone is not sufficient evidence to assert that competition is the primary driver of parapatric distributions.

INTRODUCTION

Species inhabiting tropical mountains often have narrow elevational ranges with closely-related species occupying adjacent elevational zones (Terborgh 1971; Stotz *et al.* 1996; McCain 2009). This pattern leads to rapid species turnover along mountainsides (Huey 1978) and is associated with exceptional biodiversity and endemism on tropical mountains (Cadena *et al.* 2011; Merckx *et al.* 2015). Yet, the factors limiting elevational ranges of tropical species remain unclear (Jankowski *et al.* 2012).

Interspecific competition is hypothesized to be a strong force that can limit species ranges (Connell 1961; Diamond 1973) and is thought to explain adjacent but non-overlapping elevational distributions of closely related species (Heller 1971; Diamond 1973; Terborgh & Weske 1975; Stevens 1992; Jankowski, Robinson & Levey 2010; Freeman 2015). Competitive interactions are generally thought to be most important at the "warm" edge of a species range, while abiotic drivers are hypothesized to be more important at "cold" boundaries (MacArthur 1972). If this paradigm is accurate, low-elevational species should be competitively dominant over high elevation species and show stronger interspecific aggression towards their high-elevation relative than vice versa (Jankowski *et al.* 2010). This pattern of asymmetric interspecific aggression means that warming climates may drive range contractions in high elevation species as dominant low elevation competitors expand their range upward. This process is thought to drive "mountaintop extinctions", making montane species particularly vulnerable to climate change (Colwell *et al.* 2008; Sekercioglu *et al.* 2008). Understanding the role of interspecific competition in determining range boundaries is therefore critical to predicting outcomes and prioritizing conservation effort in light of climate change.

Evidence for competition shaping parapatric distributions comes primarily from observations that some species expand their range in areas where a closely-related species is absent, suggesting competitive release in the absence of a competitor (Terborgh & Weske 1975; Remsen Jr. & Graves 1995a; b; Martin & Martin 2001a; Gifford & Kozak 2011). However, what appears to be range expansion due to the absence of a presumed competitor can reflect geographic variation in the distribution of suitable habitat and not competitive release (Cadena & Loiselle 2007). Observations of interspecific aggression between closely-related species with abutting ranges are also presented as evidence that competition sets and/or maintains range limits for some species pairs (Heller 1971; Robinson & Terborgh 1995; Jankowski *et al.* 2010). However, if interference competition sets and/or maintains range boundaries between two competitors, we would expect ranges to be perfectly adjacent and non-overlapping (Terborgh 1971). Yet, in many cases of elevational 'parapatry' significant zones of overlap or gaps where neither species is present occur (Terborgh 1971). Overall, the importance of interference competition in limiting distributions of close relatives is unclear.

We examine these questions in with songbirds (passerines) across an elevational gradient in the tropics. Songbirds are a tractable system in which to examine the drivers of elevational range limits. In the tropics, many clades have parapatric distributions with congeners "stacked" on top of each other in narrow elevational bands (Terborgh 1971; Diamond 1973; Remsen Jr. & Graves 1995a; b; Stotz *et al.* 1996). Birds are easily observed both visually and aurally, and territorial singing behavior allows for straightforward identification to species and facilitates territory location. Evidence for interspecific aggression as a proximate force limiting elevational ranges of songbirds is mixed. Broadly speaking, interspecific aggression in birds is often asymmetric (reviewed in Martin, Freshwater & Ghalambor 2017a), where one species either consistently "wins" aggressive interactions, or responds more strongly to the presence of a heterospecific than the other. Along elevational gradients, asymmetric aggression has been reported, with low elevation species dominating high-elevation relatives (Jankowski *et al.* 2010; Freeman 2016a; Freeman & Montgomery 2016). This pattern has been interpreted as evidence that low-elevation species outcompete high-elevation subordinates who are forced into suboptimal habitat (Martin & Martin 2001b; Jankowski *et al.* 2010). However, interspecific aggression was absent in some other pairs, calling into question the general importance of competition in setting elevational range limits in birds (Freeman 2016a). Furthermore, strong interspecific aggression has been documented in co-occurring (sympatric) species pairs (Robinson & Terborgh 1995; Freeman 2016b), suggesting that observations of interspecific aggression alone are not sufficient evidence to infer interference competition as a driver of elevational parapatry. Thus, studies assessing strength and directionality of interspecific aggression in both sympatric and parapatric species pairs are needed.

Here, we perform reciprocal playback experiments to assess the presence and directionality of interspecific aggression in two closely-related species pairs that replace each other along an elevational gradient. We also performed reciprocal playback experiments on two sympatric species to assess whether patterns of interspecific aggression is equally strong between co-occuring and parapatric species pairs.

METHODS

Study system

All data were collected at Kinabalu Park, Sabah, Malaysia (6°N, 116°E), a large tract of tropical forest spanning 400 – 4100m on the island of Borneo. Playback experiments were performed in mid-elevation submontane cloud-forest at Park HQ (1560 – 1850m) and high-elevation elfin forest at Laban Rata (3000 – 3450m) (Rafiqpoor & Nieder 2006). The two sites are connected by continuous, undisturbed forest bounded below by the park boundary at ~1450m, and above by a zone of bare granite from ~3800m to Low's Peak at 4095m. All fieldwork was conducted from February – June, 2012-2016.

Elevational ranges

To describe elevational distributions of bird species at our study site and to identify species pairs with parapatric distributions we conducted repeated point count surveys along a continuous transect from 1450m – 3800m on Mt. Kinabalu. Points were placed at least 200m straight-line distance apart, at a density of 5 points per 200 vertical meters. Counts were 10 minutes in duration, during which we recorded all individuals detected visually or aurally. Counts were conducted between civil twilight and 08:00 with a maximum of 5 counts per morning. All counts were conducted by AJB. The entire transect was sampled either two (2014-2015) or three (2012-2013) times per season. The order in which each cluster of points was sampled was reversed after each transect to avoid sampling bias related to time of day. The park boundary limited the low-elevation extent of our point counts at ~1450m, obscuring variation in lower range boundary for many species. To address this, we characterized the full extent of species elevational ranges in the park using elevational distribution data from Harris et al. (2012). This dataset is based on multiple data sources including direct sampling by the authors, citizen science projects, the literature, and unpublished data from experienced observers. To improve data quality, elevational ranges were broadened where direct observations from our field data fell outside of the published elevational range. Furthermore, where elevational ranges included single observations that were more than 200m either above or below all other known observations, we assumed these were misidentifications or represented temporary movements. These records were discarded and the elevational ranges re-described based on the remaining data.

Playback experiments

We selected two pairs of elevationally parapatric relatives and one pair of sympatric relatives for playback experiments. All species are common year-round residents. Parapatric species pairs included bulbuls *(Pycnonotidae);* Ochraceus Bulbul *(Alophoixus ochraceus)* and Pale-faced Bulbul *(Pycnonotus leucops)*, and white-eyes *(Zosteropidae);* Black-capped White-eye *(Zosterops atricapilla)* and Mountain Black-eye *(Chlorcharis emeliae)*. For bulbuls, *A. ochraceus* occupies submontane and montane forest, and *P. leucops* is restricted to montane and elfin forest surrounding high mountain summits (Harris *et al.* 2012; Sheldon 2015). The low elevation *A. ochraceus* (49.0g) is larger than the high elevation *P. leucops* (29.8g) (Boyce, Wolf & Martin 2018b). Both bulbul species are primarily frugivorous, forage in the subcanopy and understory and build nests in small saplings and shrubs (Smythies 1999, pers obs). For white-eyes, *Z. atricapilla* inhabits submontane and montane forest and scrub, while *C. emeliae* is restricted to montane forest and high-elevation elfin forest (Harris *et al.* 2012; Sheldon, Lim & Moyle 2015). Although not congeners by current taxonomy, both pairs are each other's closest relative at the site. Furthermore, recent phylogenetic studies show *Chlorocharis* nested within the *Zosterops* clade (Moyle *et al.* 2009), suggesting these two species are best treated as congeners. The high elevation *C. emeliae* (15.3g) is larger than the lower elevation *Z. atricapilla* (8.6g) (Boyce *et al.* 2018b). White-eyes feed primarily on fruit and nectar throughout forest strata and along habitat edges and build nests in a variety of substrate in the subcanopy (Smythies 1999, pers obs). We chose two understory flycatchers

(*Muscicapidae*) as our sympatric species pair; Snowy-browed Flycatcher *(Ficedula hyperythra)* and Eyebrowed Jungle-Flycatcher *(Vauriella gularis)*. Both species are common residents in submontane and montane forest and, feed primarily on insects and small invertebrates taken on the ground, and construct nests of live moss in trees/shrubs from 1-3m above ground (Smythies 1999, pers obs). *V. gularis* (25.3g) is larger than *F. hyperythra* (8.3g) (Boyce, Wolf & Martin 2018c). All three species pairs have easily recognizable songs that differ qualitatively within species pairs in both sound and pattern of delivery (Supplementary material S1-S6). Playback experiments for mid-elevation species and sympatric flycatchers were conducted in the vicinity of Park Headquarters (1450m – 1850m). Experiments for high elevation species were conducted in the vicinity of Laban Rata substation (3000 – 3450m).

Territories of focal species for both recordings and playback trials were located opportunistically throughout the study area during point counts and other concurrent fieldwork. Locations of singing birds were recorded using a Garmin GPSMap 60CSx portable GPS unit (Garmin International, Olathe, KS, USA). Song recordings were made using a Sennheiser ME67 shotgun microphone (Sennheiser, Old Lyme, CT, USA) and a Marantz PMD661 digital recorder (Marantz, Chatsworth, CA, USA). All recordings were post-processed in Raven Pro (Bioacoustics Research Program 2014) to filter out low-frequency background noise (< 750hz), to amplify recordings to normalize amplitude across all recordings, and to clip recordings to identical length. Each recording was only used once, and was chosen at random to avoid pseudo-replication (Kroodsma *et al.* 2001).

Each playback trial was structured to include three auditory stimuli; conspecific song, putative competitor song, and control species song. We chose Golden-naped Barbet *(Psilopogon pulcherrimus)* as a control because it occupies a divergent niche from all focal species as a canopy frugivore and cavity-nester and is common and vocal at both mid and high elevation sites. Observations of the focal bird were made during 1 minute of playback and 1 subsequent minute of silence. We then waited a further 2 minutes before continuing the trial with the next stimulus. Conspecific playback was always played last to avoid elevating the focal bird to a heightened state of territoriality before control or heterospecific playback. Heterospecific and control stimuli were shuffled randomly.

To broadcast playback stimuli, we used a waterproof speaker (Grace Digital Inc., San Diego, CA, USA) and an Apple iPod Nano (Apple Inc., Cupertino, CA, USA). During playback trials we noted distance from the focal individual to the speaker following all movements of more than 1m and noted all vocalizations of the focal individual. Distances were estimated visually and aurally during trials and calibrated afterwards using a digital rangefinder. In some cases, the focal individual left the immediate area during or in between stimuli or became silent and obscured such that observation was impossible. In other cases, conspecific (non-target) individuals responded to stimuli making it difficult to keep track of the target individual and potentially altering the behavior of the target individual. If data had been successfully collected for at least 1 stimulus, the trial was resumed within 48hrs. If not, the trial was abandoned and re-attempted at a later date.

Statistical Analyses

Behavioral observations were transformed into 3 indices of aggression; closest approach to speaker, latency to approach speaker, and number of vocalizations. If the focal individual did not approach the speaker, we recorded the maximum value of 120s. Closest approach to speaker was square-root transformed due to a right-skewed distribution. We performed principle components analysis to reduce these three behavioral variables into a single index of aggressiveness (Freeman 2016b). Because species may respond aggressively in different ways (i.e. vocalizations vs. physical approach) we performed separate PCAs for each species. All three behavioral variables were scaled prior to PCA. We generated PCA scores for each stimulus for each individual based on the first principle component as our index of overall aggression. We then fit linear mixed-effects models for each species with aggression (PC1) as the dependent variable, stimuli type as a fixed effect and focal individual as a random effect. We performed post-hoc Tukey multicomparison tests in package ‘multcomp’ to compare the intensity of aggression between control, conspecific and heterospecific stimuli. Identical analyses were performed on each behavioral variable independently to characterize species-specific aggressive responses. All statistical analyses were performed in R (R Core Team 2015).

RESULTS

Elevational ranges

Bulbul species on Mt. Kinabalu were almost perfectly parapatric. Ochraceus Bulbul *(A. ochraceus)* occupied forest from the park boundary at 1450m to 1810m. Pale-faced Bulbul *(P. leucops)* occupied forest from 1890m to 3332m. This species pair showed no zone of overlap, so were never detected on the same point count. White-eyes showed a broadly parapatric distribution, but overlapped slightly at their mutual boundary. Black-capped White-eye *(Z. atricapilla)* occupied forest from the nearest park boundary at 1450m to 2131m. Mountain Blackeye *(C. emeliae)* was present from 1845m to 3681m. The two species both occupied an approximately 300m zone of overlap and were sometimes detected on the same point counts within this zone. Of 27 point counts during which a *Zosteropidae* species was detected in the zone of overlap, both species were present 18.5% (5 of 27) of the time. However, this low percentage was mainly driven by the lower overall abundance of *Z. atricapilla*. On counts where *Z. atricapilla* was detected, both species were present on 50% (5 of 10) of the time. The two focal flycatcher species were sympatric throughout our mid elevation study site. Eyebrowed Jungle-Flycatcher (*V. gularis)* was present from the park boundary at 1450m to 1850m. Snowy-browed Flycatcher *(F. hyperythra)* occurred from the park boundary at 1450m to 2924m. Both species were regularly encountered on the same point count, with both present on 16% (4 of 25) of counts with at least one species of flycatcher. This estimate likely understates their degree of overlap due to difficulty in detecting *V. gularis*. On counts where *V. gularis* was detected, both species were present on 80% (4 of 5) of counts. Based on mark recapture studies, both species are widespread and abundant between 1450 and 1850m (Martin *et al.* 2015, 2017b).

Playback experiments

We conducted a total of 47 playback experiments on 6 species ($\bar{x} = 7.83$, range: 6 – 11 individuals). All species showed an aggressive response to conspecific playback compared to a control, but responses to parapatric or sympatric relatives varied (Fig 1-2). The first principal component from our PCA had parallel loadings for all three behavioral variables across all species. That is, positive scores indicate closer approach to the speaker, shorter latency to approach and increased vocalization rate.

Among parapatric bulbuls, interspecific aggression was strongly asymmetric (Fig 1A , 2A). The first principle component explained 67% of the total variance in behavioral variables for *A. ochraceus* and 75% of total variance for *P. leucops*. *A. ochraceus*, the low-elevation species, responded aggressively to both conspecific playback and heterospecific playback compared with the control ($P < 0.01$, $P = 0.02$) and with equal intensity to both ($P = 0.12$). *P. leucops*, the high-elevation species, frequently showed sentineling behavior and short approach flights in response to heterospecific playback, such that the response differed significantly from a control (Fig 1A, $P = 0.04$). However, the response to conspecific playback was stronger ($P < 0.01$) and was characterized by frequent vocalizations and a rapid, close approach.

