

# Basal metabolism in tropical birds: latitude, altitude, and the ‘pace of life’

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## Summary

1. Life history varies across latitudes, with the ‘pace of life’ being ‘slower’ in tropical regions. Because life history is coupled to energy metabolism via allocation tradeoffs and links between performance capacity and energy use, low metabolic intensity is expected in tropical animals. Low metabolism has been reported for lowland tropical birds, but it is unclear if this is due to ‘slow’ life history or to a warm, stable environment.

2. We measured basal metabolic rates (BMR) of 253 bird species across a 2–6 km altitude gradient in Peru. We predicted higher BMR at high altitude due to lower temperatures leading to elevated thermoregulatory costs. We also tested for BMR differences between widely separated tropical regions (Peru and Panama), and between tropical- and temperate-breeding birds.

3. We found no effect of altitude on BMR in Peruvian species and no difference in BMR between Peruvian and Panamanian birds, suggesting that BMR in Neotropical birds is consistent and independent of environmental temperature. In a data set encompassing more than 500 species, tropical birds had significantly lower BMR than temperate-breeding birds.

4. In contrast to several recent analyses, we found higher BMR in passerine birds than in non-passerines, independent of breeding latitude.

5. Breeding latitude affects BMR, but diversity in avian life history within and between temperate and tropical regions may explain some of the residual variation in BMR after accounting for body mass and breeding latitude. Future studies of links between life history, metabolism and environmental factors might benefit from examining these variables within individual species as well as across broad geographic contrasts.

**Key-words:** allometry, Andes mountains, birds, BMR, body size, elevation, energy metabolism, life-history, temperature

## Introduction

Life histories are fitness-maximizing solutions to environmental challenges that evolve in response to numerous ecological factors, both abiotic (e.g. temperature, rainfall) and biotic (e.g. competition, predation, pathogens and parasites). Theory predicts that life history is largely driven by resource limitations and allocation tradeoffs (Roff 1992; Stearns 1992; Reznick 2014). This view stems from the assumption that food is limited (in acquisition or processing), and the largely mutually exclusive ways that animals can allocate energy: for maintenance (resting and activity

metabolism, immunity), somatic growth or reproduction. These constraints, coupled with selection imposed by expected longevity on the urgency of reproduction, should generate a ‘slow-fast’ continuum of life histories ranging from long-lived species that invest heavily in maintenance but relatively little in fecundity to short-lived species that invest little in self-maintenance and produce numerous rapidly-growing offspring.

In addition to extrinsic ecological influences, life history is inescapably dependent on intrinsic organismal properties (physiology). The ‘slow-fast’ continuum is coupled to energy metabolism via allocation tradeoffs and by linkages between organismal performance and the physiological

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systems that support it (Ricklefs & Wikelski 2002; Williams *et al.* 2010). For example, high rates of offspring production require high rates of resource acquisition and hence intense foraging and rapid food processing; in turn, these require costly high-capacity musculoskeletal, cardio-respiratory and digestive systems. The flux of energy through the animal, sometimes called the 'rate of living' (Pearl 1928) or the 'pace of life' (Ricklefs & Wikelski 2002), is expected to be high at the 'fast' end of the life-history continuum and low at the 'slow' end. These predictions have been tested, with varying support, in species ranging from nematodes (Van Voorheis & Ward 1999) to mammals (Speakman *et al.* 2002; White & Seymour 2004).

Contrasts in the 'pace of life' between temperate and tropical birds are of special interest (we use latitude as a proxy for major environmental characteristics: e.g. the tropics have stable, warm temperatures, low seasonality and high biotic diversity). Compared to temperate birds, tropical birds – particularly those from humid forests – are thought to have 'slow' life histories: small clutches (Moreau 1944; Kulesza 1990), slow nestling growth and maturation (Ricklefs 1976; Russell, Yom-Tov & Geffen 2004; Schaefer *et al.* 2004; Martin *et al.* 2011) and low adult mortality (Fogden 1972; Snow & Lill 1974; Francis, Terborgh & Fitzpatrick 1999; Gill & Haggerty 2012). Tropical birds tend to be sedentary whereas many temperate breeders migrate over long distances, a behaviour requiring massive use of energy (Jetz, Freckleton & McKechnie 2008). Accordingly, if life history predicts the energetic 'pace of life', then tropical birds should have lower metabolic rates than temperate birds.

Early work on tropical bird energetics was ambivalent, with low metabolic rates reported in some species (Weathers 1979; Hails 1983; Tieleman *et al.* 2006) but not others (Scholander *et al.* 1950; Bennett & Harvey 1987; Vleck & Vleck 1979). Two recent studies support the 'pace of life' hypothesis. Wikelski *et al.* (2003) found lower resting metabolic rates in a tropical population of stonechats (*Saxicola torquata*) than in stonechats native to temperate areas (but see Tieleman 2007). An interspecific comparison of lowland tropical birds and north-temperate breeders found lower basal metabolic rate (BMR) and lower maximal metabolism during exercise and thermogenesis in tropical species (Wiersma, Chappell & Williams 2007; Wiersma *et al.* 2007). The low limits may be functionally related to small visceral organs (Wiersma, Nowak & Williams 2012) and differences at the cellular and subcellular levels (Jimenez *et al.* 2014). These authors interpreted low metabolic rates as manifestations of a 'slow' life history. However, the limited set of tropical species (primarily from lowland rain forest in Panama) does not rule out other explanations. For example, low metabolic rates might result from residence in a benign tropical climate (White *et al.* 2007; Wiersma, Chappell & Williams 2007; Jetz, Freckleton & McKechnie 2008).

