

RESEARCH ARTICLE

Functional Ecology



Survival is negatively related to basal metabolic rate in tropical Andean birds

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Abstract

1. Life-history theory postulates that physiological traits, such as energy metabolism, can be understood in terms of allocation trade-offs between self-maintenance and reproduction over an organism's life span, and data show that metabolic intensity and survival vary inversely with latitude, with tropical birds exhibiting a "slow" pace of life relative to temperate species. However, tropical regions harbour strong environmental gradients of their own, and it remains to be shown whether similar life-history trade-offs between metabolism and longevity are reflected among tropical birds of the same latitude.
2. We estimated apparent annual survival in 37 species of tropical passerine birds along an elevational gradient (400–3,000 m) in Peru to test whether variation in survival was influenced by basal metabolic rate (BMR; estimated at the same sites), elevation or both factors. We used path analysis to test our prediction that survival would decline as BMR increased, while accounting for the potential direct effects of elevation on survival due to differences in predation pressure or environmental conditions as well as potential indirect effects of elevation on BMR via temperature and the costs of thermoregulation.
3. Higher BMR in tropical passerine birds predicted lower apparent survival, regardless of the elevation at which species occurred. In addition, elevation had a direct negative effect on apparent survival, perhaps due to harsher abiotic conditions, low site fidelity or both at high elevations.
4. We provide evidence of a link between metabolic rate and longevity previously undescribed in populations of free-living birds. Our results illustrate that tropical montane species may be characterized by a unique suite of traits in their pace of life, in which BMR does not differ from lowland birds, but survival does.

KEYWORDS

energy metabolism, life-history trade-offs, Manu Biosphere Reserve, mark-recapture, pace-of-life, Peru, phylogenetic path analysis, tropical birds

1 | INTRODUCTION

Life-history strategies are thought to optimize fitness given constraints on species' physiology and ecology (Roff, 2002; Stearns, 1992) and can be viewed as occurring along a slow-fast continuum (Stearns, 1983). According to this view, finite resources impose an allocation trade-off between current versus future reproduction or survival—time and/or energy invested in current reproduction is made unavailable for other purposes. “Slow” species are characterized as investing less in reproduction, but more in self-maintenance, increasing survival overall; whereas “fast” species display opposite patterns. These life-history strategies are coupled to sets of physiological traits, including metabolic, immunological and hormonal, that have coevolved in response to ecological conditions to form a “pace-of-life” syndrome (Ricklefs & Wikelski, 2002). Birds have proved useful to “pace-of-life” studies because they are well-sampled globally and have life-history and physiological traits that vary predictably over temperate to tropical latitudes. For example, tropical species lay smaller clutches (Jetz, Sekercioglu, & Böhning-Gaese, 2008; Kulesza, 1990; Lack, 1947), have higher survival (Muñoz, Kéry, Martins, & Ferraz, 2018; Peach, Hanmer, & Oatley, 2001), and display lower basal metabolic rates (BMR) than north temperate species of similar body mass (Bushuev, Tolstenkov, Zubkova, Solovyeva, & Kerimov, 2017; Londoño, Chappell, Castañeda, Jankowski, & Robinson, 2015; Wiersma, Muñoz-Garcia, Walker, & Williams, 2007). Because BMR provides an integrated view of the maintenance energy requirements of an individual associated with its ecological conditions (Daan, Masman, & Groenewold, 1990), it is one of the most widespread and useful measures in linking the flux of energy through an animal with key aspects of their life history (Wiersma, Chappell, & Williams, 2007), such as survival.

Attempts to link energy metabolism to survival date to the early 20th century, when Pearl (1928) advanced “rate-of-living theory,” a tenet of which is that species with lower metabolic rates live longer. Harman (1956) theorized further that long life spans are achieved at lower metabolic rates due to reductions in reactive oxygen species (ROS) and the damage they do to cells as a byproduct of aerobic respiration (Selman, Blount, Nussey, & Speakman, 2012; Speakman, 2005; Vágási et al., 2019). As a result, evolutionary ecologists and physiologists often assume negative correlations between metabolic rate and survival (Speakman et al., 2015), even though relationships between energy metabolism, oxidative stress and survival are complex and also affected by antioxidant defence and cellular repair pathways (Speakman, 2005; Vágási et al., 2019). Moreover, individual BMR can be highly flexible in some species and varies to accommodate seasonal changes in temperature, breeding or as part of the migratory cycle (McKechie, 2008). Thus, while the over-arching prediction of a negative relationship between avian BMR and survival are strongly supported by patterns in latitudinal gradients (Ricklefs & Wikelski, 2002; Williams, Miller, Harper, & Wiersma, 2010), considerable uncertainty surrounds this relationship, and few empirical studies have compared metabolic rate and survival across multiple species at a single site (but see Williams et al., 2010).