Among parapatric white-eyes, interspecific aggression was completely absent (Fig 1B, 2B). The first principal component explained 72% and 68% of total variance in behavioral variables for *Z. atricapilla* and *C. emeliae*, respectively. *Z. atricapilla*, the low-elevation species, responded aggressively to conspecific playback ($P < 0.01$), but did not show any difference in behavior in response to heterospecific playback and the control ($P = 0.92$). Similarly, *C. emeliae*, showed a strong aggressive response to conspecific playback ($P < 0.01$), but was unresponsive to heterospecific playback ($P = 0.68$).

Among sympatric flycatchers, interspecific aggression was strongly asymmetric (Fig 1C, 2C). The first principal component explained 79% and 61% of total variance in behavioral variables for *F. hyperythra* and *V. gularus*, respectively. *F. hyperythra*, responded aggressively to conspecific playback ($P < 0.01$), but did not show a difference in aggression in response to heterospecific playback compared with the control ($P = 0.31$). *V. gularis*, showed a strong aggressive response to both conspecific ($P = 0.02$) and heterospecific playback ($P < 0.01$) compared to the control.

DISCUSSION

Interspecific competition mediated by interspecific aggression is thought to drive parapatric distributions of closely-related species on environmental gradients (Terborgh & Weske 1975; Robinson & Terborgh 1995; Jankowski *et al.* 2010). However, climatic stability in the tropics is thought to result in a narrowing of species' physiological niche and is also thought to play a role in setting range limits, particularly across elevational gradients (Janzen 1967; Ghalambor *et al.* 2006). Here, we found interspecific aggression between one pair of elevationally parapatric species but a complete absence of aggression in another. Our results suggest interspecific aggression may set elevational range limits in some species pairs, but it is not a prerequisite for elevational parapatry.

An absence of aggression has been observed in parapatric species pairs with significant elevational gaps, leading to the suggestion that frequent interactions may be a necessary prerequisite for interspecific aggression (Freeman 2016a).While that possibility remains, our results in white-eyes suggest that spatial separation is not required to facilitate benign interactions between closely-related species (Fig 1B). More importantly, if interspecific aggression consistently evolves in the presence of interference competition, we can rule out interference competition as a driver of elevational parapatry in white-eyes.

Causes for the variation in heterospecific response between bulbuls and white-eyes are not readily apparent. Theory predicts that interspecific competition should be strongest between species with the greatest niche overlap (MacArthur & Levins 1967). We did not attempt to quantify niche overlap between species pairs, but due to niche conservatism, niche overlap is generally expected to be highest between close relatives (Peterson, Soberon & Sanchez-Cordero 1999) and phylogenetic relatedness appears to be a good proxy of functional traits in Bornean passerines (Boyce *et al.* 2018a). Of the three pairs studied here, white-eyes share the most recent common ancestor at no more than 2.3 mya (Moyle *et al.* 2009). In contrast, our focal pairs of bulbuls and flycatchers are far more phylogenetically distant (Boyce *et al.* 2018a; Fig 1). Therefore, it seems unlikely that niche divergence explains variation in heterospecific responses in these groups.

Phylogenetic relatedness may not provide the best proxy for expected intensity of heterospecific interactions. The abundance and distribution of resources can also influence the degree of aggression between species such that highly dispersed or clustered resources may not be easily defendable and lead to selection against territorial aggression (Brown 1964; Peiman & Robinson 2010). For example, both white-eyes are primarily nectarivorous and rely on flowers that are typically patchy and ephemeral food sources. Aggression may not be favored in this situation if these characteristics mean that resources are not easily defendable and thus interspecific aggression may play a weaker role in influencing elevational range limits in this group.

In parapatric species pairs, asymmetric aggression has been interpreted as a force causing spatial segregation (Jankowski *et al.* 2010). However, interspecific aggression in co-occurring relatives appears to be common, with the vast majority of interactions being asymmetric (Martin & Martin 2001b; Freeman 2016b; Martin *et al.* 2017a, Fig 2C). Because there is no categorical difference between asymmetric aggression in broadly sympatric species pairs and between parapatric pairs near their mutual boundary, interspecific aggression alone is not sufficient evidence to suggest competition is the primary driver of parapatric distributions. While interference competition may play a role in driving parapatry, the presence of asymmetric aggression between species that occasionally interact is a reasonable null hypothesis rather than confirmation of particularly intense competition driving complete parapatry. Interspecific aggression may still be important in both contexts. Interspecific aggression can drive niche displacement in co-occurring species with consequences for fitness and demography (Martin & Martin 2001b; Grether *et al.* 2009). Thus, costs of coexistence mediated by interspecific aggression may act to influence range boundaries in combination with other factors in both sympatric and parapatric species pairs.

The intensity of interspecific aggression often increases with proximity to a zone of interaction, suggesting a learned component as opposed to an evolved response (Jankowski *et al.* 2010; Freeman 2016a; b). We did not conduct a sufficient number of trials to explore whether proximity to range boundary was related to response intensity in our focal species, but our results still speak to this question. *P. leucops* showed a significant heterospecific response (Fig 1A) during playback trials at between 3000 and 3450m, at least 1200m above the closest territory of *A. ochraceus*. We find it unlikely that dispersal over such a distance is common in a small, territorial songbird, suggesting that interspecific aggression in songbirds may have both evolved and learned components in bulbuls. Observations of interspecific aggression in completely allopatric populations of sunbirds (Nectarinidae) indicate that evolved aggressive responses may be widespread in songbirds (McEntee 2014).

Increasingly, interspecific interactions are being incorporated into species distribution models and models aiming to predict future range shifts (i.e. Engler *et al.* 2017). Our results provide evidence that interspecific aggression is present between some pairs of parapatric species. However, we also show that interspecific aggression is not a prerequisite for parapatry. Thus, workers seeking to identify biotic interactions that may influence range dynamics must be cautious when inferring biotic processes from distributional patterns. Drivers of elevational range boundaries may differ substantially among clades. Understanding the causes and correlates of this variation is critical to accurately predicting range dynamics in light of changing biotic and abiotic conditions.

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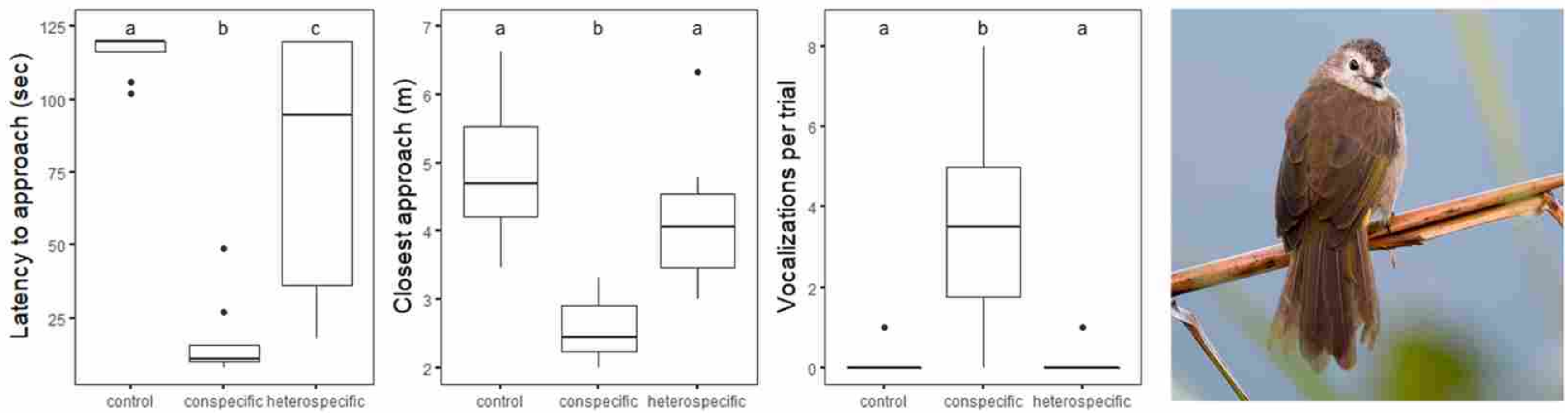
Figure Legends

Figure 1. Behavioral responses (distance of closest approach, latency to approach, and number of calls) to control, conspecific and heterospecific playback stimuli in two elevationally parapatric species pairs (**A-B**) and one sympatric species pair (**C**). Letters above boxplots indicate significant differences ($P < 0.05$) between stimuli based on post-hoc Tukey multicomparison tests. An asterisk (*) indicates a difference with marginal significance ($0.05 < P < 0.10$). For parapatric pairs, high elevation species are shown in the upper panels. Photo credits: *A. ochraceus*; Chien Lee, *C. emeliae*; Cede Prudente.

Figure 2. Aggressive responses to control, conspecific and heterospecific playback stimuli in two elevationally parapatric species pairs (**A-B**) and one sympatric species pair (**C**). Higher aggression scores indicate a stronger response. Letters above boxplots indicate significant differences between stimuli based on post-hoc Tukey multicomparison tests. High elevation species are shown in the upper panels and vice versa. Elevational distributions within our study site based on point count surveys are depicted in the vertical panel.

Figure 1A



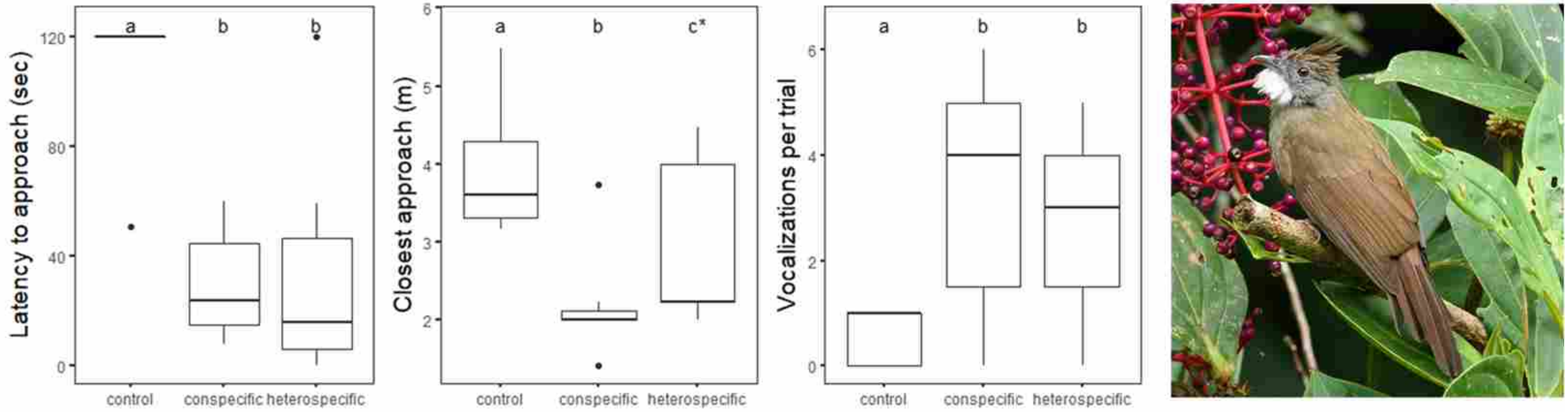


Figure 1B

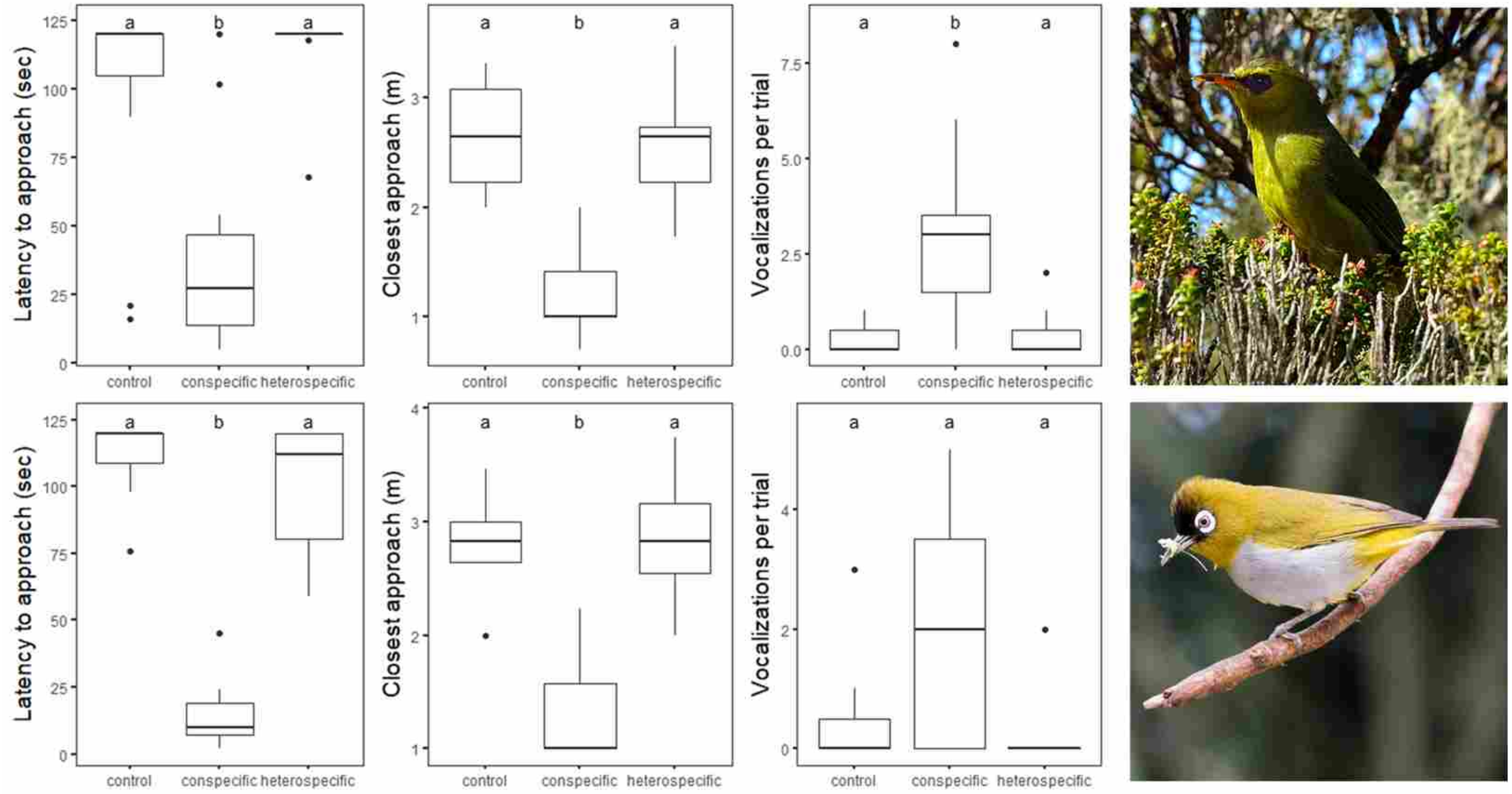

a
b
a
Latency to approach (sec)
125
100
75
50
25
0
control
conspecific
heterospecific
Closest approach (m)
3
2
1
Vocalizations per trial
7.5
5.0
2.5
0.0
a
b
a
Latency to approach (sec)
Closest approach (m)
4
Vocalizations per trial
a
a
a