Comparisons of bird species from adjacent habitats with stable but contrasting thermal regimes, such as along

tropical altitude gradients, could offer insights into relationships between environment, life history and energy metabolism. We used BMR from a large sample of forest birds inhabiting a 2–6 km altitude gradient in south-eastern Peru to address four questions. First, we tested if differences in native altitude influenced BMR. Low ambient temperatures at high altitude should increase costs of thermoregulation and result in higher BMR according to the 'pace of life' hypothesis (higher maintenance costs and possible cold acclimatization; Cooper & Swanson 1994; McKechnie & Swanson 2010). Secondly, we asked if the low BMR of Panamanian birds is also characteristic of geographically distant Peruvian species, as expected if the tropical environment *per se* is important in determining BMR. Thirdly, we combined our results with published data to test whether BMR is lower in tropical birds than in temperate birds, another 'pace of life' prediction that to date has been confirmed for Panamanian lowland forest species. Finally, we used this large data set to explore a long-standing question in avian ecological and evolutionary physiology: whether BMR differs between passerines and non-passerines. We used both conventional and phylogenetically informed statistics, and this is the first major analysis of avian BMR based on the Hackett *et al.* (2008) phylogenetic tree rather than that of Sibley, Ahlquist & Monroe (1988). Given the many differences between the two phylogenies, our results have implications for understanding how BMR varies across avian orders, as well as how it is influenced by latitude and altitude.

## Materials and methods

### FIELD SITES

We worked at three field stations in south-eastern Peru. Two are in steep mountain terrain along the south-eastern edge of Parque Nacional del Manu. Wayqecha (altitude 2550–3200 m; 13°10'S, 71°35'W) is in cloud forest near tree line. San Pedro (1300–1600 m; 13°03'S, 71°32'W) spans montane rain forest and lower cloud forest (Jankowski *et al.* 2013). Pantiacolla (380–500 m; 12°39' S, 71°13'W) is in lowland rain forest. The stations are roughly aligned along a 70 km northeast–southwest axis. Annual temperature means ranged from 11.2 °C (Wayqecha) to 23.2 °C (Pantiacolla), and for all stations, monthly means differed by 3 °C or less (Table S1, Supporting information).

### BIRD CAPTURE AND HANDLING

We measured metabolism between July and December 2011–2013. Birds were mist-netted in the afternoon (15:00–17:00 h local time); individuals with brood patches or other indications of active reproduction were released. Non-reproductive birds were held in cloth-covered cages in quiet rooms and provided with water but not food (except for hummingbirds, which were given 25% sugar water). After sunset (*c.* 19:00 h), birds were weighed ( $\pm 0.05$  g for birds <125 g; FlipScale F2, www.myweigh.com/pocket/;  $\pm 0.5$  g for larger species; Pesola 300 g spring scale; Baar, Switzerland) and placed in the respirometry system. Measurements of BMR began several hours later, usually after 23:00 h, to ensure that birds were postabsorptive. All birds (except hummingbirds) had been fasting for at least 4–5 h prior to BMR measurements. Fast

duration in hummingbirds was > 2 h, sufficient for absorption of sugar (Karasov *et al.* 1986). All individuals were tested for BMR at 30 °C and most were also tested at 32–34 °C; in addition, we measured metabolism at 10 and 20 °C for nearly all individuals. Body temperature ( $T_b$ ) was obtained immediately after BMR measurements using fine-gauge thermistors inserted at least 5–10 mm into the cloaca. After the conclusion of measurements, birds were reweighed and the mean of initial and final weights was used as body mass. Birds were released the following morning at the site of capture.

In addition to Peruvian species, we report BMR measured in the laboratory of one of the authors (M.A. Chappell) at the University of California, Riverside ('UCR' data set). Specimens were wild-caught or captive-bred; all were housed in large outdoor flight cages.

Capture and handling procedures were approved by the Institutional Animal Care and Use Committees at the University of California, Riverside (protocol # 0408026, 20070023, 20100048) and the University of Florida (Protocol #: 201106068), and by permits from the government of Peru (0239-2013 MINAGRI-DGFFS/DGEFFS 2013).