Negative correlations of survival, BMR and latitude suggest that similar trade-offs in life-history traits should also be expected across other environmental gradients, such as elevation (Boyle, Sandercock, & Martin, 2016; Hille & Cooper, 2015). Birds in particular have developed physiological machinery that has allowed them to adapt and thrive at high elevations more so than any other group of endotherms, including a greater capacity to tolerate and exercise in hypoxia (Scott, Meir, Hawkes, Frappell, & Milsom, 2011). High-elevation populations of birds in both temperate and tropical regions must deal with decreased partial pressure of oxygen as well as colder temperatures relative to adjacent lowland/low-latitude species and larger daily fluctuations in temperature, the latter of which can both reduce food availability and challenge individual physiology (Kwit et al., 2004). We might therefore expect the “pace-of-life” syndrome of birds living in high-elevation environments to reflect increased rates of energy expenditure due to higher maintenance costs and acclimatization to colder temperatures (McKechie & Swanson, 2010). For instance, populations of White-crowned Sparrows (*Zonotrichia leucophrys*; Weathers et al., 2002) in temperate North America, and Amethyst Sunbirds (*Chalcomitra amethystina*; Lindsay, Downs, & Brown, 2009) and Fiscal Shrikes (*Lanius collaris*; Soobramoney, Downs, & Adams, 2003) in austral Africa all display increased BMR at high elevation. Thus, if high BMR characterizes high-elevation populations, then we might also expect them to exhibit low survival. However, in contrast to temperate regions, data from the tropical Andes failed to find an effect of elevation on metabolism when examining >250 species from Peru across a 2.6 km elevational gradient (Londoño et al., 2015). This result implies that low BMR in tropical birds is unrelated to ambient temperature, changes in oxygen partial pressure, or is offset by the costs of metabolic heat production and reduced thermal conductance at high elevations (Londoño, Chappell, Jankowski, & Robinson, 2017). Links between survival and elevation do receive support from several intraspecific studies of birds at temperate and Holarctic latitudes, with most reporting higher survival in populations at higher elevation (Boyle et al., 2016). High-elevation sites in tropical regions differ from the temperate zone in important ways—they are less seasonal and lack the productivity pulses experienced at higher latitudes—so it remains unclear whether populations of tropical mountaintop birds also display higher survival relative to lowland species.

We examined relationships among survival, BMR and elevation in tropical birds from southeastern Peru to test whether (a) BMR and survival are negatively related and (b) survival rates differ between birds living at low versus high elevation. First, we estimated apparent annual survival in 37 Passerine species along an Amazon-to-Andes elevational gradient (400–3,000 m) using multi-year mark-recapture data. We then asked whether BMR (previously measured at the same study sites; Londoño et al., 2015), elevation or both predicted apparent survival. Second, we asked if the relationship between BMR and apparent survival was mediated through elevation whereby lower temperatures at higher elevations led to an increase in BMR and subsequent reduction in survival. To disentangle direct and indirect effects of physiology and environment, we used a path analysis while

controlling for non-independence of species due to their common ancestry (Felsenstein, 1985) and positive allometric effects of body mass on BMR (Londoño et al., 2015; McNab, 2009; Williams et al., 2010) and survival (McCarthy, Citroen, & McCall, 2008). These data represent the first test of elevation, representing an important environmental gradient within the tropics, and BMR, long believed to be negatively related to longevity, to explain variation in apparent survival for tropical birds.

2 | MATERIALS AND METHODS

We conducted our study at three research stations in the Manu Biosphere Reserve, Peru, at 400–3,000 m elevation and oriented along a 70 km-long northeast–southwest axis (Figure S1). Pantiacolla is located at the base of the Andean foothills in humid lowland rainforest (12°38′31.3″S, 71°14′21.2″W). San Pedro includes both humid montane rainforest and lower-elevation cloud forest (13°3′19.4″S, 71°32′48.5″W). Wayqecha is at the upper boundary of Andean cloud forest near tree line (13°11′14.4″S, 71°35′9.3″W). A rainy season occurs from November through March with highest rainfall generally in January and February, while May through July form the dry season (Rapp & Silman, 2012). Mean annual rainfall is highest at mid elevations (>4,500 mm) while both low- and high-elevations stations average >3,000 mm/year (Rapp & Silman, 2012). Annual mean temperature ranges from a low of 11.2°C at Wayqecha to 23.2°C at Pantiacolla (Londoño et al., 2015) with a difference of <4°C between the warmest and coolest months (Rapp & Silman, 2012).

2.1 | Mark-recapture and mist-netting

At each research station, we surveyed for birds at 10 plots in continuous forested habitat using mist-nets (12 × 3 m, 36-mm mesh). Plots were typically positioned adjacent to one another along trails and spanned elevational ranges between 385 and 575 m at Pantiacolla, 1,250 and 1720 m at San Pedro and 2,515 and 2,985 m at Wayqecha. Each plot covered an area of approximately 1–1.5 ha and consisted of a linear array of 10–15 nets set at ground level placed 5–50 m apart at the same location each year. We timed data collection to overlap with the end of the dry season (August–November), which is also the breeding period for most birds in the region (Londoño et al., 2015). We visited plots for three consecutive days and checked nets regularly from ~0600 to 1600 hr. During 2012–2015, a repeat 3-day visit was made to each plot 7–14 days after initial sampling for a total of 6 days of mist-net surveys per plot. Each plot was surveyed for 6 years at Pantiacolla and San Pedro, and 5 years at Wayqecha, where mist-netting began in 2012. Sampling effort varied somewhat among years but was relatively equal across stations overall (Table S1).