Figure 1C

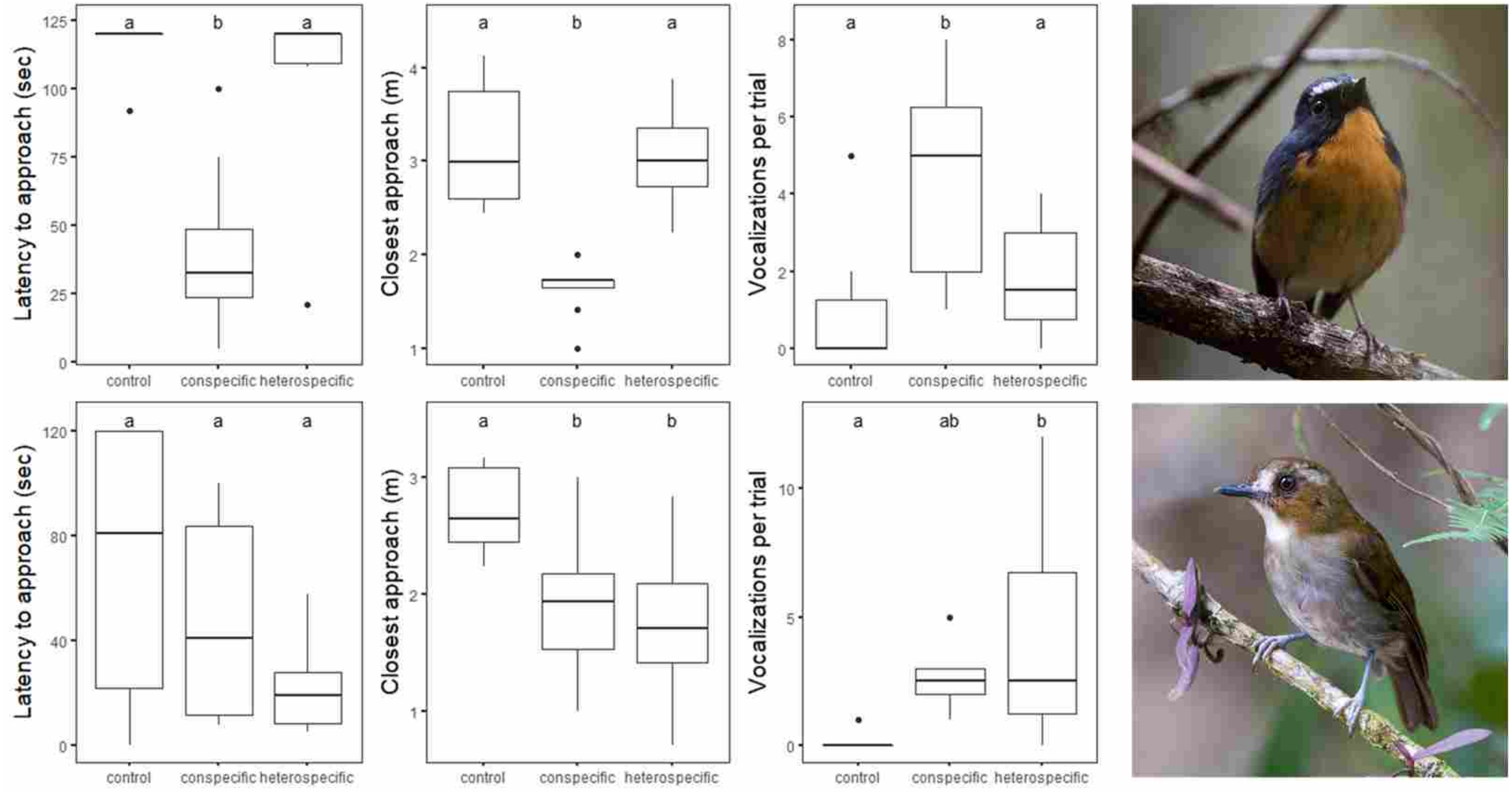
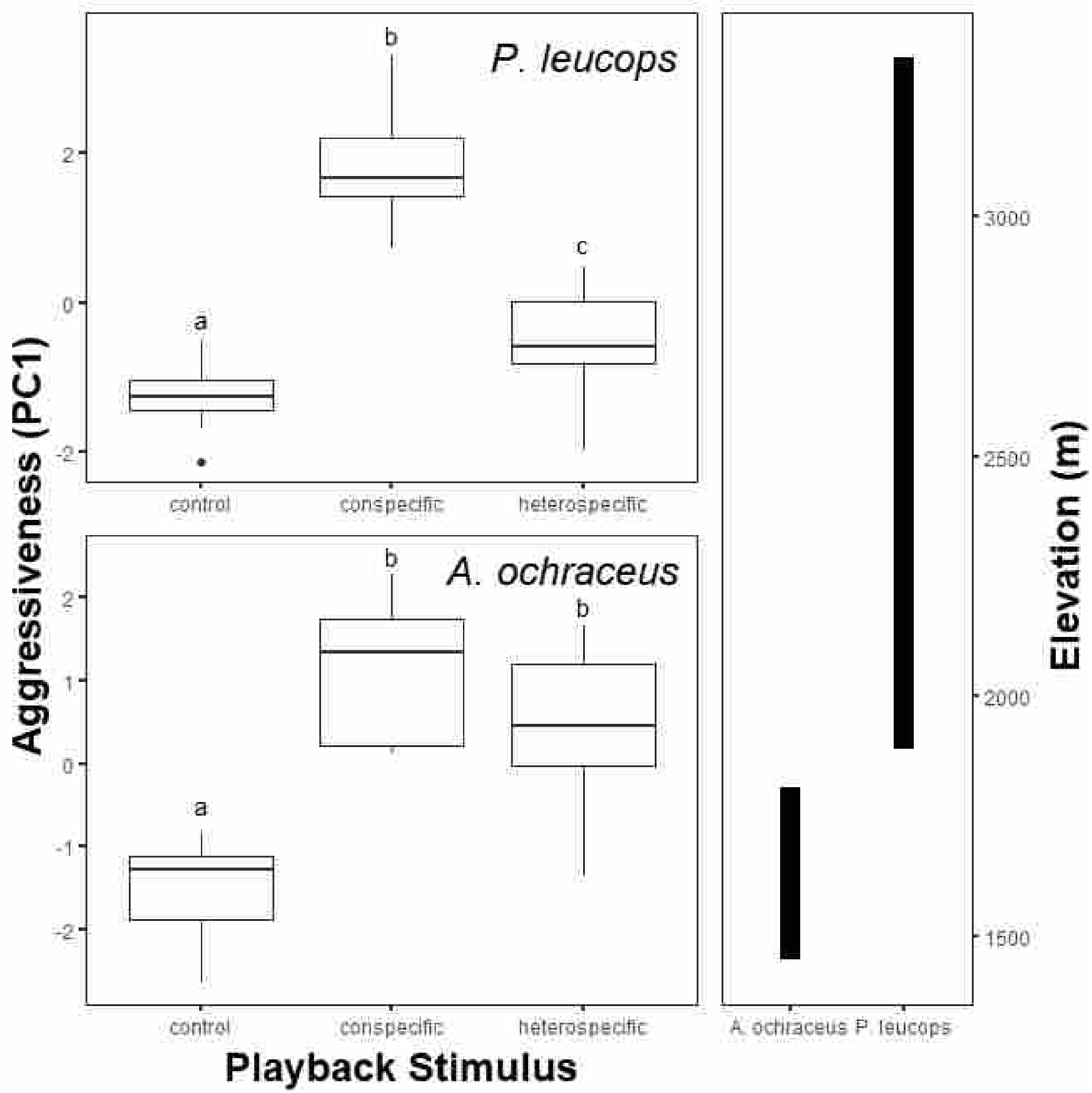

Latency to approach (sec)
125
100
75
50
25
0
a
b
a
control
conspecific
heterospecific
Closest approach (m)
4
3
2
1
a
b
a
control
conspecific
heterospecific
Vocalizations per trial
8
6
4
2
0
a
b
a
control
conspecific
heterospecific
Latency to approach (sec)
120
80
40
0
a
a
a
control
conspecific
heterospecific
Closest approach (m)
3
2
1
a
b
b
control
conspecific
heterospecific
Vocalizations per trial
10
5
0
a
ab
b
control
conspecific
heterospecific

Fig 2A



P. leucops
A. ochraceus
a
b
c
a
b
b
2
0
-2
2
1
0
-1
-2
control
conspecific
heterospecific
control
conspecific
heterospecific
Aggressiveness (PC1)
Playback Stimulus
3000
2500
2000
1500
Elevation (m)
A. ochraceus
P. leucops

Fig 2B

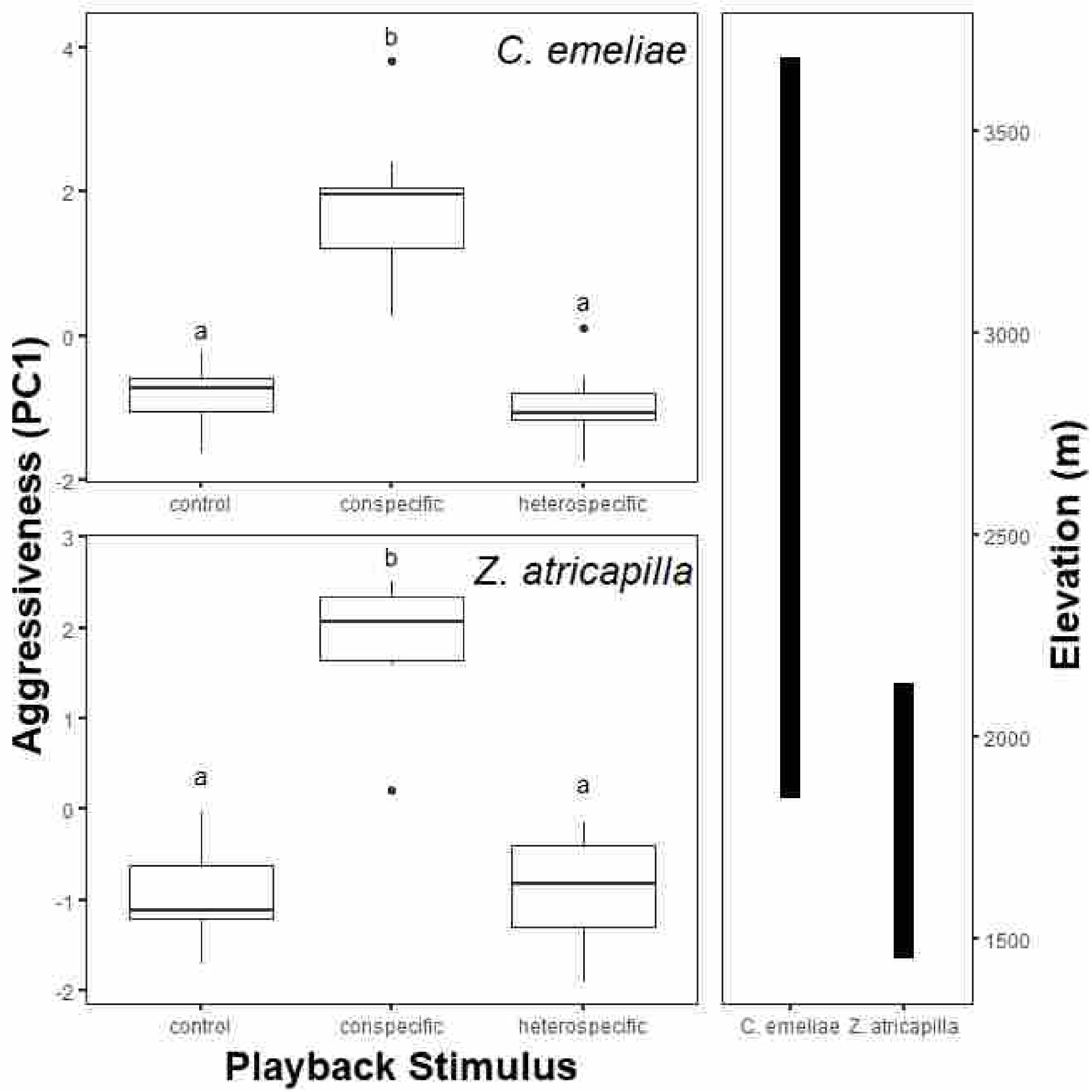

C. emeliae
Z. atricapilla
Aggressiveness (PC1)
Elevation (m)
Playback Stimulus
control
conspecific
heterospecific
a
b
a
4
2
0
-2
3
1
-1
3500
3000
2500
2000
1500
C. emeliae
Z. atricapilla

Fig. 2C

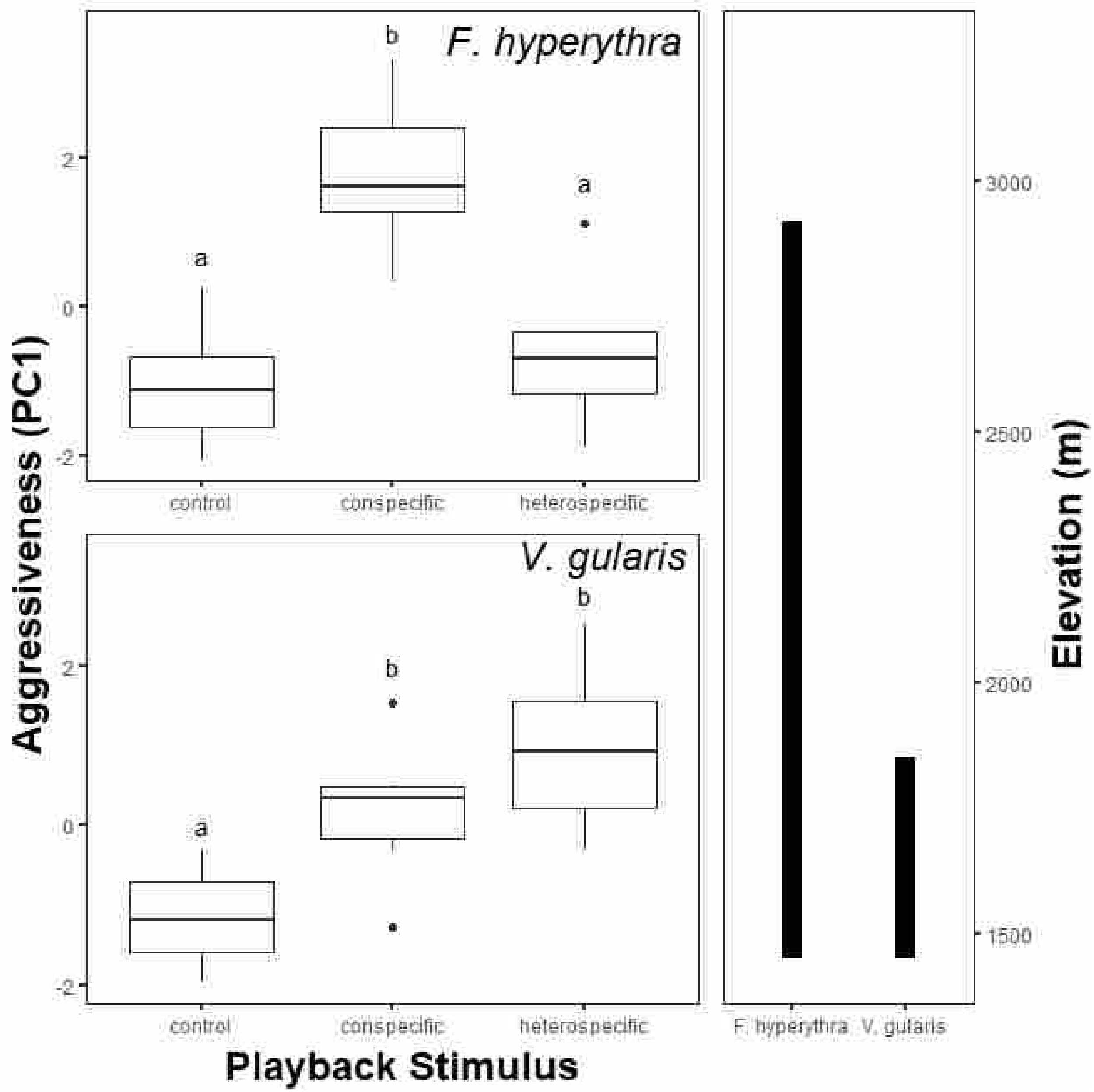

F. hyperythra
V. gularis
Aggressiveness (PC1)
Playback Stimulus
Elevation (m)
a
b
a
b
b
a
2
0
-2
control
conspecific
heterospecific
3000
2500
2000
1500
F. hyperythra
V. gularis

Figure S1. Sonogram of a representative song phrase of Pale-faced Bulbul *(Pycnonotus leucops)*.