## RESPIROMETRY

We measured energy metabolism as rates of oxygen consumption ( $\dot{V}O_2$ ) with open-circuit respirometry (identical equipment and procedures were used at all stations). Air flow (supplied with aquarium pumps) was dried with silica gel and divided among four metered channels (FlowBar; Sable Systems, Las Vegas, NV, USA) calibrated with a mass flow controller (Sensirion 4200, Stafa, Switzerland) verified against a dry volume meter (DTM115; Singer American, Stanford, CN, USA; Stromme & Hammel 1968). One channel was used for reference air; each of the others could supply continuous flow to a metabolism chamber, and we usually measured three birds per night. Chambers were constructed from opaque airtight plastic and equipped with thermistors to measure ambient temperature ( $T_a$ ). We matched chamber volume (1, 2, or 4 L) and airflow (200–1200 mL min<sup>-1</sup> STPD) to the size of tested birds, with larger chambers and higher flows used for larger species. Excurrent air was routed through a multiplexer (Sable Systems RM-8) that selected one flow at a time for analysis. The selected flow was subsampled (50–100 mL min<sup>-1</sup>) at constant pressure, scrubbed of CO<sub>2</sub> and water vapour (soda lime and silica gel) and analysed for O<sub>2</sub> content with a Sable Systems FoxBox. Flow rate,  $T_a$  and O<sub>2</sub> content were recorded every 1 s (Sable Systems ExpeData or Warthog LabHelper; www.warthog.ucr.edu). The system monitored each bird for 15 min, switched to reference air for 2.5 min, then switched to the next bird in sequence. Accordingly, the fraction of time each bird's metabolism was monitored was 29% if three birds were being measured, 43% if two birds were measured, and 86% for single birds. Airflows were sufficient to keep O<sub>2</sub> concentrations above 20.4%; subsampled air attained steady-state values within 1–2 min after switching from reference readings to chamber air. Chamber  $T_a$  was maintained  $\pm 0.5$  °C with PELT-5 controllers and PTC-1 cabinets (Sable Systems). Data were baseline-corrected and converted to  $\dot{V}O_2$  (mL O<sub>2</sub> min<sup>-1</sup>) with LabAnalyst (www.warthog.ucr.edu) using the 'Mode 1' formula:

$$\dot{V}O_2 = \dot{V}(FiO_2 - FeO_2)/(1 - FeO_2)$$

where  $\dot{V}$  is flow rate (mL min<sup>-1</sup> STPD),  $FiO_2$  is incurrent fractional oxygen concentration (0.2095), and  $FeO_2$  is excurrent fractional oxygen concentration. BMR was calculated as the lowest continuous average  $\dot{V}O_2$  over at least 2 min (usually 5 min) during periods when  $\dot{V}O_2$  was low and stable and birds had been at constant  $T_a$  for at least

1 h. We rejected data from birds that did not become quiescent or had  $T_b < 35.0$  °C. For birds tested at both 30 and at 32–34 °C, we used the lowest of the two metabolic rates as BMR. In a few cases, the lowest  $\dot{V}O_2$  occurred at 20 °C and we used that value as BMR. We converted  $\dot{V}O_2$  to watts using a coefficient of 19.8 Joules mL<sup>-1</sup> O<sub>2</sub> (Gessaman & Nagy 1988).

Procedures for UCR data were similar, except for the use of a different oxygen analyzer (S-3A; Applied Electrochemistry, Sunnyvale, CA, USA) and flow controllers (Applied Materials or Tylan). Only one bird was tested per night, with baseline readings every 42–45 min.

## ANALYSES AND STATISTICS

We log<sub>10</sub>-transformed species means of body mass and BMR to account for nonlinear metabolic scaling. Several Peruvian species were captured at two stations; none were captured at three. For species with multiple captures at one station and a single capture at another ( $N = 7$ ), the single value was discarded. For species with multiple captures at two stations (four tropical, one temperate migrant), we computed means for each station; no species showed between-station differences in BMR ( $P > 0.10$ ). Because many species were represented by single individuals, we tested for sample size effects by performing duplicate analyses, one including all species and a second that excluded species with single measurements. Results of duplicate analyses were qualitatively identical and quantitatively similar. Accordingly, we present results for the entire data set only.

To compare between two Neotropical sites (Peru and Panama), and between tropical and temperate-breeding birds, we combined our measurements with data from three other studies (McKechnie & Wolf 2004; White *et al.* 2007; Wiersma *et al.* 2007). McKechnie & Wolf (2004) did not specify latitude and White *et al.* (2007) did not specify breeding habitats, so we categorized species from these studies from published distribution data. Multiple measurements were available for several species. Our conventional analyses included all independently-measured BMR. For phylogenetic statistics, species were represented once and we handled replicate measurements as follows. For species with more than one literature value, we used the first-published datum. For Peruvian species also represented in the literature, we used our data (in all such cases we measured more individuals). The pooled data (534 measurements of 176 temperate and 350 tropical species) include several species that breed in both temperate and tropical regions, and some tropical species inhabiting climatically variable regions such as deserts or seasonal grasslands. To emphasize possible contrasts in BMR between cool, variable temperate climates and warm, stable tropical climates, we analysed a subset of 496 measurements of 488 species that, to our knowledge, breed exclusively in either temperate regions or humid tropical forests.

Because there is uncertainty over differences in BMR among avian lineages (Lasiewski & Dawson 1967; Reynolds & Lee 1996; McKechnie & Wolf 2004), we used our pooled data set to test for differences in BMR among major avian groups.