All birds captured were banded with a uniquely marked aluminium leg band (National Band and Tag, Newport, United States). We recorded wing chord, tail length, bill width and length (in mm), and mass for all birds (± 0.05 g, FlipScale F2, <https://myweigh.com>). Sex

and reproductive status were determined by brood patch, cloacal protuberance or dichromatic plumage. We aged birds using a combination of plumage characteristics, skull ossification and the extent of body and flight feather moult (Kennedy, Heavyside, Jankowski, & Scholer, 2018).

2.2 | Basal metabolic rate, elevational range and body mass

BMR was estimated as the mean per species at each of the three field stations as part of a study of energy metabolism in tropical birds (Appendix S1; Londoño et al., 2015). Similar to Pollock, Brawn, Agin, and Cheviron (2019), who found tropical birds exhibited more modest seasonal acclimatization compared with their temperate counterparts, we found little evidence of seasonal variation in BMR and thus did not include sampling date as a potential nuisance parameter in our analysis (Appendix S1, Table S2 and Figures S2,S3). We calculated the mean of each species' elevational range based on capture locations within stations. Because our coverage of the elevational gradient was not complete, and also due to the high species turnover with elevation in the study area (Jankowski, Merkord, et al., 2013), few species were captured at multiple stations and no species was captured in sufficient numbers to model survival at more than one station. We calculated body mass as the mean mass of each species based on capture data.

2.3 | Estimating adult survival

We used 5,531 capture records (1,732 recaptures of 3,799 individuals) of 37 Passerine species to estimate apparent annual survival (minimum number of captures = 34; mean ratio of captures/recaptures = 2.34, $SD = 1.26$). Because we were interested in adult survival, we excluded data from 35 cases when we captured birds determined to have recently fledged. For each individual, we created a capture history of their initial capture and subsequent recaptures to model apparent annual survival—the product of true survival and site fidelity—using Cormack–Jolly–Seber (CJS) models with time intervals adjusted to fractional years to reflect unequal sampling (Table S2). All mark-recapture analyses and goodness-of-fit (GOF) testing were carried out using *RMark* (Laake, 2013) in R environment 3.4.0 (R Core Team, 2017).

We fitted four a priori models that varied in their assumptions of apparent survival (ϕ) and capture probability (p) to each of the 37 species (Table S3). To estimate ϕ , we considered time-constant (.) and time-since-marking (TSM) models, the latter of which accounts for underestimation of survival due to transient individuals moving through the study area (Johnston, White, Peach, & Gregory, 1997). We used TSM models because the proportion of transients in populations of tropical birds are known to be high (e.g., >40% for birds in Panama; Brawn, Karr, Nichols, & Robinson, 1999), especially for frugivorous species, such as tanagers, manakins and some flycatchers (Martin & Karr, 1986). The TSM model allows apparent survival to differ for birds during their first interval after capture (ϕ^1) from

survival in the second (φ^{2+}) and subsequent intervals. Because φ^{2+} is a less-biased estimate of true survival whenever $\varphi^1 < \varphi^{2+}$ (Sandercock, 2006), we did not use estimates of survival from the first time interval (φ^1) in our analysis. Due to differences in capture effort among years (Table S1), we considered models where capture probability varied or remained constant (Table S3).

To assess model fit, we quantified overdispersion by calculating a variance inflation factor (\hat{c}) obtained by dividing the deviance of each species' most general model by the deviance estimated from 1,000 parametric bootstrap simulations. We used the resulting \hat{c} to adjust corrected Akaike information criterion (AIC_C) values to their quasi-likelihood analogue ($QAIC_C$). We considered the model with the lowest $QAIC_C$ the most appropriate model if it had fewer parameters and was at least 2 $QAIC_C$ less than the next most competitive model (Arnold, 2010; Burnham & Anderson, 2002). Models assuming constant survival and recapture probabilities had the most support (Table S3), and for the majority of species, there was more than one top model within 2 $QAIC_C$ of the lowest value (Table S4). When models were within 2 $QAIC_C$, we used a likelihood-ratio test for all nested sub-models to assess whether the additional parameter significantly improved model fit.

2.4 | Analysis

We used a multi-step approach to model relationships between BMR, elevation and survival. First, to account for potential nonlinear relationships between elevation and dependent variables, we compared model fit where elevation was continuous (mean capture elevation), categorical (Pantiacolla, San Pedro, Wayqecha) or binary (lowland <1,000 m vs. montane > 1,000 m). Model fit was best for the binary structure (Table S5) and was carried forward to the next stage of model development that considered the simultaneous effects of all variables within a multivariate framework.