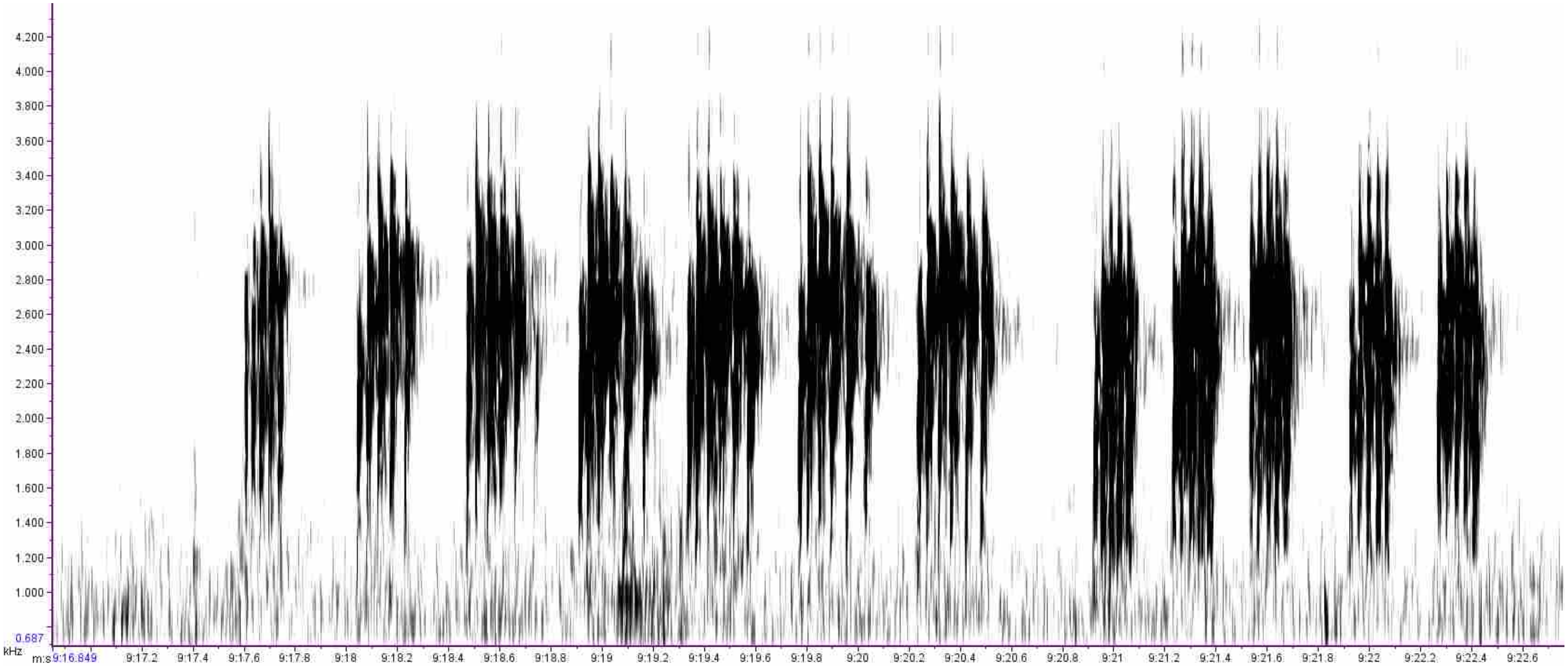


Figure S2. Sonogram of a representative song phrase for Ochraceus Bulbul *(Alopohixus ochraceus)*.

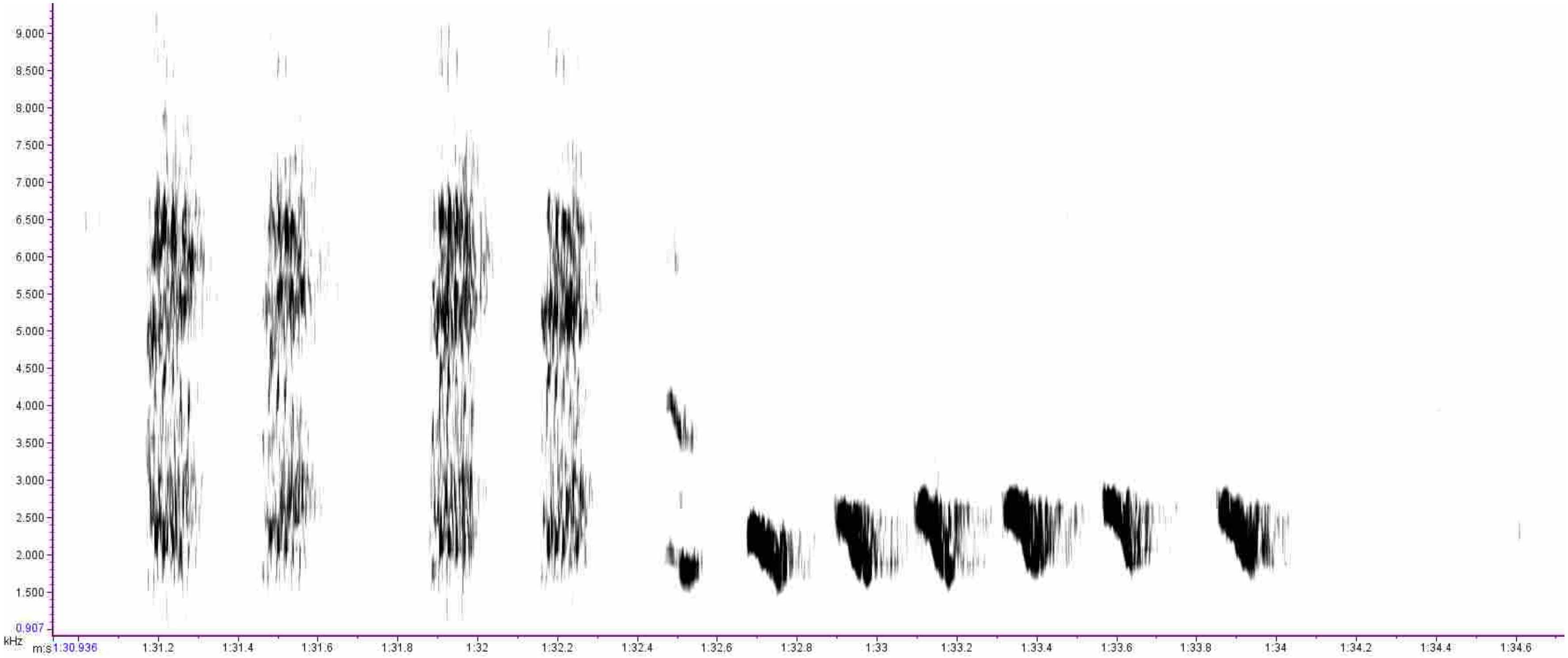


Figure S3. Sonogram of a representative song phrase for Snowy-browed Flycatcher *(Ficedula hyperythra)*.

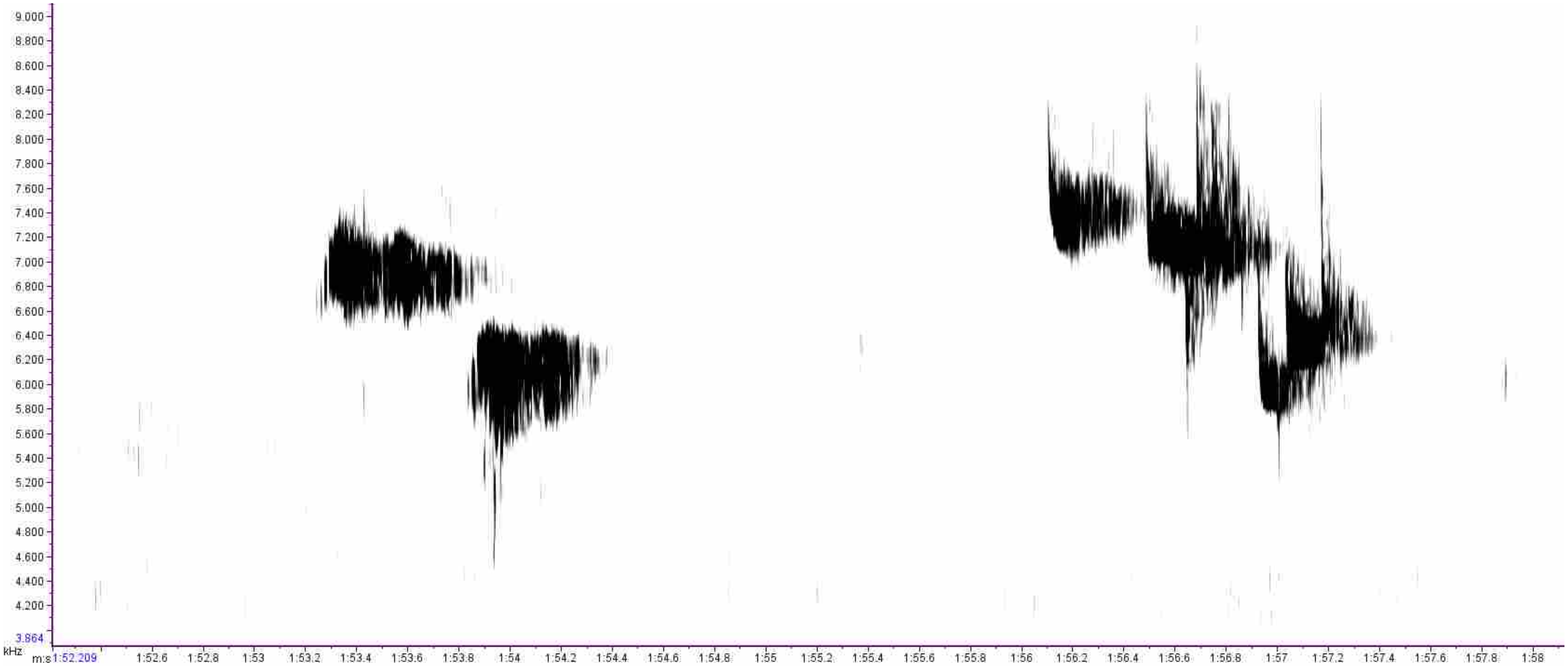


Figure S4. Sonogram of a representative song phrase for Eyebrowed Jungle-Flycatcher *(Vauriella gularis)*.

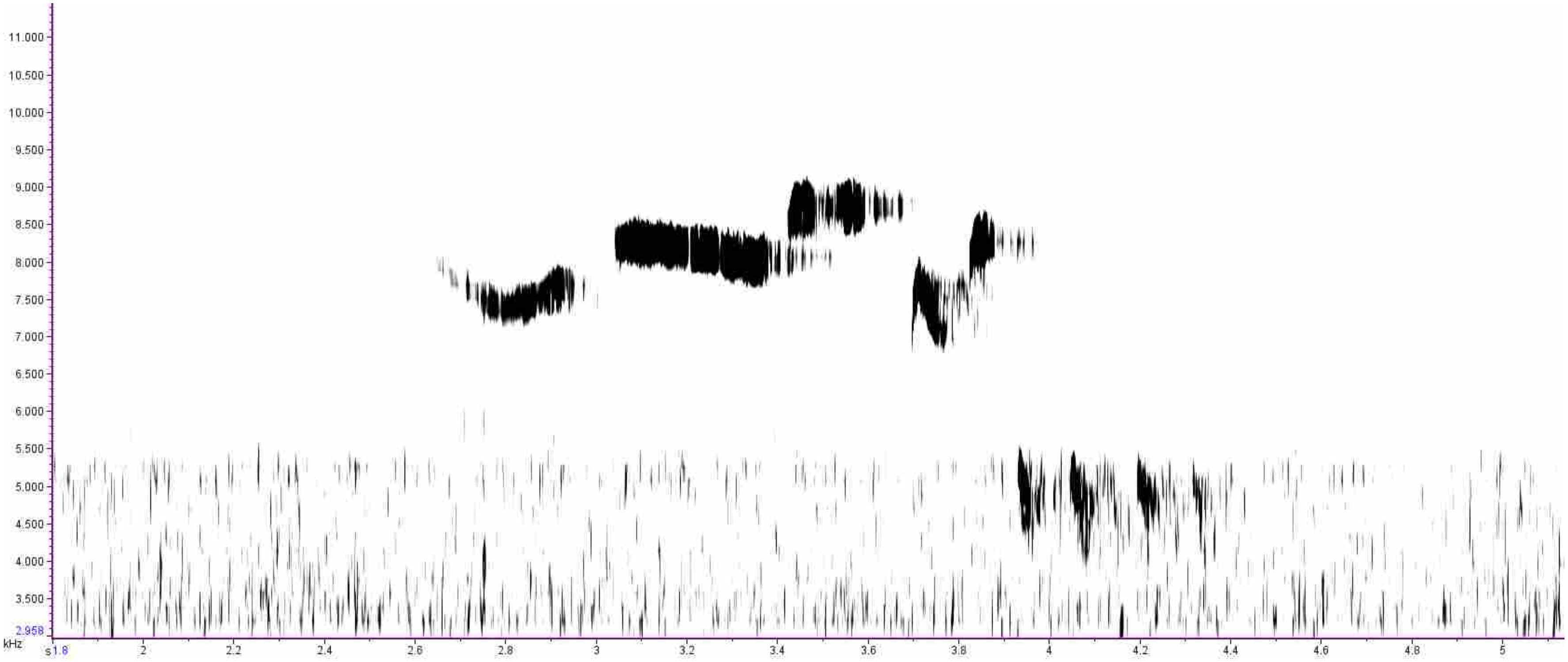


Figure S5. Sonogram of a representative song phrase for Black-capped White-eye *(Zosterops atricapilla)*.