We compared BMR with ordinary least squares analysis of covariance (OLS ANCOVA) where altitude (Peru species only) and breeding latitude were fixed factors and body mass was the covariate. To account for potential sampling bias or methodological differences, we also included the data source. These analyses were performed with JMP 10 (SAS Institute, Cary, NC, USA).

Equivalent tests were performed within a phylogenetic context using a phylogeny derived from the avian 'tree of life' (Jetz *et al.* 2012), using Hackett *et al.* (2008) as a backbone. We downloaded 5000 randomly-selected topologies that included all species in our data set (<http://birdtree.org/>; Hackett backbone, 'genetic data

only' trees), and computed a maximum clade credibility consensus (MCC) tree (TREEANNOTATOR v. 1.8.0; Drummond & Rambaut 2007). Subsequent calculations were performed using the MCC tree as a point estimate, and the entire sample of 5000 trees was used to evaluate how accurately the consensus tree represented the entire distribution (Tables S2, S3).

Forty-four species lacked molecular data. For tree construction, we substituted molecular data from a congener for 37 of these (Table S4); the rest were excluded from phylogenetic analyses. For Peruvian species with data from two altitudes, we removed data from the elevation with the lowest sample size for phylogenetic analysis (Table S3). Tree structures and raw data are available in <http://datadryad.org>.

Phylogenetic tests were performed in R (R Core Team 2013). To justify use of phylogenetically informed regressions, we computed Pagel's  $\lambda$  (Pagel 1999) to estimate phylogenetic signal in BMR, body mass and residuals of regressions between BMR and mass ('phytools' package; Revell 2010, 2012). We used phylogenetic independent contrasts (Felsenstein 1985; Garland *et al.* 1992) to estimate correlations between BMR and body mass ('ape' package; Paradis, Claude & Strimmer 2004). We performed phylogenetic generalized least squares (PGLS) to examine relationships of BMR with body mass, altitude, breeding latitude and data set ('nlme' package; Pinheiro *et al.* 2013). For PGLS, we compared five models of evolution (Table S5): Brownian Motion, Grafen (1989), Pagel (1999), Accelerated/Decelerated (Blomberg, Garland & Ives 2003), and Ornstein-Uhlenbeck (Martins & Hansen 1997). According to akaike information criterion tests ('qpcR' package; Ritz & Spiess 2008), Pagel's model best fit our data, indicating that the traits in question are best described as having evolved in a directional manner in which patterns of similarity reflect shared evolutionary histories (Pagel 1999). We used this model for all PGLS analyses (Table S5).

## Results

We measured BMR in 253 species of tropical breeders from Peru, and three species of temperate North American breeders wintering in Peru (Table S4). The body mass ( $M_b$ ) range was 2.77–322.4 g; mass distributions were similar at the three stations (Fig. 1). The mean number of individuals sampled per species was  $5.1 \pm 6.7$  (range = 1–41). The UCR data (Table S4) included BMR from 185 individuals of 27 species of tropical- and temperate-breeding birds ( $M_b$  range 13.8–1140 g).

In all comparisons, strong phylogenetic signal was present in  $M_b$ , BMR and the regression residuals ( $\lambda = 0.73$ – $1.00$ ,  $P < 0.0001$ ).

### ALTITUDE

Ordinary least squares analysis of covariance (OLS ANCOVA;  $N = 253$  species, three of which had data from two altitudes) showed no significant effect of altitude on BMR ( $F_{2,250} = 1.80$ ,  $P = 0.17$ ). BMR was highly correlated with  $M_b$ , but there was an altitude  $\times M_b$  interaction ( $F_{2,250} = 7.0$ ,  $P = 0.0011$ ): highland natives had a larger mass exponent than low- and mid-altitude species, but had lower BMR at small  $M_b$  (Fig. 2). The overall relationship between  $M_b$  and BMR (watts) was  $BMR = 0.056 \times M_b^{0.551 \pm 0.017 SE}$  ( $r^2 = 0.80$ ,  $t = 32.3$ ,  $P < 0.0001$ ).

The data set for phylogenetic analyses was reduced to 227 species, but PGLS results were similar: BMR was not

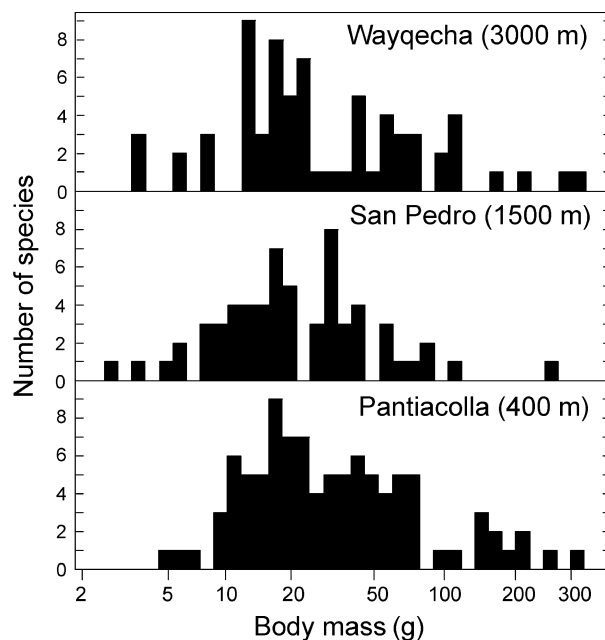


Fig. 1. Body mass of birds at three field sites in south-eastern Peru along a 2.6 km altitude gradient encompassing lowland forest (400 m;  $N = 97$ ), cloud forest (1500 m;  $N = 63$ ) and highland forest (3000 m;  $N = 70$ ).