An additional complicating factor when modelling interspecific species relationships is that closely related species may display similar

life-history traits because of shared ancestry (Felsenstein, 1985). We therefore included phylogeny in the analysis using phylogenetic trees obtained from Jetz, Thomas, Joy, Hartmann, and Mooers (2012; <https://birdtree.org>) and the Hackett et al. (2008) backbone. A majority rules consensus tree was derived from a set of 1,000 randomly selected trees, which we then pruned to include only our 37 species of interest (Figure S4). We used this consensus tree to specify values for the phylogenetic correlation matrix and then fit a general least squares model to the data to find the maximum likelihood value for Pagel's λ (Pagel, 1999). Estimates of λ approach 0 if data are distributed independent of phylogeny and 1 when trait variation between species is proportional to their shared evolutionary history (Pagel, 1999).

To account for both potential effects of phylogeny and indirect effects of mass on BMR and survival and elevation on BMR, we used a phylogenetic path analysis (PPA). PPA is an extension of multiple regression to assess direct and indirect paths among variables as well as the relative importance of various causal models while also incorporating the expected covariance due to shared ancestry (von Hardenberg & Gonzalez-Voyer, 2013). Model fit of PPA was evaluated using Fischer's C statistic to test whether the correlation structure observed in the data fits a set of minimal conditional independencies given by a causal model (Shipley, 2000). A significant C statistic indicates that the model fit is poor (von Hardenberg & Gonzalez-Voyer, 2013). To facilitate comparisons between non-nested models, an analogous approach to model selection with $QAIC_C$ can be employed based on the C statistic and is referred to as CIC_C (von Hardenberg & Gonzalez-Voyer, 2013). As with $QAIC_C$, models within 2 CIC_C are considered to be competitive with the top model if they had the same or fewer parameters with minimal change in the GOF estimate (Arnold, 2010; Burnham & Anderson, 2002).

We developed six models that explored different causal relationships among variables based on theoretical and empirical evidence. Specifically, we developed hypotheses testing scenarios in which BMR, elevation or both had a direct effect on apparent survival and whether an indirect effect of elevation on BMR improved model fit (Figure 1). Well-established

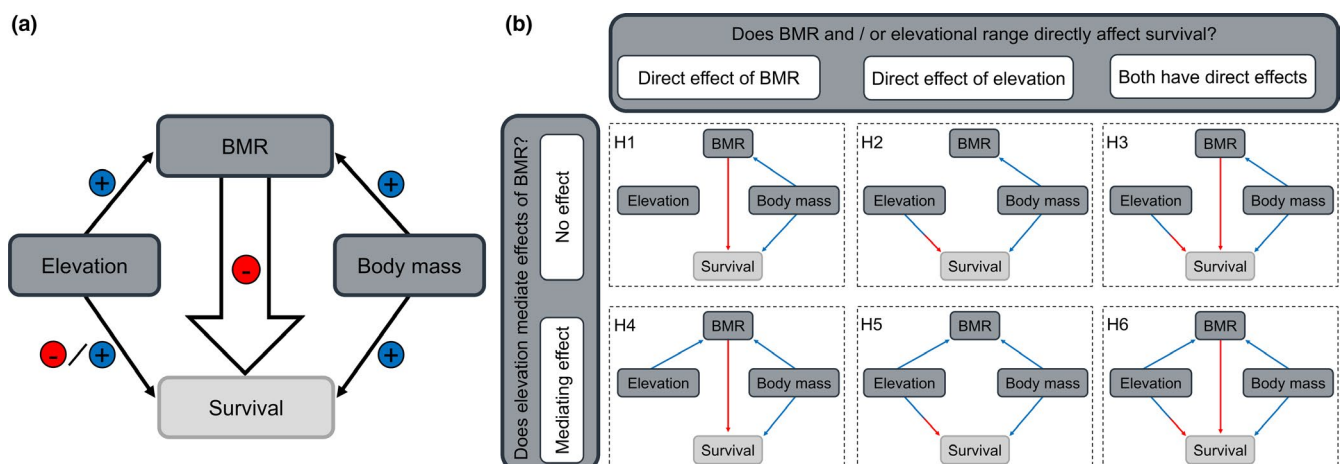


FIGURE 1 Conceptual framework used to test relationships among survival, physiology, and the environment (a), which suggests that a combination of metabolic costs and abiotic factors that vary between high and low elevations as well as allometric effects influence life history traits. For each alternative hypothesis (b), the predicted effect between variables is indicated as either positive (blue arrow), negative (red arrow), or a combination of both effects (blue and red arrow).

relationships between body mass and BMR (Londoño et al., 2015) and body mass and survival (McCarthy et al., 2008; Speakman, 2005) were included in all tested models. By incorporating a causal link with mass, we accounted for allometric effects of body mass on both BMR and survival (von Hardenberg & Gonzalez-Voyer, 2013). We calculated the C statistic, CIC_C and standardized path coefficients and associated 95% confidence intervals from each model using PGLS with an error structure following Pagel's λ (Pagel, 1999). Compared to the best supported model, which accounted for 56% of model weights, all competing models were >2 CIC_C larger or included additional noninformative parameters (Table 1). We therefore present results from only the top model H3 (Figure 1), although results of coefficients averaged over all models were qualitatively the same. All PPA were conducted with R using the *phylo_path* function in *phylopath* (van der Bijl, 2018; von Hardenberg & Gonzalez-Voyer, 2013).