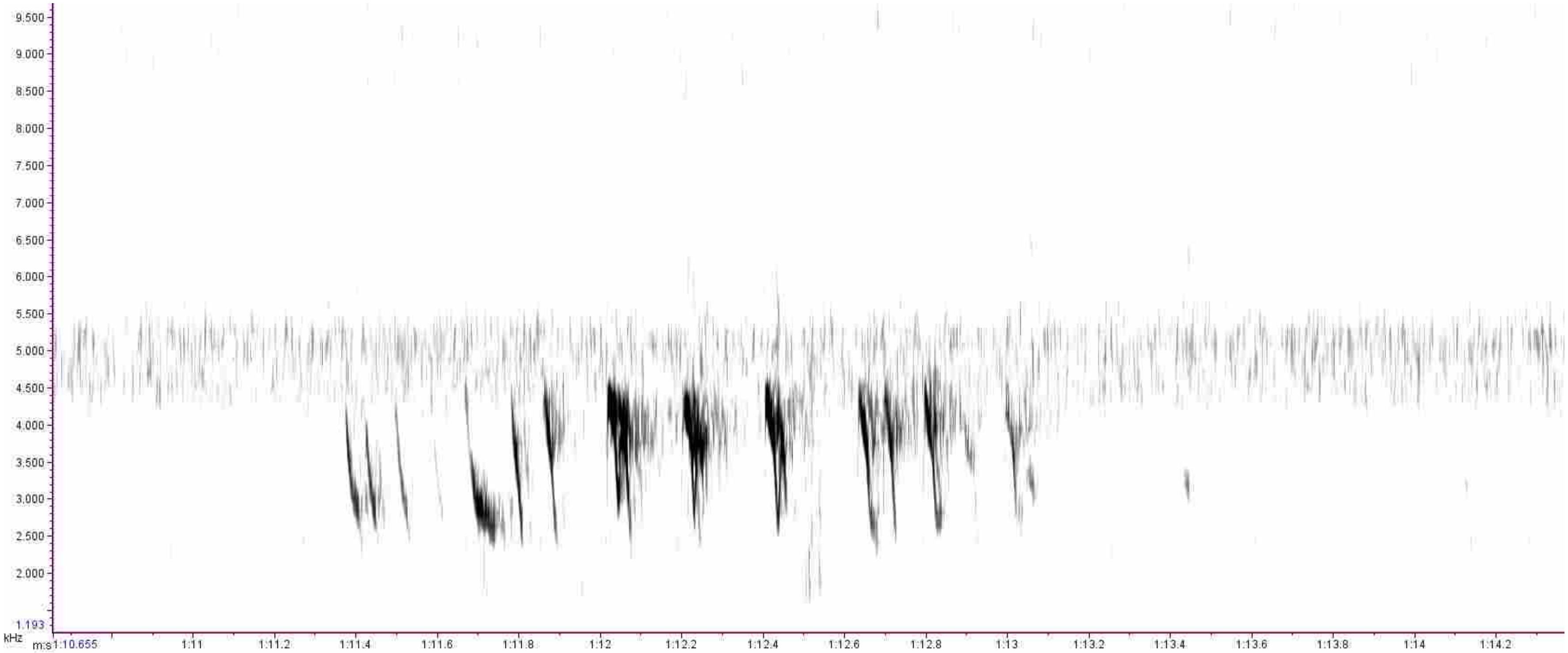
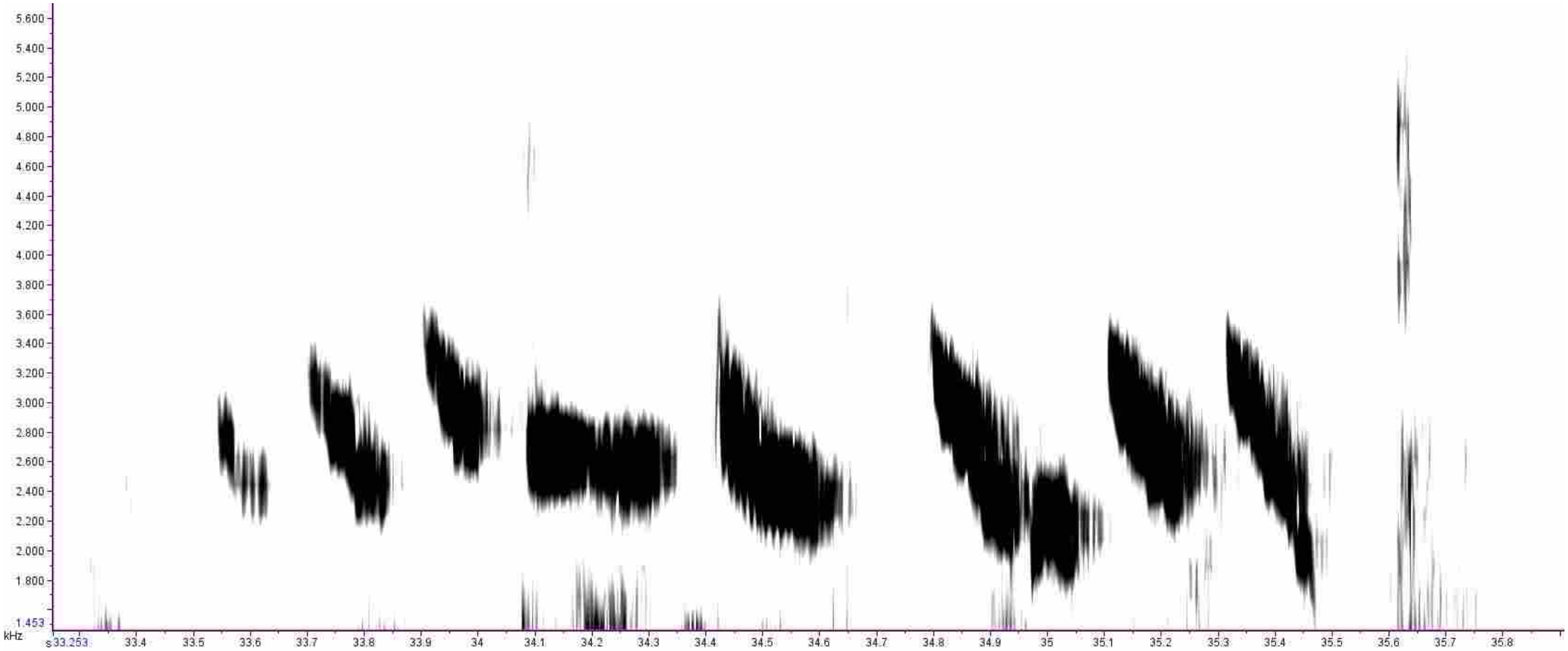


Figure S6. Sonogram of a representative song phrase for Mountain Blackeye *(Chlorocharis emeliae)*.



Chapter 4: Metabolic rate explains variation in adult mortality probability within but not across latitudes in songbirds.

Andy J. Boyce, Blair O. Wolf and Thomas E. Martin

ABSTRACT

The rate of living hypothesis posits that physiological damage from cellular metabolism causes species with faster metabolic rates to be shorter-lived. Here, we sought to test whether metabolic rate explained variation in mortality rates among songbirds within and across latitudes. We measured resting metabolic rate (RMR) and estimated adult mortality probability for 28 species of passerine birds at tropical and temperate sites and compiled analogous data for 104 passerine species from the literature. In both field-based and literature datasets, we found that metabolic rates were similar between temperate and tropical regions. As a result, metabolic rate failed to explain lower rates of adult mortality in tropical species although it explained some variation in adult mortality probability within latitudes. The inability of metabolic rate to explain adult mortality between may reflect a larger role of extrinsic sources of mortality across latitudes or the evolution of physiological mechanisms that mitigate damage from metabolism.

INTRODUCTION

Adult mortality rate varies extensively among species and is a major influence on fitness, demography and life-history evolution (Ashmole 1963; Stearns 1977; Promislow & Harvey 1990; Martin 2015). The rate of living hypothesis has been proposed as a physiological mechanism driving variation in mortality rate. Pearl (1928) posited a causal link between metabolic rate and longevity. Production of damaging reactive oxygen species (ROS) from metabolism has been posited as the primary physiological mechanism of aging, such that higher metabolic rates cause greater oxidative damage and shorter life (Pearl 1928; Harman 1956; Balaban, Nemoto & Finkel 2005; Brys, Vanfleteren & Braeckman 2007; Monaghan, Metcalfe & Torres 2009). Yet, metabolism may be decoupled from senescence because mechanisms to prevent or repair damage (e.g. endogenous antioxidants, mitochondrial membrane composition and telomere dynamics) may coevolve with metabolic rate (Brand 2000; Monaghan & Haussmann 2006; Hulbert *et al.* 2007; Costantini 2008; Salin *et al.* 2015; Skrip & Mcwilliams 2016). Consequently, the relationship between metabolic rate and adult mortality remains unclear (Costantini 2008).

Mortality rates may be unrelated to the accumulation of physiological damage entirely. The evolutionary theory of aging posits that adaptations to slow senescence should be favored in populations with low extrinsic adult mortality, meaning extrinsic and intrinsic mortality rates should be correlated (reviewed in Charlesworth 1994, 2000). Indeed, actuarial studies in birds and mammals suggest intrinsic mortality rate increases with extrinsic mortality rate (e.g. weather, predation) (Promislow 1991; Ricklefs 1998, 2000). However, the proportion of deaths from intrinsic sources are greater when overall mortality rates are low, suggesting that adaptations to slow the rate of aging are limited, such that extrinsic and intrinsic rates become increasingly decoupled as extrinsic mortality declines (Ricklefs & Scheuerlein 2001). Furthermore, the onset of senescence is commonly delayed until well after the age of maturity (Promislow 1991), suggesting that intrinsic and extrinsic mortality rates may also be unrelated when extrinsic mortality is very high.

Comparative studies show that metabolic rate is negatively correlated with maximum observed lifespan (MLS) in birds and mammals at broad taxonomic scales (Trevelyan, Harvey & Pagel 1990; Hulbert *et al.* 2007). However, the overriding influence of mass on both lifespan and metabolism obscures the independent effect of metabolic rate on lifespan in such studies (Speakman 2005). Moreover, other comparisons raise questions about this relationship. Bats and birds have higher metabolic rates but are longer-lived than terrestrial mammals of similar size, weakening the relationship between metabolism and lifespan (Holmes & Austad 1995; Holmes, Fluckiger & Austad 2001; Munshi-South & Wilkinson 2010). Furthermore, measurements of MLS represent exceptional rather than an average of individuals and are sensitive to variation in sample size, recapture probability and quality of record keeping (Krementz, Sauer & Nichols 1989; Promislow 1993). MLS is often based on captive individuals that are well-fed and isolated from disease, predation and other extrinsic sources of mortality that are ubiquitous in wild populations (i.e. de Magalhães & Costa 2009). Model-based estimates of annual mortality rate are not susceptible to these issues and are thus a more appropriate index of average lifespan for comparative studies (Krementz *et al.* 1989; Promislow 1993). Ultimately, studies that directly compare metabolic rates with robust estimates of adult mortality from wild populations are needed.

Passerine birds (songbirds) are a good group in which to examine these issues. Passerines are diverse (~ 6,000 species) and show broad ecological and morphological variation (del Hoyo *et al.* 2017). They show large interspecific variation in both metabolic rate (McKechnie & Wolf 2004; Wiersma *et al.* 2007; Londoño *et al.* 2015; McKechnie 2015) and adult mortality probability (Johnston *et al.* 1997; Sandercock *et al.* 2000; Martin 2015; Martin *et al.* 2015, 2017b). Evidence of a link between metabolic rate and longevity in songbirds is mixed. For example, lower avian metabolic rates have been found in tropical birds which are typically longer-lived than temperate relatives (Wikelski *et al.* 2003; Wiersma *et al.* 2007; Londoño *et al.* 2015). However, other studies found no difference in metabolic rates across latitudes in either adult birds (Vleck & Vleck 1979; Bennett & Harvey 1987) or embryos (Martin, Ton & Niklison 2013). Furthermore, using latitude as a proxy for mortality rate is problematic due to large variation within latitudes (Johnston *et al.* 1997; Martin *et al.* 2015). Metabolic rate and adult mortality were positively correlated across latitudes in songbirds in one study (Williams *et al.* 2010). However, methods used for estimating mortality rates differed between latitudes in this study, which can yield problematic variation (Martin *et al.* 2017b). Finally, adult mortality is not strongly influenced by body mass in passerines (Martin *et al.* 2015), which alleviates the issue of collinearity in analyses involving metabolic rate, mass and mortality rate (i.e. Speakman 2005).

Here, we test for a relationship between adult mortality probability and metabolic rate. We directly measured RMR and estimated adult mortality probability for 30 species of songbirds at tropical and temperate field sites. We also compiled basal metabolic rate (BMR) and adult mortality data for 104 species from the literature. We used phylogenetically-informed methods to test whether metabolic rate explained interspecific variation in adult mortality within and across latitudes.

METHODS

Study system

Resting metabolic rate measurements and estimation of adult mortality probability were conducted on populations of passerine birds at Kinabalu Park, Sabah, MY (6°N, 116°E), and the Coconino National Forest, Arizona, USA (35°N, 111°W). Metabolic measurements were performed during the breeding season at both sites (Malaysia; February – June, 2013 – 2016, Arizona; May – July, 2015).

Birds were captured for metabolic measurements by both passive and targeted mist-netting. Breeding females (based on presence of a brood patch) were excluded to minimize disruption of nesting and because the extreme vascularization of the avian brood patch is likely to alter RMR. Birds were transported to the lab and held for 1-2 hrs, depending on mass, to insure they were post-absorptive during measurements. Birds were watered before and after measurements and returned to point of capture upon completion of metabolic measurements.

Adult mortality probability was estimated by banding, resighting and recapturing birds, using the same long-term protocols at both sites (Martin *et al.* 2015). Birds were captured by both passive mist-netting and target-netting for 6 hours each day beginning at sunrise. Twelve nets were deployed at each netting plot, which were distributed uniformly across accessible areas of each site. Each plot was visited 3 times at equal intervals over the course of the field season. Birds were marked with unique combinations of one alpha-numeric aluminum band and three color-bands to facilitate individual identification via resighting. In addition to subsequent recaptures, birds were resighted opportunistically each day for the duration of each field season. Resulting estimates (see Statistical Analyses) are based on 21 consecutive years of banding and resighting effort in Arizona site and 8 consecutive years in Borneo.