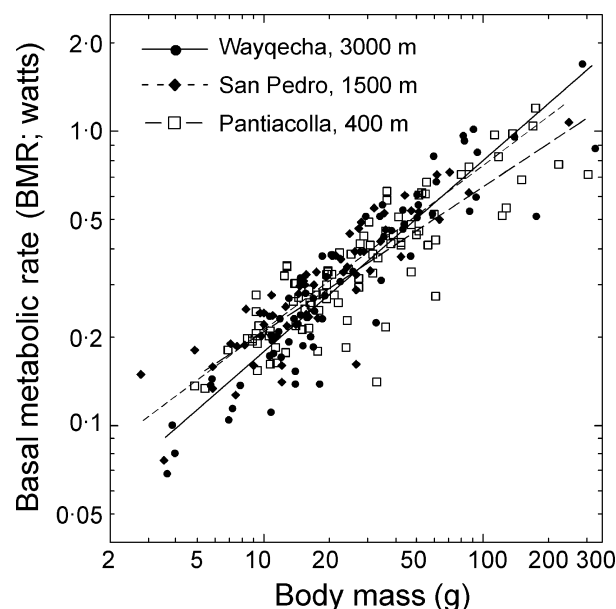


Fig. 2. Basal metabolic rates (BMR) of birds inhabiting a 2.6 km altitude gradient encompassing lowland forest (400 m;  $N = 97$ ), cloud forest (1500 m;  $N = 63$ ) and highland forest (3000 m;  $N = 70$ ) in south-eastern Peru. OLS ANCOVA (shown here) and phylogenetic generalized least squares (PGLS) revealed strong correlations with body mass, but no difference among altitudes ( $P > 0.09$ ).

affected by altitude ( $F_{2,221} = 0.02$ ,  $P = 0.98$ ), but there was a significant  $M_b \times$  altitude interaction ( $F_{2,221} = 5.07$ ,  $P = 0.007$ ). BMR was highly correlated with  $M_b$ , and the overall equation for BMR (watts) was  $BMR = 0.052 \times M_b^{0.543 \pm 0.026 SE}$  ( $r^2 = 0.74$ ;  $P < 0.0001$ ).



## PERU VS. PANAMA

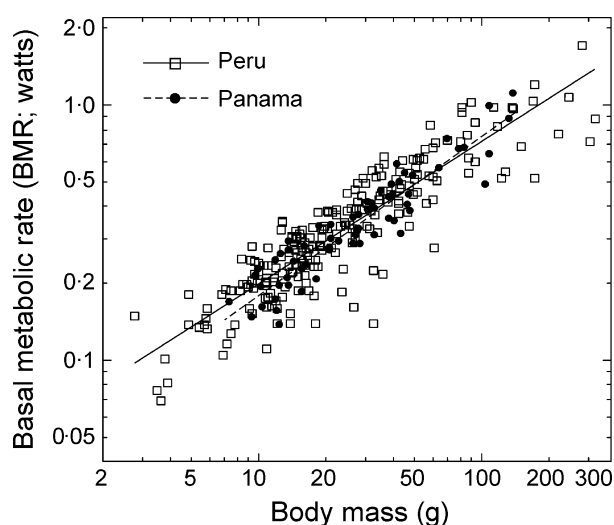
OLS ANCOVA revealed no difference in BMR between 64 Panamanian lowland forest species reported by Wiersma *et al.* (2007) and 253 Peruvian birds ( $F_{1,316} = 0.43$ ,  $P = 0.56$ ; Fig. 3). Thirteen species occurred in both locations; these were included in the analyses as independent measurements. There was no  $M_b \times$  data set interaction ( $P = 0.18$ ). The combined regression was  $\text{BMR (watts)} = 0.055 \times M_b^{0.558 \pm 0.015 \text{ SE}}$  ( $r^2 = 0.81$ ,  $P < 0.0001$ ).

PGLS analysis (278 species) also found no difference between Peruvian and Panamanian species ( $F_{1,274} = 1.81$ ,  $P = 0.18$ ), a strong effect of  $M_b$  on BMR ( $F_{1,274} = 629$ ,  $P < 0.0001$ ), and a marginally significant  $M_b \times$  data set interaction ( $P = 0.052$ ). The combined equation was  $\text{BMR (watts)} = 0.050 \times M_b^{0.557 \pm 0.012 \text{ SE}}$  ( $r^2 = 0.75$ ;  $P < 0.0001$ ).