3 | RESULTS

3.1 | Mark-recapture analysis

Mean annual survival probability for all species based on their top models was 0.50 with a standard error of 0.10. For families of birds represented by more than one species, survival probability was highest in Turdidae (mean $\varphi = 0.56$, $SE = 0.07$), lowest for Troglodytidae ($\varphi = 0.42$, $SE = 0.03$) and ranged most widely within the Thraupidae (range of $\varphi = 0.35$ – 0.70 ; Figure 2, Table S6). Not all families of birds were equally represented across the elevational gradient in our dataset, with some (e.g., Thraupidae, Parulidae) only occurring above 1,000 m and others (e.g., Thamnophilidae) in lowland habitat. Of the 37 species, estimates of apparent annual survival were highest for *Pipra fasciicauda* ($\varphi = 0.72$, $SE = 0.13$) and lowest ($\varphi = 0.34$, $SE = 0.13$) for *Myiothlypis bivitata* (Figure 2, Table S6).

3.2 | Covariation in survival, basal metabolic rate and elevation

Accounting for effects of phylogeny, body mass and elevation, we found that BMR maintained a significant negative association with survival ($\beta = -0.76$, 95% CI = -1.23 to -0.05 ; Figure 3a,b). Similarly,

when elevation was modelled as a direct effect, survival was higher for species living in lowland versus montane habitats ($\beta = -0.75$, 95% CI = -1.28 to -0.08 ; Figure 3c). Model structures that incorporated an indirect effect of elevation on survival via BMR, however, received little support relative to models that assumed independence between elevation and BMR (Table 1). Body mass also had a strong significant effect on BMR ($\beta = 0.90$, 95% CI = 0.74 – 1.01 ; Figure 3d), and a weaker, nonsignificant effect on survival ($\beta = 0.48$, 95% CI = -0.25 to 1.08 ; Figure 3e). Estimates of Pagel's λ were low (-0.11) indicating that there was little effect of phylogeny on survival.

4 | DISCUSSION

We found that for a phylogenetically diverse group of Passerine birds representing 10 avian families, apparent survival was negatively related with BMR and elevation (Figure 3). This means birds with low BMR and living at low elevation showed the highest apparent annual survival, on average. Path models incorporating an indirect effect of elevation on apparent survival fitted the data poorly. Thus, although high-elevation birds had similar BMRs to those at low elevation, we found no clear benefit of living at higher elevation in terms of apparent survival. As expected, we also found a positive, allometric relationship between body mass, BMR and apparent annual survival. These results were unchanged when averaging effects over all path models, or when conducting path analyses ignoring phylogeny. Together, these observations suggest a functional link between BMR and survival in tropical birds, which exists independent of a species' elevational distribution, body mass or phylogenetic history.

BMRs used here were a subset of estimates for 253 species of tropical birds, which showed no association between BMR and elevation (Londoño et al., 2015). In contrast, high-elevation bird populations in temperate regions exhibited higher BMRs than birds in lowland populations (McNab, 2009). One reason BMR might vary with elevation is that thermoregulatory costs are thought to increase at high elevation due to lower temperatures. For example, avian BMR increased 50% over a 20°C decrease in temperature across latitudes (Jetz, Freckleton, & McKechnie, 2008). At our study area, daily mean temperature decreases by $\sim 0.55^\circ\text{C}$ for every 100 m increase in elevation (Rapp & Silman, 2012). Several reasons may account for the lack of relationship between elevation and BMR in the birds we studied. First, birds have adapted to cold climates largely independent of body mass via coordinated changes in BMR and thermal conductance (i.e. as the rate of heat gained from or lost to the environment; Fristoe et al., 2015). These physiological traits vary in a compensatory way; for example, although birds at Wayqecha ($>2,500$ m) expressed similar BMRs to those at Pantiacolla (<550 m), the former had reduced thermal conductance (i.e., better insulation) and lower body temperatures (Londoño et al., 2017), suggesting higher resistance to heat loss. More generally, physiological adaptations to high elevations may not be obvious in standard field measurements of tropical birds such as BMR (Londoño et al., 2015) or thermal tolerances (Freeman, 2015). Although BMR is the one of the most frequent and repeatable measures of energy expenditure,

TABLE 1 Results of the phylogenetic path analysis (PPA) where k is the number of linear models tested, q corresponds to the number of parameters estimated, and C is Fischer's C statistic. Hypothesized causal models are ranked according to a theoretical information criterion (CIC_C), ΔCIC_C is the difference in CIC_C values between models, and w_i is the model weight. Causal models are depicted in Figure 1

Model	K	Q	C	CIC_C	ΔCIC_C	w_i
H3	2	8	2.20	23.34	0.00	0.59
H6	1	9	0.75	25.42	2.07	0.21
H2	3	7	9.15	27.02	3.67	0.09
H1	3	7	10.51	28.37	5.03	0.05
H5	2	8	7.70	28.84	5.5	0.04
H4	2	8	9.06	30.20	6.85	0.02