Metabolic measurements

We measured RMR using an open-flow respirometry system similar to that described in Gerson et al. (2015). We used 2L and 5L transparent plastic containers (Rubbermaid, Atlanta, GA, USA) as metabolic chambers, depending on the size of the study species. These containers were modified to include incurrent and excurrent air ports, with wire mesh platforms and plastic perches to allow the subject to rest comfortably. The bottom of the chamber contained a 2cm layer of mineral oil to trap moisture and gas associated with feces. Containers were placed inside a large cooler, which was modified to hold an integral peltier device (model AC-162, TE Technology, Traverse City, MI), with a custom temperature control device (Gerson *et al.* 2015) to regulate chamber temperature. Incurrent air was provided by a high capacity vacuum pump (model DAA-V515-ED, Gast Manufacturing, Benton Harbor, MI, USA), and was routed through a coil of copper tubing prior to entering the inner chamber to facilitate rapid temperature equilibration. Air flow rates were regulated by mass-flow controllers (Alicat Scientific, Tucson, AZ). Flow rates varied between 2-15 L/min depending on mass of study species. Incurrent and excurrent air were both subsampled at rates between 250 and 500 ml/min and CO_2 and H_2O were measured using a portable gas-analyzer (LI-COR model LI-840a, Lincoln, NE, USA). These data were sampled every second and recorded using Expedata (Sable Systems, Las Vegas, NV, USA).

Humidity of incurrent air was regulated using a dew-point generator constructed of three Nalgene bottles connected in series. Air was bubbled through water in the first two bottles, and the third was empty and served as a water trap. The entire device was then submerged in a water bath kept at approximately 10°C by the addition of small ice-packs. This device prevented rapid fluctuations in humidity due to either ambient air temperature or ambient humidity and also prevented condensation occurring in the system. By adjusting water bath temperature and incurrent air pressure, we maintained relative humidity between 50 and 70%, which is within the range of normal conditions at both sites during the breeding season.

Each individual was sampled at multiple temperatures as part of a concurrent study of thermal tolerance. We subsetted data for analysis by selecting the longest continuous period of resting behavior after chamber temperature had reached equilibrium for at least 30 minutes. Subject activity was monitored in real-time via an infrared security camera connected with an external LCD screen. If no period of complete rest greater than two minutes was observed, no data was analyzed for that temperature. We pooled measurements from 27, 30, and 33°C, which are within the thermoneutral zone of most passerines (McKechnie & Wolf 2004; McNab 2009) and selected the lowest measurement for each individual as RMR.

We corrected mass flow rates of humid air, and calculated CO_2 and H_2O production using equations in Lighton (2008). Metabolic rate (W) was calculated as in Walsberg and Wolf (1995). CO_2 production was converted to metabolic energy using a respiratory quotient (RQ) value of 0.71, as suggested for post-absorptive, non-granivorous birds (Gessaman & Nagy 1988).

Literature data

We compiled basal metabolic rate data (BMR) from the literature, drawing primarily from 3 manuscripts that use large BMR datasets to investigate allometric and latitudinal variation in avian BMR (McKechnie & Wolf 2004; Wiersma *et al.* 2007; Londoño *et al.* 2015). Estimates of annual adult mortality were compiled by searching the literature, and were greatly aided by manuscripts containing large literature datasets (Martin 1995; Martin & Clobert 1996). We restricted estimates of adult mortality probability to model-based estimates based on mark-recapture datasets from wild populations. Where multiple estimates of either BMR or adult mortality probability for a single species were present in the literature, we chose the estimate based on the most recent study.

Statistical Analyses

We employed Cormack-Jolly-Seber models to estimate apparent annual adult survival (ϕ) and detection probability (p) for each species based on live encounters in an open population using program MARK

(White & Burnham 1999; Burnham & Anderson 2002). A suite of models were built for each species, allowing parameters to vary based on sex and/or age-structure (time since marking; Pradel *et al.* 1997). Top models were selected based on Akaike's information criterion (AICc) adjusted for small sample size. Estimates used here are a subset of those presented in Martin et al. (Martin *et al.* 2015, 2017b), where additional methodological details are provided. Apparent annual survival rate (ϕ) was converted to annual adult mortality probability (μ) by the simple equation: $\mu = (1- \phi)$.

For field data we log-transformed RMR (W) and body mass (g). We regressed metabolic rate on body mass to obtain residual metabolic rate values for each individual. We used species mean values of both residual metabolic rate and body mass to analyze the relationships between residual metabolic rate, adult mortality probability and latitude.

We used phylogenetic least-squares regression (PGLS), implemented in the package ‘ape’ (Paradis, Claude & Strimmer 2004; Popescu, Huber & Paradis 2012), to control for the non-independence of species-level data points associated with phylogenetic relatedness (Felsenstein 1985). We used the scaling parameter Pagel’s λ to quantify phylogenetic signal in our data (Pagel 1999). Typical λ values range from 0-1, from no phylogenetic signal (random covariance with respect to phylogenetic distance) to Brownian motion (covariance directly proportional to phylogenetic distance) (Pagel 1999). Phylogenetic trees were acquired from birdtree.org (Jetz *et al.* 2012) using the Hackett backbone (Hackett *et al.* 2008). We sampled a distribution of 1000 trees for each analysis and produced majority-rules consensus trees using Mesquite (Maddison & Maddison 2011). In one case (*Troglodytes aedon*), we include both a tropical (*T. a. musculus*) and temperate (*T. a. aedon*) subspecies in our dataset. To facilitate phylogenetic analysis in which duplicate estimates for a single species are problematic, we assigned one estimate to a closely-related congener (*T. cobbi*) for tree construction.

For our field data, we tested whether residual metabolic rate and/or site explained interspecific variation in adult mortality probability by fitting a generalized least-squares regression model with adult mortality probability as the dependent variable and residual metabolic rate and site as independent variables. We tested whether body mass was associated with adult mortality probability separately because including mass as a covariate in a model including metabolic rate would introduce issues of collinearity. We also tested for differences in metabolic rate between sites using a generalized least-squares model with metabolic rate as the dependent variable, site as an independent variable and body mass as a covariate. We followed an identical procedure for analysis of our literature data, substituting region for site. Finally, we combined field and literature datasets and tested for differences in allometric relationships between RMR and BMR. All analyses were performed in R (R Core Team 2015).

RESULTS

We obtained field-based estimates of adult mortality probability and resting metabolic rate for 28 species; 14 in Arizona and 14 in Malaysia. We measured RMR in a total of 207 individuals with an average of 7.4 individuals per species (Table 1). Body mass explained the majority of variation in metabolic rates ($P < 0.01$, Fig 1), and metabolic rates were similar across sites ($P = 0.72$). The allometric scaling exponent was 0.65, which is consistent with known values for birds (Bennett & Harvey 1987; McKechnie & Wolf 2004). There was no phylogenetic signal in RMR for our field dataset ($\lambda = -0.95$). Adult mortality probability increased with increasing residual (i.e. corrected for mass) metabolic rate ($P = 0.04$), but was lower in Malaysian than Arizona species for the same RMR ($P < 0.01$, Fig 2). Body mass was not a significant predictor of adult mortality probability for our field data ($P = 0.26$). There was no phylogenetic signal in adult mortality probability ($\lambda = -0.61$).

We compiled literature data for BMR and adult mortality probability for 104 species; 70 temperate and 34 tropical (Table 2). Sample sizes for metabolic measurements were available for 90 of these species, which averaged 8.54 individuals per species. Similar to our field data, body mass explained variation in metabolic rates ($P < 0.01$, Fig 3), and we detected no difference in basal metabolic rate between tropical and temperate regions ($P = 0.72$). The allometric scaling exponent was 0.68, which is consistent with known values for birds (Bennett & Harvey 1987; McKechnie & Wolf 2004). Residual

BMR showed a moderate phylogenetic signal (λ = 0.39). Adult mortality probability increased with increasing residual BMR, but the relationship was marginally significant ($P = 0.08$, Fig. 4). Adult mortality was lower in tropical than temperate species for the same metabolic rate ($P < 0.01$, Fig 4). Larger species had lower adult mortality probability but the relationship was marginally significant ($P = 0.08$). Adult mortality probability showed a strong phylogenetic signal in in our dataset (λ = 0.76).

RMR was 17.4% higher than BMR ($P < 0.01$) and the relationship between mass and metabolism did not differ between active (RMR) and resting (BMR) phases ($P = 0.49$).

DISCUSSION

Our results from both field and literature data suggest that residual metabolic rate is positively correlated with adult mortality probability but that large variation in adult mortality probability exists beyond that explained by metabolism (Fig 2,4). This finding may provide support for the rate-of-living hypothesis within latitudes, but highlights the inability of the rate-of-living hypothesis to explain latitudinal differences in mortality rates and life-history strategies in songbirds.

We found similar metabolic rates between temperate and tropical regions based on both field and literature data. This result contrasts with recent studies that identified lower BMR in tropical species (Wiersma *et al.* 2007; Londoño *et al.* 2015) but agrees with earlier work in both adult birds (Vleck & Vleck 1979; Bennett & Harvey 1987) and embryos (Martin *et al.* 2013). Metabolic rates may increase with elevation (McNab 2009; but see Londoño *et al.* 2015) such that our field measurements of RMR in montane birds may be higher than a 'typical' tropical species. This has the potential to minimize latitudinal differences in RMR in our field data set but is unlikely to bias our literature dataset which spans elevations in the tropics. Most importantly, any difference in metabolic rate among latitudes is tiny in comparison to variation within latitudes (see Wiersma *et al.* 2007, Fig 1; Londono *et al.* 2015, Fig 4). In contrast, adult mortality probability shows large variation across latitudes (Martin *et al.* 2017b).

The absence of a strong relationship between metabolic rate and adult mortality across latitudes does not discount the possibility that physiological damage from cellular metabolism underpins life-history tradeoffs. On the contrary, investment in mechanisms to mitigate damage, such as endogenous production of antioxidants (Parolini *et al.* 2017) or mitochondrial membrane composition (Hulbert *et al.* 2007), can reduce damage from cellular metabolism. If tropical species invest in these mechanisms with allocation costs for growth or reproduction, such a tradeoff could explain the longer life and slower life-history strategies of tropical species despite similar metabolic rates across latitudes.

BMR and RMR are the most easily measurable and comparable metrics of metabolic expenditure in wild organisms. However, these measures only encompass minimal energy expenditure to sustain life and thus exclude energy allocated to essential activities such as reproduction, thermoregulation, locomotion and digestion. Physiological damage from metabolism may be more tightly linked to measures of total energy expenditure that describe all energetic expenditures in free-living organisms. Measurements of total energy expenditure, such as field metabolic rate (FMR) or daily energy expenditure (DEE) are comparatively rare in the literature, especially for tropical species (McKechnie 2015), but do show a relationship with adult mortality probability in the temperate zone (Martin 2014). However, BMR and RMR are strongly correlated with each other, and with measures of total energy expenditure across species (Daan, Masman & Groenewold 1990; Auer, Killen & Rezende 2017a), making BMR and RMR reasonable proxies for total energy expenditure. Nonetheless, future studies should examine the relationship between FMR and adult mortality within and across latitudes.

Latitudinal variation in avian mortality rates may be driven primarily by differences in extrinsic mortality probability. Extrinsic mortality is thought to account for 80-95% of all mortality for birds with total annual mortality rates similar to those in our study (Ricklefs 1998). Thus, variation in extrinsic mortality is likely to have a much larger effect on total mortality rates than intrinsic physiological differences. However, extrinsic mortality could exert selection on metabolic costs to survival (Charlesworth 1994, 2000). High adult mortality rates in temperate birds may reflect high rates of extrinsic mortality imposed by abiotic factors (Macarthur 1972) that better explain latitudinal differences in mortality (Martin *et al.* 2015).

Lambda values from PGLS analyses indicate moderate to strong phylogenetic signal for both metabolic rate and adult mortality probability in our literature dataset but were negative for analyses based on field data. Negative values indicate that closely-related species have significantly more divergent trait values than expected by chance, meaning that trait variation in both adult mortality and residual metabolic rate is primarily driven by differences in environmental factors between our study sites than by phylogenetic inertia (see Martin et al. 2015).

Our study provides correlational support for the rate-of-living hypothesis within latitudes while also suggesting that it is unable to explain latitudinal differences in adult mortality in birds. This contradiction provides obvious opportunity for future studies. Tropical birds have longer developmental periods and parents invest more energy per-offspring compared with temperate species (Martin 1996; Martin *et al.* 2011; Gill & Haggerty 2012). These differences may facilitate longer life in tropical species if they facilitate greater investment in physiological adaptations to combat oxidative damage in the face of similar metabolic rates. Quantifying interspecific and latitudinal variation in physiological mechanisms capable of mitigating oxidative damage may reveal how tropical species maintain low adult mortality without a major reduction in basal metabolic rate. Mortality rate differences among latitudes may also be due to variation in extrinsic mortality. Studies quantifying latitudinal differences in cause-specific mortality are necessary to test this hypothesis.

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Table 1. Mean (± SE) values of mass, resting metabolic rate (RMR) and annual mortality probability for species in our field study. N (sample size) values represent the number of unique individuals measured for metabolic rate and the number of unique individuals marked for annual mortality probability.

	Metabolism					Mortality Probability		
Species	Mass (g)	SE	RMR (W)	SE	N	Rate (Yr^{-1})	SE	N
Arizona								
Empidonax occidentalis	11.72	0.34	0.277	0.019	5	0.401	0.034	674
Parus gambeli	11.65	0.16	0.326	0.019	5	0.495	0.033	709
Certhia americana	7.47	0.26	0.227	0.011	4	0.452	0.072	408
Sitta canadensis	10.38	0.24	0.291	0.015	6	0.529	0.058	547
Sitta carolinensis	17.67	0.34	0.410	0.019	4	0.574	0.057	164
Sialia mexicana	23.68	0.55	0.440	0.017	3	0.517	0.096	73
Catharus guttatus	29.07	0.39	0.571	0.01	7	0.482	0.023	1,875
Turdus migratorius	73.00	2.75	0.944	0.111	3	0.461	0.035	655
Pipilo chlorurus	30.25	0.75	0.575	0.025	6	0.445	0.088	158
Junco hyemalis	21.99	1.14	0.448	0.01	7	0.433	0.014	1,885
Vermivora celata	8.98	0.17	0.267	0.013	7	0.411	0.027	976
Dendroica coronata	12.67	0.21	0.345	0.028	8	0.494	0.038	1,008
Cardellina rubrifrons	9.99	0.63	0.266	0.015	6	0.429	0.051	694
Piranga ludoviciana	28.30	0.71	0.512	0.023	5	0.435	0.035	728
Malaysia								
Pachycephala hypoxantha	22.79	0.30	0.406	0.007	12	0.267	0.030	193
Rhipidura albicollis	12.11	0.18	0.307	0.016	10	0.358	0.055	127
Alophoixus ochraceus	48.57	0.82	0.769	0.021	20	0.213	0.043	90
Orthotomus cuculatus	7.07	0.12	0.218	0.01	8	0.289	0.098	20
Yuhina everetti	13.73	0.23	0.359	0.008	2	0.319	0.063	94
Stachyris nigriceps	15.50	0.28	0.340	0.011	17	0.238	0.015	410
Trichastoma pyrrogenys	18.90	0.24	0.372	0.008	12	0.208	0.049	72

Napothera crassa	28.11	0.72	0.471	0.028	9	0.028	0.036	37
Rhinomyias gularis	25.33	0.32	0.460	0.025	11	0.191	0.026	146
Brachypteryx montana	20.27	0.28	0.438	0.023	4	0.175	0.070	39
Enicurus leschenaulti	35.69	1.14	0.634	0.026	7	0.104	0.101	22
Myophonus borneensis	116.71	3.87	1.393	0.063	8	0.275	0.080	18
Ficedula hyperythra	8.32	0.13	0.218	0.014	9	0.365	0.033	155
Aethopyga siparaja	5.96	0.77	0.176	0.019	2	0.269	0.103	19

Table 2. Mean values and sources for mass, basal metabolic rate (BMR) and annual mortality probability for species in our literature dataset. Sample size (N) values are provided for BMR estimates when available from the original sources.