## TROPICAL VS. TEMPERATE SPECIES

OLS ANCOVA (534 measurements of 350 tropical and 176 temperate species) showed a significant effect of breeding latitude, with the BMR of temperate breeders averaging 14.1% higher than that of tropical species ( $F_{1,533} = 16.0$ ,  $P < 0.0001$ ). However, there was an  $M_b \times$  breeding latitude interaction ( $F_{1,533} = 28.7$ ,  $P < 0.0001$ ) and data set was a significant factor ( $F_{4,526} = 12.9$ ,  $P < 0.0001$ ), with BMR in the McKechnie & Wolf (2004) and UCR data sets averaging lower than the other data sets after correction for  $M_b$  and latitude. BMR scaled in proportion to  $M_b^{0.636 \pm 0.010 \text{ SE}}$  (overall  $r^2 = 0.92$ ,  $P < 0.0001$ ).

Exclusion of species with ambiguous distributions reduced sample size to 496 measurements of 488 species (331 tropical, 157 temperate) and removed the ostrich (*Struthio camelus*), by far the largest species. Nevertheless,



**Fig. 3.** Basal metabolic rate (BMR) of tropical forest birds from Peru ( $N = 227$ ) and Panama ( $N = 64$ ; Wiersma *et al.* 2007). OLS ANCOVA (shown here) and phylogenetic generalized least squares (PGLS) showed no difference in BMR between the two regions ( $P > 0.18$ ).

results were similar. There was an effect of breeding latitude, with BMR of temperate breeders averaging 16.4% higher than that of tropical species ( $F_{1,495} = 18.6$ ,  $P < 0.0001$ ), and an  $M_b \times$  breeding latitude interaction ( $F_{1,495} = 32.1$ ,  $P < 0.0001$ ). Data set was a significant factor ( $F_{4,488} = 8.8$ ,  $P < 0.0001$ ), with lower BMR in the McKechnie & Wolf (2004) and UCR data sets. Overall, BMR scaled in proportion to  $M_b^{0.625 \pm 0.0096 \text{ SE}}$  ( $r^2 = 0.92$ ,  $P < 0.0001$ ).

Results from phylogenetic analyses were broadly similar: there was an effect of breeding latitude on BMR ( $F_{1,477} = 15.8$ ,  $P = 0.0001$ ) and interactions between  $M_b$  and both breeding latitude ( $F_{1,477} = 20.8$ ,  $P < 0.0001$ ) and data set ( $F_{4,477} = 6.06$ ,  $P = 0.0001$ ). PGLS indicated that BMR was strongly affected by  $M_b$  ( $F_{1,477} = 2176$ ,  $P < 0.0001$ ), but not by data set ( $F_{4,477} = 1.01$ ,  $P = 0.41$ ). For tropical species,  $\text{BMR (watts)} = 0.031 \times M_b^{0.665 \pm 0.0245 \text{ SE}}$  ( $r^2 = 0.797$ ,  $P < 0.0001$ ); for temperate-breeding species,  $\text{BMR (watts)} = 0.023 \times M_b^{0.731 \pm 0.018 \text{ SE}}$  ( $r^2 = 0.875$ ,  $P < 0.0001$ ).

PGLS results were qualitatively identical when species with ambiguous distributions were excluded. There was an effect of breeding latitude on BMR ( $F_{1,457} = 25.5$ ,  $P < 0.0001$ ), no effect of data set ( $F_{4,457} = 1.91$ ,  $P = 0.11$ ), and interactions between  $M_b$  and both breeding latitude ( $F_{1,457} = 24.8$ ,  $P < 0.0001$ ) and data set ( $F_{4,457} = 5.20$ ,  $P = 0.0004$ ). For tropical species,  $\text{BMR (watts)} = 0.044 \times M_b^{0.589 \pm 0.0214 \text{ SE}}$  ( $r^2 = 0.745$ ,  $P < 0.0001$ ); for temperate-breeding species,  $\text{BMR (watts)} = 0.023 \times M_b^{0.729 \pm 0.0221 \text{ SE}}$  ( $r^2 = 0.867$ ,  $P < 0.0001$ ).

## COMPARISONS AMONG ORDERS

In contrast with recent reports (McKechnie & Wolf 2004; White *et al.* 2007), phylogenetic analyses indicated that BMRs of passerine birds are higher than those of non-passerines ( $F_{1,485} = 54.6$ ,  $P < 0.0001$ ), but with an order  $\times M_b$  interaction ( $F_{1,485} = 5.9$ ,  $P = 0.02$ ). Passerine  $\text{BMR (watts)} = 0.0448 \times M_b^{0.627 \pm 0.0228 \text{ SE}}$  ( $r^2 = 0.719$ ;  $P < 0.0001$ ); for non-passerines,  $\text{BMR (watts)} = 0.025 \times M_b^{0.701 \pm 0.0228 \text{ SE}}$  ( $r^2 = 0.88$ ;  $P < 0.0001$ ). OLS results were similar, except that there was no order  $\times M_b$  interaction ( $P = 0.84$ ):  $\text{BMR scaled to } a \times M_b^{0.644 \pm 0.0098 \text{ SE}}$ , where the mass coefficient  $a = 0.0401$  for passerines and 0.0378 for non-passerines (i.e. passerine BMR averaged 12.2% higher than that of non-passerines;  $F_{1,533} = 15.6$ ,  $P < 0.0001$ ).