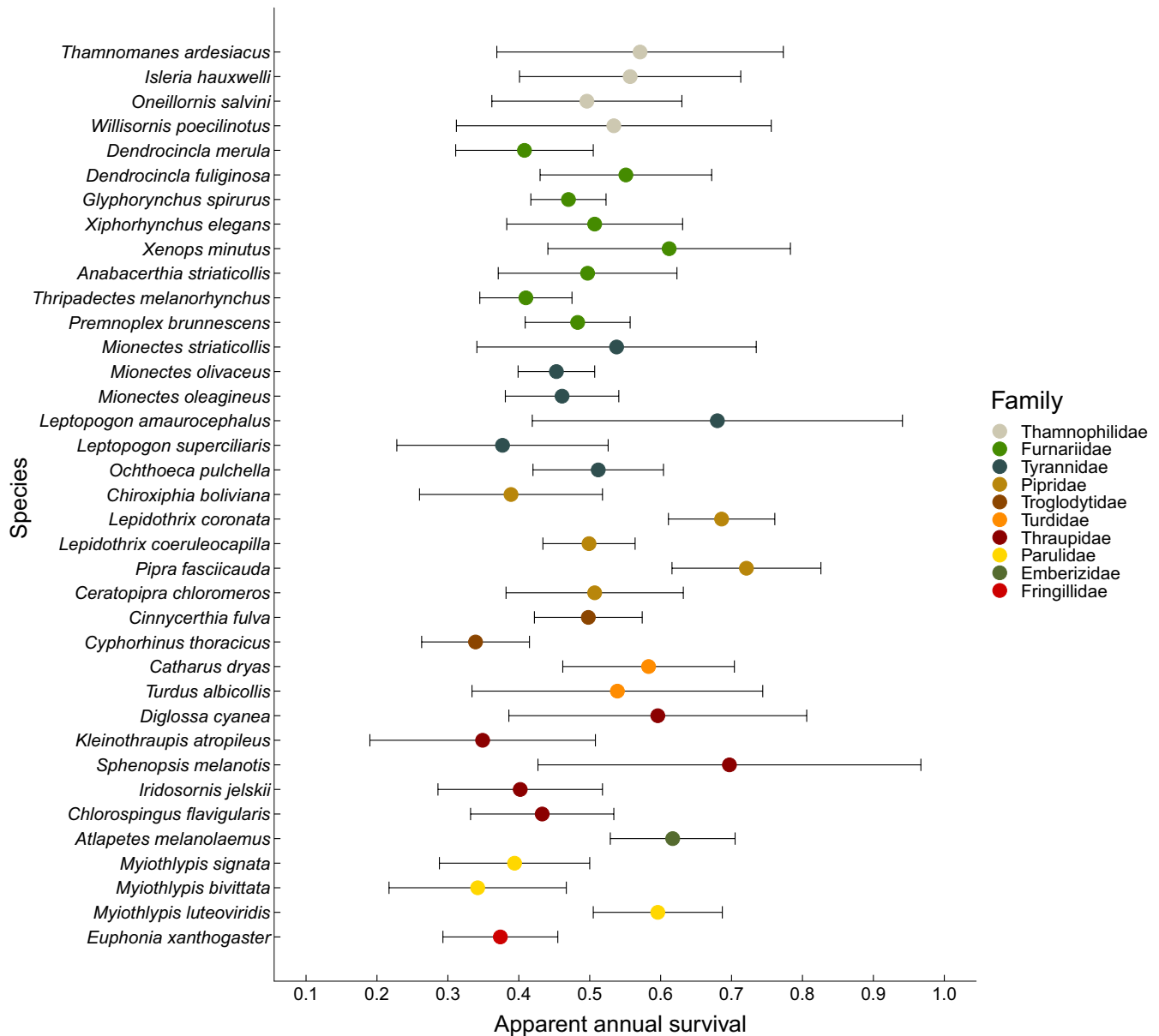


FIGURE 2 Apparent annual survival estimates and their associated standard errors for 37 species of tropical passerines from southeastern Peru

it accounts for only a portion of total energy used. Measures such as field metabolic rate (FMR) or thermogenic capacity may therefore better reflect energetic conditions experienced by birds daily (Daan et al., 1990). While BMR tends to covary positively with FMR (White & Seymour, 2004) and exercise-induced metabolism (Wiersma, Chappell, et al., 2007), it does so with high variability. Furthermore, measurements of FMR are particularly sparse for tropical birds (Anderson-Teixeira & Jetz, 2005) with only a handful (<5) available for birds from humid montane forests such as those found at our study sites.