	Metabolism				Mortality probability	
Species	Mass (g)	BMR (W)	N	Source	Rate (Yr^{-1})	Source
Temperate						
Acanthorhynchus tenuirostris	9.7	0.25	6	Weathers et al. 1996	0.40	Macfarland & Ford 1987
Acrocephalus arundinaceus	21.9	0.26	4	Hails 1983	0.41	Peach et al. 2001
Acrocephalus schoenobaenus	11.5	0.22	3	Kendeigh et al. 1977	0.63	Martin & Clobert 1996
Aegithalos caudatus	8.9	0.20	17	Makarieva et al. 2008	0.53	Martin & Clobert 1996
Agelaius phoeniceus	47.1	0.56	-	Wiersma et al. 2007	0.47	Martin 1995
Alauda arvensis	31.7	0.72	14	Tieleman et al. 2002	0.34	Martin & Clobert 1996
Ammodramus savannarum	13.8	0.18	3	Yarbrough 1971	0.40	Martin 1995
Anthus pratensis	18.9	0.30	3	Kendeigh et al. 1977	0.58	Martin & Clobert 1996
Anthus trivialis	19.7	0.34	5	Kendeigh et al. 1977	0.57	Martin & Clobert 1996
Cardinalis cardinalis	40.5	0.50	8	Hinds & Calder 1973	0.44	Martin 1995
Carduelis chloris	28.2	0.47	17	Kendeigh et al. 1977	0.51	Martin & Clobert 1996
Carduelis tristis	13.6	0.33	-	Dawson & Carey 1976	0.56	Middleton & Webb 1984
Carpodacus mexicanus	20.4	0.31	13	Weathers 1981	0.45	Martin 1995
Catharus ustulatus	28.2	0.43	38	Londono et al. 2015	0.65	Martin 1995
Dendroica coronata	11.5	0.19	4	Yarbrough 1971	0.49	Martin et al. 2015
Emberiza citrinella	26.8	0.44	27	Makarieva et al. 2008	0.47	Martin & Clobert 1996
Emberiza schoeniclus	17.6	0.30	3	Kendeigh et al. 1977	0.49	Martin & Clobert 1996
Empidonax virescens	12.3	0.18	7	Yarbrough 1971	0.54	Martin 1995
Erithacus rubecula	15.5	0.28	1	Daan et al. 1990	0.52	Martin & Clobert 1996
Ficedula hypoleuca	11.7	0.23	9	Kendeigh et al. 1977	0.50	Martin & Clobert 1996
Fringilla coelebs	21.0	0.37	35	Makarieva et al. 2008	0.44	Martin & Clobert 1996
Geothlypis trichas	10.6	0.17	4	Yarbrough 1971	0.46	Martin 1995
Hippolais icterina	12.5	0.25	6	Kendeigh et al. 1977	0.50	Martin & Clobert 1996
Hirundo rustica	18.0	0.32	4	Makarieva et al. 2008	0.63	Martin & Clobert 1996

Junco hyemalis	18.0	0.30	12	Weathers & Sullivan 1993	0.44	Martin 1995
Lichmera indistincta	9.0	0.21	12	Collins et al. 1980	0.44	Robertson & Woodall 1987
Melithreptus lunatus	14.3	0.25	-	Vitali et al. 1999	0.42	Rowley & Russell 1991
Melospiza melodia	19.1	0.25	7	Yarbrough 1971	0.45	Martin 1995
Mimus polyglottos	44.2	0.68	-	Wiersma et al. 2007	0.51	Martin 1995
Mniotilta varia	8.2	0.13	1	Yarbrough 1971	0.46	Dugger et al. 2004
Motacilla alba	18.0	0.30	8	Makarieva et al. 2008	0.51	Martin & Clobert 1996
Motacilla flava	14.7	0.26	2	Kendeigh et al. 1977	0.52	Martin & Clobert 1996
Parus atricapillus	10.3	0.25	-	Rising & Hudson 1974	0.60	Martin 1995
Parus major	18.0	0.32	10	Hissa & Palonkangas 1970	0.51	Martin & Clobert 1996
Passer domesticus	24.2	0.28	1	Daan et al. 1990	0.45	Martin & Clobert 1996
Passer montanus	17.5	0.20	10	Hails 1983	0.56	Martin & Clobert 1996
Passerculus sandwichensis	15.9	0.22	6	Williams & Hansell 1981	0.52	Martin 1995
Phoenicurus phoenicurus	13.0	0.23	4	Kendeigh et al. 1977	0.57	Martin & Clobert 1996
Phylloscopus collybita	8.2	0.17	6	Kendeigh et al. 1977	0.62	Martin & Clobert 1996
Phylloscopus trochilus	10.7	0.21	7	Kendeigh et al. 1977	0.64	Martin & Clobert 1996
Pica pica	158.9	1.20	9	Hayworth & Weathers 1984	0.33	Martin & Clobert 1996
Pooectes gramineus	21.5	0.27	8	Yarbrough 1971	0.50	Martin 1995
Protonotaria citrea	12.8	0.20	3	Yarbrough 1971	0.57	Martin 1995
Prunella modularis	16.8	0.32	4	Kendeigh et al. 1977	0.53	Martin & Clobert 1996
Regulus regulus	5.5	0.18	22	Kendeigh et al. 1977	0.86	Martin & Clobert 1996
Riparia riparia	13.6	0.23	3	Kendeigh et al. 1977	0.64	Martin & Clobert 1996
Sayornis phoebe	21.6	0.34	4	Yarbrough 1971	0.69	Martin 1995
Seiurus aurocapilla	19.0	0.24	5	Yarbrough 1971	0.36	Martin 1995
Seiurus noveboracensis	18.7	0.28	3	Yarbrough 1971	0.35	Martin 1995
Sialia mexicana	27.5	0.42	9	Mock 1991	0.52	Martin et al. 2015
Sitta carolinensis	19.4	0.36	4	Liknes & Swanson 1996	0.57	Martin et al. 2015
Spizella passerina	11.9	0.19	5	Yarbrough 1971	0.42	Martin 1995
Spizella pusilla	13.0	0.26	5	Dutenhoffer & Swanson 1996	0.54	Martin 1995
Sturnus vulgaris	75.0	0.88	13	Kendeigh et al. 1977	0.53	Martin & Clobert 1996
Sylvia atricapilla	21.9	0.42	8	Kendeigh et al. 1977	0.51	Martin & Clobert 1996

Sylvia borin	24.8	0.42	12	Kendeigh et al. 1977	0.46	Martin & Clobert 1996
Sylvia curruca	10.6	0.20	8	Kendeigh et al. 1977	0.56	Martin & Clobert 1996
Tachycineta bicolor	16.4	0.29	-	Wiersma et al. 2007	0.60	Martin 1995
Troglodytes a. aedon	10.2	0.21	-	Wiersma et al. 2007	0.54	Martin et al. 2015
Troglodytes troglodytes	9.0	0.21	16	Makarieva et al. 2008	0.65	Martin & Clobert 1996
Turdus iliacus	58.0	0.72	9	Kendeigh et al. 1977	0.58	Martin & Clobert 1996
Turdus merula	66.8	0.74	2	Daan et al. 1990	0.47	Martin & Clobert 1996
Turdus migratorius	62.4	0.76	-	Wiersma et al. 2007	0.46	Martin et al. 2015
Turdus philomelos	62.8	0.73	12	Makarieva et al. 2008	0.47	Martin & Clobert 1996
Tyrannus tyrannus	35.7	0.44	1	Yarbrough 1971	0.57	Martin 1995
Vireo olivaceus	16.2	0.24	-	Wiersma et al. 2007	0.45	Martin 1995
Wilsonia citrina	12.0	0.21	4	Yarbrough 1971	0.45	Martin 1995
Zonotrichia albicollis	20.2	0.28	6	Yarbrough 1971	0.46	Martin 1995
Zonotrichia leucophrys	26.1	0.34	6	Yarbrough 1971	0.50	Martin 1995
Zosterops lateralis	11.0	0.15	9	Maddocks & Geiser 1997	0.17	Willis 1974
Tropical						
Basileuterus tristriatus	12.6	0.25	11	Londono et al. 2015	0.24	Martin et al. 2015
Cercomacra tyrannina	15.4	0.19	-	Wiersma et al. 2007	0.18	Morton & Stutchbury 2000
Coereba flaveola	11.0	0.24	3	Londono et al. 2015	0.35	Johnston et al. 1997
Conopophaga peruviana	24.5	0.34	4	Londono et al. 2015	0.43	Blake & Loiselle 2013
Corythopis torquatus	18.7	0.28	5	Londono et al. 2015	0.36	Blake & Loiselle 2013
Cyanocompsa cyanoides	25.0	0.38	3	Londono et al. 2015	0.57	Blake & Loiselle 2013
Dendrocincla fuliginosa	33.1	0.37	9	Londono et al. 2015	0.23	Johnston et al. 1997
Dendrocincla merula	52.8	0.62	11	Londono et al. 2015	0.29	Francis et al. 1999
Formicarius analis	54.9	0.62	3	Londono et al. 2015	0.51	Karr et al. 1990
Glyphorynchus spirurus	15.5	0.25	21	Londono et al. 2015	0.38	Blake & Loiselle 2013
Gymnopithys bicolor	27.7	0.33	-	Wiersma et al. 2007	0.29	Willis 1974
Henicorhina leucophrys	15.3	0.31	6	Londono et al. 2015	0.22	Martin et al. 2015
Himatione sanguinea	13.5	0.30	8	Weathers et al. 1983	0.28	Ralph & Fancy 1994
Hylophylax naevioides	16.1	0.24	-	Wiersma et al. 2007	0.41	Karr et al. 1990
Lepidothrix coronata	10.6	0.20	20	Londono et al. 2015	0.39	Blake & Loiselle 2013

Loxioides bailleui	36.0	0.46	12	Weathers & van Riper 1982	0.37	Lindsey et al. 1995
Manacus vitellinus	15.5	0.23	7	Bartholomew et al. 1983	0.53	Karr et al. 1990
Microcerculus marginatus	19.4	0.33	3	Londono et al. 2015	0.49	Blake & Loiselle 2013
Mionectes oleagineus	11.4	0.18	7	Londono et al. 2015	0.49	Brawn et al. 1995
Myadestes ralloides	28.8	0.39	7	Londono et al. 2015	0.29	Martin et al. 2015
Myioborus miniatus	9.8	0.20	6	Londono et al. 2015	0.21	Martin et al. 2015
Myrmoborus myotherinus	21.2	0.28	3	Londono et al. 2015	0.40	Blake & Loiselle 2013
Myrmotherula axillaris	8.9	0.19	4	Londono et al. 2015	0.31	Blake & Loiselle 2013
Pipra fasciicauda	16.4	0.26	38	Londono et al. 2015	0.23	Francis et al. 1999
Rhynchocyclus olivaceus	21.0	0.30	-	Wiersma et al. 2007	0.43	Karr et al. 1990
Saltator maximus	44.8	0.55	-	Wiersma et al. 2007	0.39	Martin et al. 2015
Thamnomanes ardesiacus	19.3	0.27	9	Londono et al. 2015	0.19	Jullien & Thiollay 1998
Thamnomanes schistogynus	19.7	0.34	3	Londono et al. 2015	0.22	Francis et al. 1999
Thamnophilus atrinucha	20.5	0.28	-	Wiersma et al. 2007	0.27	Karr et al. 1990
Thamnophilus punctatus	21.0	0.34	-	Wiersma et al. 2007	0.46	Greenberg & Gradwohl 1986
Thraupis palmarum	32.6	0.40	-	Wiersma et al. 2007	0.33	Johnston et al. 1997
Troglodytes a. musculus	13.3	0.21	-	Wiersma et al. 2007	0.41	Martin et al. 2015
Turdus albicollis	51.3	0.46	15	Londono et al. 2015	0.34	Blake & Loiselle 2013
Xiphorhynchus guttatus	60.1	0.52	7	Londono et al. 2015	0.24	Johnston et al. 1997

Figure Legends

Figure 1. The allometric relationship between resting metabolic rate (RMR) and body mass (M_b) for species measured at our Malaysia (filled circles) and Arizona (open circles) field sites. Associated data is presented in Table 1. The dashed line represents the phylogenetic generalized least-squares regression line described by the equation in the figure.

Figure 2. The relationship between residual resting metabolic rate and adult mortality probability based on our field data from Malaysia (filled circles) and Arizona (open circles).

Figure 3. The allometric relationship between basal metabolic rate (BMR) and body mass (M_b) based on data compiled from the literature and presented in Table 2. Each data point represents one species. Filled circles are tropical species and open circles are temperate species. The dashed line represents the phylogenetic generalized least-squares regression line described by the equation in the figure.

Figure 4. The relationship between residual basal metabolic rate and adult mortality probability based on data compiled from the literature.