Because hummingbirds may have different metabolic constraints than other non-passerine orders, they could have a disproportionate influence on contrasts between passerines and non-passerines. Our data contained 34 Apodiformes (32 hummingbirds and two swifts; 2.8–44.9 g). Accordingly, we tested for differences in BMR between Apodiformes, Passeriformes and the pooled data from other non-passerine orders. PGLS revealed differences among these groups ( $F_{2,483} = 70.0$ ,  $P < 0.0001$ ), and an order  $\times M_b$  interaction ( $F_{2,483} = 6.1$ ,  $P = 0.003$ ). BMR differed between Apodiformes

and Passeriformes ( $P < 0.0001$ ), Apodiformes and non-passerines ( $P < 0.0001$ ), and non-passerines and Passeriformes ( $P < 0.0001$ ). For Passeriformes, BMR (watts) =  $0.045 \times M_b^{0.627 \pm 0.0228 SE}$  ( $r^2 = 0.719$ ;  $P < 0.0001$ ); for Apodiformes, BMR (watts) =  $0.067 \times M_b^{0.450 \pm 0.140 SE}$  ( $r^2 = 0.554$ ;  $P = 0.0033$ ); for other non-passerine orders, BMR (watts) =  $0.021 \times M_b^{0.724 \pm 0.0243 SE}$  ( $r^2 = 0.89$ ;  $P < 0.0001$ ).

## Discussion

Our latitudinal comparison supports the 'slow pace of life' concept for tropical species (Ricklefs & Wikelski 2002), as we found lower BMR in tropical-breeding birds compared to temperate-breeding birds. Contrary to predictions based on thermoregulatory costs, the BMR of Peruvian forest birds did not differ across a 2.6 km altitude gradient. We found no BMR differences between Neotropical birds from Peru and Panama (Wiersma *et al.* 2007), even though the sites are separated by 2500 km and are in opposite hemispheres. Together, these findings indicate consistently 'slow' energy metabolism in tropical birds across broad geographical regions and a wide range of altitudes (and therefore temperatures).

Two caveats must be kept in mind when considering the biological significance of these findings. First, BMR is easily and frequently measured, but it includes only a fraction of an endotherm's total energy expenditures; moreover, it probably has minimal ecological importance as it encompasses none of the costs of growth, activity, thermoregulation, reproduction or other critical life-history traits. Nevertheless, BMR is often used as a proxy for metabolic intensity. Several studies found positive correlations between BMR and maximal metabolism in exercise or thermogenesis (Dutenhoffer & Swanson 1996; Chappell, Bech & Buttemer 1999; Wiersma, Chappell & Williams 2007) although others have not (Hammond *et al.* 2000). Daily energy expenditures or field metabolic rates (FMR) – the most direct measure of the metabolic 'pace of life' – often covary with BMR or resting metabolism, albeit with considerable variance (Daan *et al.* 1991; Ricklefs, Konarzewski & Daan 1996; White & Seymour 2004). The association of avian FMR with latitude is not clear: FMR does tend to increase at high latitudes as predicted by the 'pace of life' concept, but variation is large, particularly in the tropics (Anderson & Jetz 2005). That may be due in part to the paucity of FMR from tropical birds (<15 species) and particularly of FMR from species inhabiting humid forests (4–5, Anderson & Jetz 2005). In one comparison, the FMR of breeding house wrens (*Troglodytes aedon*) was lower in tropical Panama than in temperate Ohio (Tieleman *et al.* 2006).

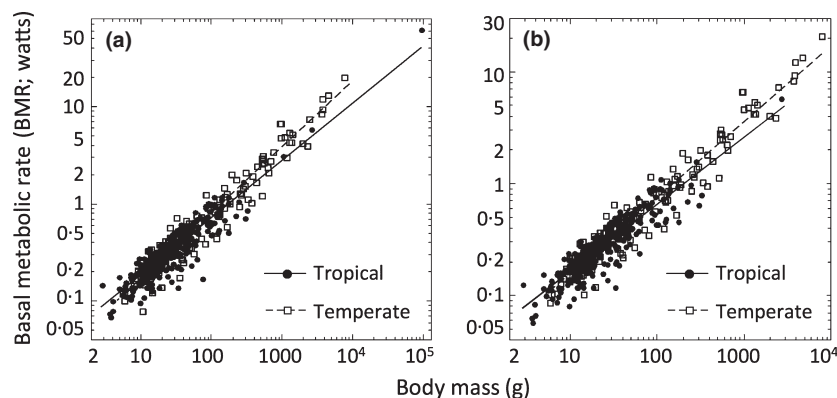
The second caveat is that like most authors of comparative studies of energy metabolism, we interpret between-group contrasts as heritable products of evolutionary change. However, we cannot be sure that differences are not manifestations of phenotypic plasticity in response to dissimilar environmental conditions, which are well known

in birds (Piersma *et al.* 1996; Kvist & Lindstrom 2001; McKechnie 2008; McKechnie & Swanson 2010). Rigorous demonstration of a genetic basis of between-group variation requires a level of experimental control (e.g. 'common garden' breeding) beyond the scope of most large comparative studies, including this one.