Although we detected no indirect effect of elevation via BMR, apparent survival was lower for highland birds. This was unexpected as many avian predators such as raptors (Thiollay, 1996) and snakes (McCain, 2010) decline with elevation. Predation rates are an important driver of both juvenile and adult survival (Martin, 1995) and are

thought to be lower for birds living at higher elevations (Badyaev & Ghalambor, 2001; Jankowski, Londoño, Robinson, & Chappell, 2013). It is possible that low predation rates at high elevations are offset by higher adult mortality due to a harsher environment. For instance, male White-ruffed Manakins (*Corapipo altera*) at high elevations in Costa Rica exhibited greater physiological stress after major storms compared to lowland males (Boyle, 2008). As far as we are aware, no studies examining demographic processes and other characteristics of the physical environment known to covary with elevation, such as temperature, partial pressure of oxygen, wind and ultraviolet radiation, exist between high and low elevation populations of tropical birds. Some evidence of higher survival at high elevations is supported by case studies at north temperate latitudes (Badyaev, 1997; Bears, Martin, & White, 2009; Sandercock, Martin, & Hannon, 2005). However, in a review of intraspecific variation

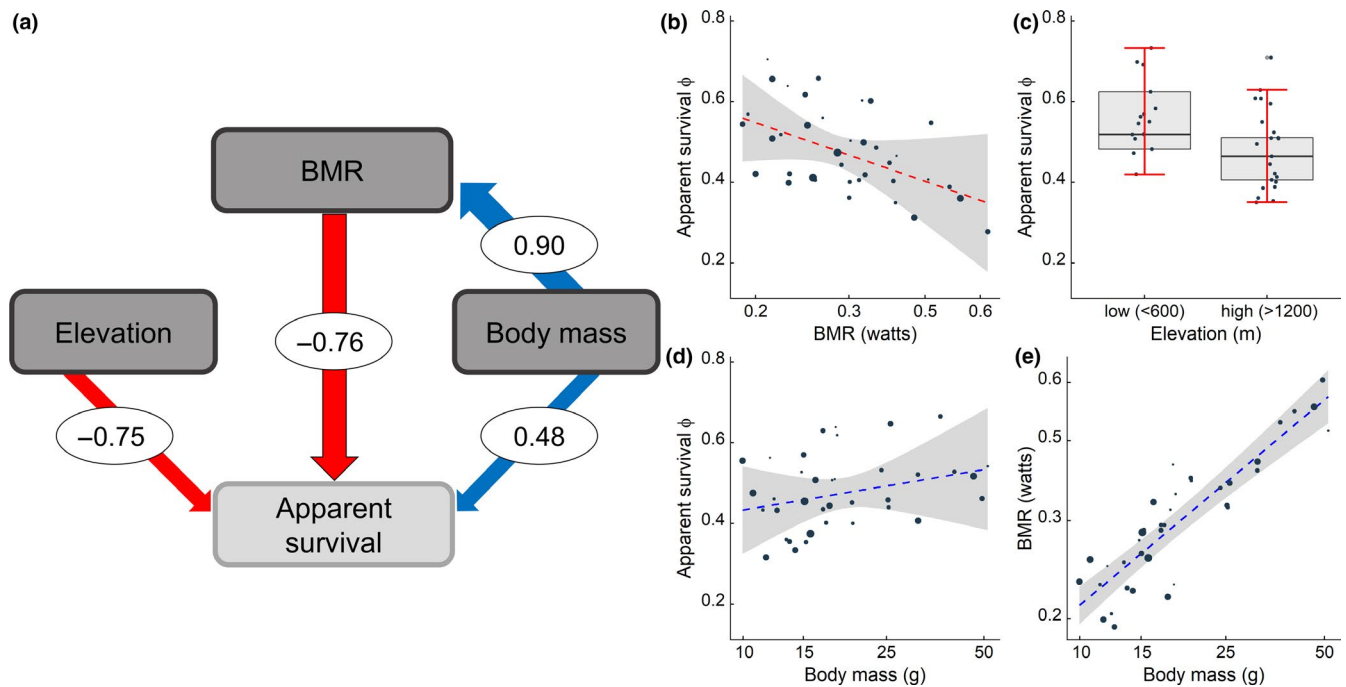


FIGURE 3 Best supported causal model from the phylogenetic path analysis (a). Arrows indicate the direction of the relationship between variables, arrow width indicates the strength of relationships, colors correspond to negative (red) or positive (blue) associations and values represent standardized regression coefficients. (b–e) Show the univariate linear relationships and associated 95% confidence intervals between survival and basal metabolic rate (BMR), the effect of elevation (coded as a binary variable) on survival, BMR and body mass and survival and body mass. Point sizes are drawn proportional to the inverse of their standard error

of life-history traits, Boyle et al. (2016) found that studies reporting higher versus lower survival for high-elevation birds were nearly equally represented in the literature—37% of comparisons showed a significant decrease in survival with elevation, whereas 42% showed increases. Overall, these contrasting results underline a species-specific variability of survival in response to environmental conditions that may differ depending on the geographic region and taxa considered.

For most tropical birds, survival estimates and other measures of life-history traits from the field remain unknown; a fact that has limited our ability to address critical questions regarding the evolution and association of life-history traits (but see Martin, 2015; Williams et al., 2010). Like other studies, our estimates of avian survival contain considerable uncertainty, but these survival probabilities remain the best estimates currently available for tropical birds (Williams et al., 2010). Studies reporting apparent annual survival for the same species of birds as our analysis were similar, and most showed overlapping confidence intervals (Figure S5) suggesting that our survival estimates are robust. Despite this, we found mean apparent survival of tropical birds was ~10% lower ($\phi = 0.50$, $SE = 0.10$) than values reported elsewhere from South America. Lower mean apparent survival may be explained by differences in survival rates between species captured above 1,000 m (mean $\phi = 0.46$, $SE = 0.08$) versus those at lower elevations (mean $\phi = 0.55$, $SE = 0.09$). For example, apparent survival was higher for most lowland species, compared to their closely related congeners occurring at higher elevations (e.g., *Leptopogon amaurocephalus* vs. *L. superciliosus*, *Mionectes oleagineus* vs. *M. olivaceus*, *Lepidothrix coronata* vs. *L. coeruleocapilla*; Figure 2 and Table S6), although this pattern did not always