Figure 1

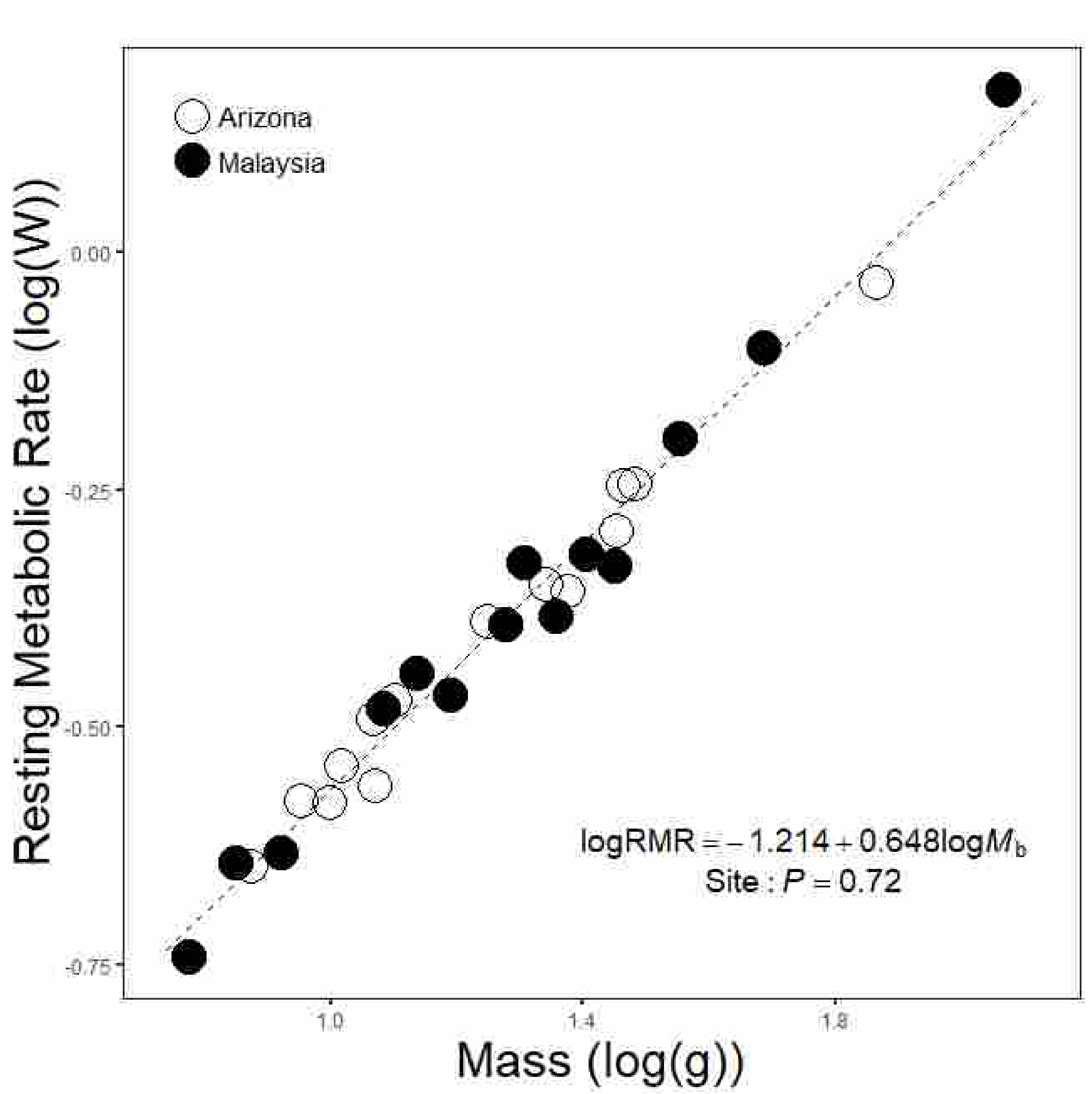

Arizona
Malaysia
Resting Metabolic Rate (log(W))
0.00
-0.25
-0.50
-0.75
1.0
1.4
1.8
Mass (log(g))
$\log RMR = -1.214 + 0.648 \log M_b$
Site : $P = 0.72$

Figure 2

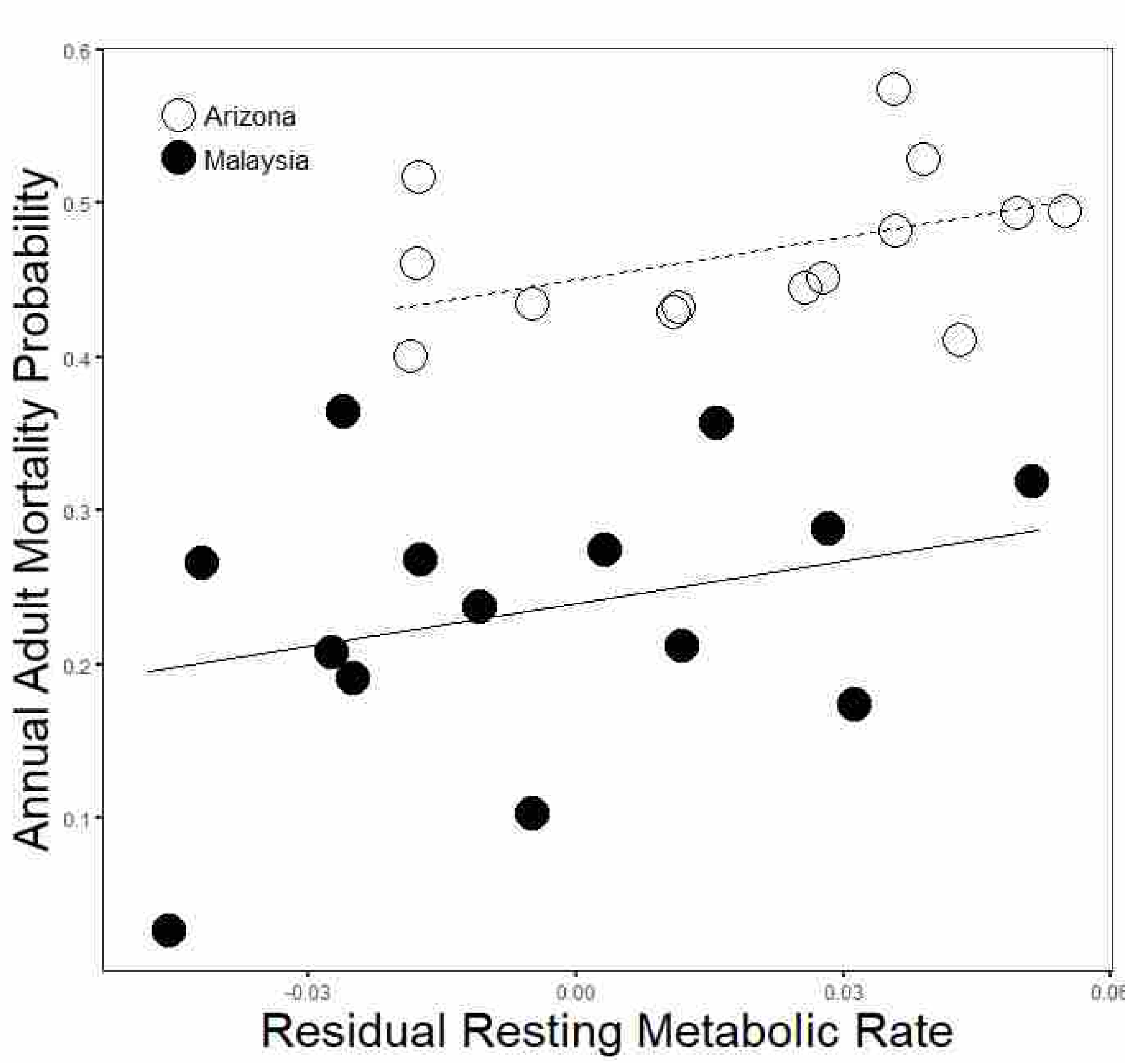

0.6
0.5
0.4
0.3
0.2
0.1
-0.03
0.00
0.03
0.0
Arizona
Malaysia
Annual Adult Mortality Probability
Residual Resting Metabolic Rate

Figure 3

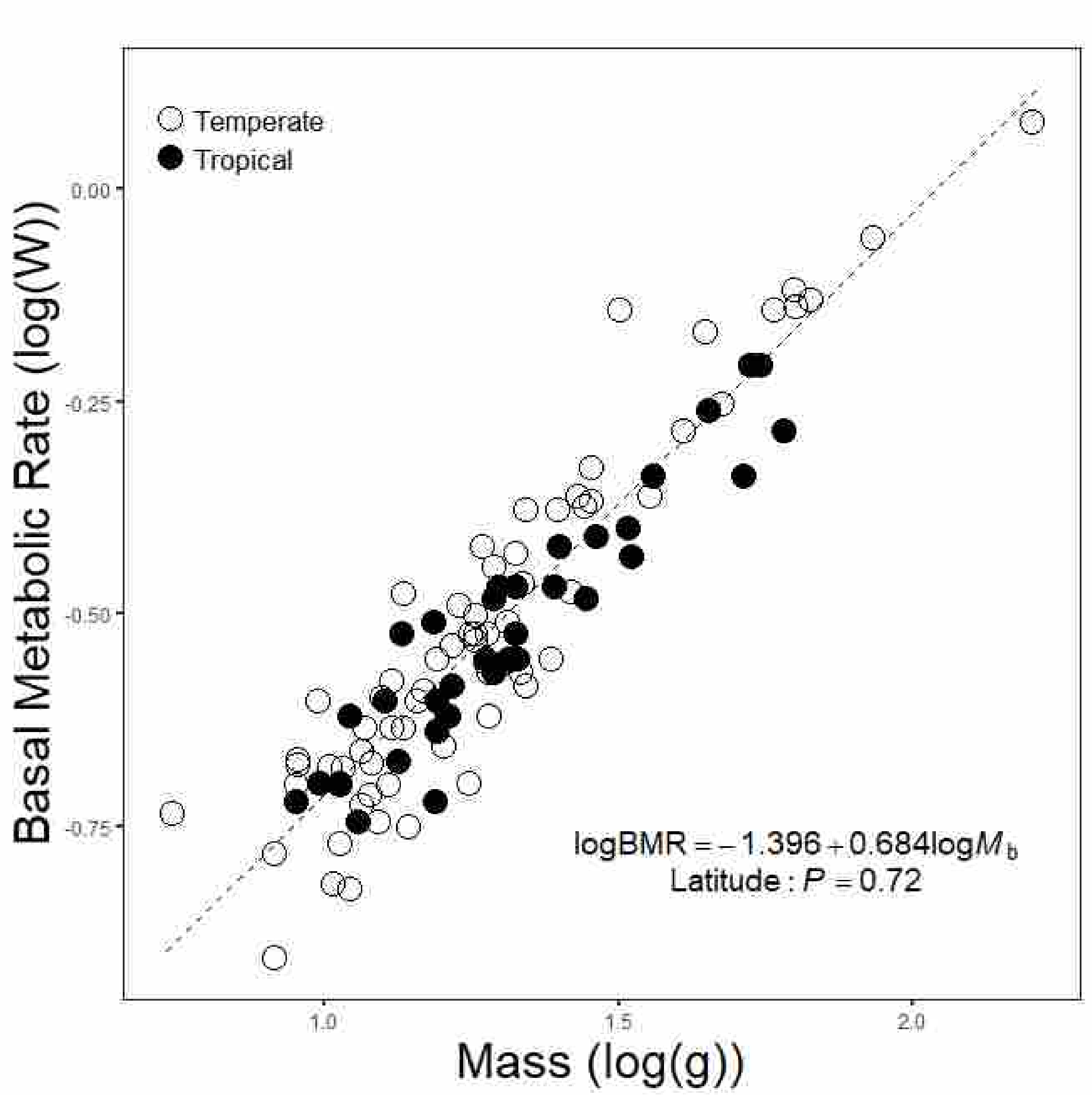
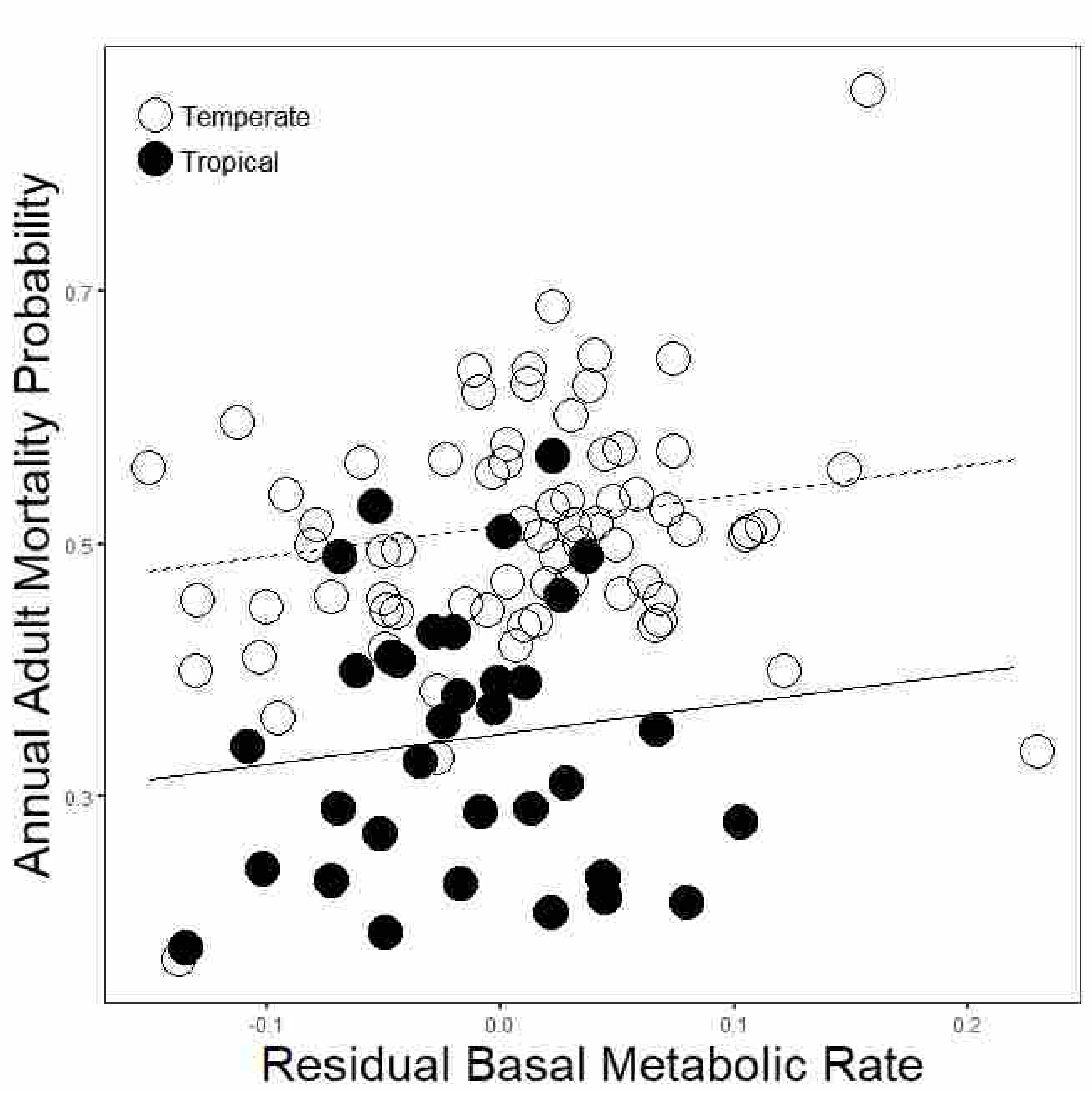

Temperate
Tropical
Basal Metabolic Rate (log(W))
0.00
-0.25
-0.50
-0.75
1.0
1.5
2.0
Mass (log(g))
logBMR = −1.396 + 0.684logM_b
Latitude : P = 0.72

Figure 4


Temperate
Tropical
Annual Adult Mortality Probability
0.7
0.5
0.3
-0.1
0.0
0.1
0.2
Residual Basal Metabolic Rate