hold (e.g., *M. striaticollis*). When considering apparent survival of lowland birds alone, mean survival from this study is similar to those from Brazil (Wolfe, Stouffer, & Seeholzer, 2014), Cocha Cashu, Peru (Francis, Terborgh, & Fitzpatrick, 1999), Ecuador (Blake & Loiselle, 2008) and French Guiana (Jullien & Clobert, 2000). Methodological differences including the size of study plots, netting effort per plot, as well as geographic variation in survival could also have contributed to the differences we observed. Comparisons of survival of high-elevation species were not possible with these other Neotropical datasets, which were conducted over a limited elevational range in lowland tropical forest.

Several caveats merit additional consideration when interpreting the biological significance of our results. First, there is a growing appreciation for the intraspecific variation in BMR due to phenotypic flexibility (McKechnie, 2008). Specifically, individuals may adjust BMR as a component of seasonal acclimatization, in response to breeding, or during migration (McKechnie, 2008). While variation in BMR is expected to be low for species living in more thermally stable climates (Pollock et al., 2019), such as the tropics, metabolic measurements of tropical birds from the rainy season are essentially unknown. In addition, significant geographic variation in BMR (Londoño et al., 2015) and survival (Wolfe et al., 2014) also exists and could lead to mismatches in physiological and life-history traits if drawn from populations experiencing different ecological conditions. While we were able to control for the latter of these possibilities, seasonal variation in BMR may have confounded our ability to detect its underlying relationship with survival. Second, variation in local movements of species with elevation could be an alternative explanation for the observed

variation in apparent survival. Low estimates of apparent survival for some species may have resulted from low site fidelity, particularly for frugivorous birds that often make wide-ranging movements in search of food (Martin & Karr, 1986), such as *Iridosornis jelskii* ($\varphi = 0.40$, $SE = 0.16$) and *Euphonia xanthogaster* ($\varphi = 0.37$, $SE = 0.11$). Another feature common to tropical birds that could lead to their permanent emigration is altitudinal migration. Although our understanding of the birds that undertake seasonal altitudinal movements is far from complete, >500 species of altitudinal migrants are currently described from the Neotropics, of which the majority are also frugivores (Barçante, Vale, & Alves, 2017; Merkord, 2010). For example, our estimate of apparent survival for *Chiroxiphia boliviana* ($\varphi = 0.39$, $SE = 0.16$), a frugivorous altitudinal migrant (Villegas, Newsome, & Blake, 2016), was between 28% and 85% lower than other sympatric manakin species. Finally, we note that in our study area Londoño et al. (2015) showed that non-passerines had BMRs about 12% lower than passerines, suggesting non-passerines should also express higher apparent survival than passerines on average. High apparent survival in the near-passerine *Galbula albirostris* (Piciformes) provides some support for this view (Wolfe et al., 2014), but additional empirical work will be needed to test whether negative relationships between BMR and apparent survival exist in avian species with dramatically different physiological and ecological life-history traits.

These caveats aside, our finding of a negative relationship between BMR and apparent annual survival in 37 species of tropical passerines provide evidence for the model of allocation trade-offs between slow-fast life histories. Our results support two main conclusions. First, BMR appears to be an intrinsic characteristic of the slow "pace-of-life" of Neotropical birds and may not be as closely linked to temperature at low latitudes, as has been demonstrated along temperate elevational gradients. Second, variation in "pace-of-life" in tropical montane species appears to be expressed as an elevational gradient in survival, but with BMR varying little between montane and lowland species. If true, this finding suggests that no suite of life-history traits is optimal for coping with the harsher abiotic factors found at high elevations of tropical mountains. One potential explanation for this pattern is that species inhabiting high elevations may be taxonomically younger than lowland species (Hawkins et al., 2012) and have not yet adapted physiologically to the local environment, or, alternatively, if higher extinction rates at high elevations preclude species from physiological adaptations. We emphasize a greater need for future studies measuring survival of tropical birds, especially those that provide information on high elevation and non-passerine species, to increase our ability to understand the fundamental question of why some species live long and others short lives.

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AUTHORS' CONTRIBUTIONS

M.N.S. conceived the ideas and designed methodology; M.N.S., G.A.L. and J.E.J. collected data on survival; G.A.L. and J.E.J. collected data on basal metabolic rate; M.N.S. and M.L.P. analysed the data; M.N.S. led the writing of the manuscript with input from the entire author team.

DATA ACCESSIBILITY

All data for this paper are available from Dryad Digital Repository <http://doi.org/10.5061/dryad.sf2gt4k> (Scholer, Arcese, Londoño, Puterman, & Jankowski, 2019).

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