Those caveats aside, why, from a mechanistic perspective, might BMR be low in tropical birds? Some authors (Wikelski *et al.* 2003; Wiersma, Chappell & Williams 2007; Wiersma *et al.* 2007) interpret low metabolic rates of tropical birds as by-products of their 'slow' life histories. Tropical environments with intense competition and predation should favour reduced fecundity. As the maximal sustained metabolic rates in birds (other than migration flights) are assumed to occur during breeding as a consequence of high requirements for parental care (Drent & Daan 1980), small, slow-growing broods should reduce parental workloads. Because BMR derives mainly from the metabolism of visceral organs that are 'scaled' to maximal power production (Daan, Masman & Groenewold 1990; Piersma *et al.* 1996; Chappell, Bech & Buttemer 1999), reduced peak energy demands should permit reductions in organ size and hence BMR. This hypothesis is consistent with a recent study showing that low BMR in tropical birds from Panama is accompanied by reduced organ and skeletal muscle masses (Wiersma, Nowak & Williams 2012).

The findings of Wiersma, Chappell & Williams (2007) and Wiersma *et al.* (2007) support the 'slow life history' concept, but the geographically limited set of tropical species, mostly from a single habitat (lowland rain forest in Panama) does not rule out other explanations. For example, low BMR could be due to residence in a warm, stable climate that does not require high activity or thermoregulatory capacity (Anderson & Jetz 2005; Wiersma, Nowak & Williams 2012). Also, many high latitude breeders migrate over long distances (Jetz, Freckleton & McKechnie 2008), which requires massive energy turnover both during migration and in preparation for it (e.g. Kersten & Piersma 1987). In this alternate scenario, reduced demands for aerobic power output (thermogenesis, long-distance flight) in benign tropical habitats – not 'slow' life history – has led to lower capacities of muscle and visceral organs and hence low BMR. This model does not require or derive from differences in reproductive investment and related life-history traits and is consistent with two analyses showing negative associations between avian BMR and environmental temperature (White *et al.* 2007; Jetz, Freckleton & McKechnie 2008). It is also analogous to shifts in energy metabolism in cold acclimatization, which elicits elevated BMR as well as thermogenic capacity (Cooper & Swanson 1994; Liknes, Scott & Swanson 2002; McKechnie & Swanson 2010).

Peruvian birds provide a test of these two hypotheses. All our field sites have stable environmental temperatures, but the high-altitude site (Wayqecha) averages 12 °C colder than the lowland site (Pantiacolla; Table S1) and



**Fig. 4.** Basal metabolic rate (BMR) of tropical- and temperate-breeding bird species. Data were obtained from McKechnie & Wolf (2004), White *et al.* (2007), Wiersma *et al.* (2007) and new measurements (Peru and UCR data sets). Duplicate analyses were performed for the entire data set (a, 491 species) and with species with ambiguous breeding distributions deleted (b, 457 species). OLS ANCOVA (shown here) and phylogenetic generalized least squares (PGLS) revealed strong correlations with body mass, a mass  $\times$  breeding habitat interaction, differences among data sets, and lower BMR in tropical species ( $P < 0.02$ ).

consequently requires higher thermoregulatory costs (M.A. Chappell and G. A. Londoño, unpublished data). Other factors being equal, daily energy requirements (DEE) should be concomitantly greater at high altitude, and if energy flux or cold acclimatization is primary 'drivers' of BMR, then BMR at Wayqecha should be higher than at Pantiacolla. An across-latitude analysis (Jetz, Freckleton & McKechnie 2008) found that a 20 °C decrease in temperature was associated with a 50% increase in avian BMR. If that relationship applies to Peruvian birds, the BMRs of highland species should be 30% greater than in lowland species. We found no difference in BMR across altitudes, which argues against the idea that warm, stable temperatures are responsible for low BMR in tropical birds. However, costs of thermoregulation are only one component of DEE, and by adjusting other aspects of the energy budget (e.g. reduced flight activity), highland birds could achieve DEE similar to that of lowland species.

White *et al.* (2007) suggested that low BMR is favoured by selection in tropical lowlands because it would reduce heat loads and risks of hyperthermia. Our Peru BMR is not consistent with that hypothesis: no species – even those from the cool highland site – showed indications of heat stress when tested at 33–34 °C, which approximates the hottest shade temperatures at Pantiacolla. Sunlight can increase heat loads, but the lowland species in our data set do not use open habitat, so prolonged unavoidable sun exposure is unlikely. Low BMR may be beneficial in more challenging habitats, such as hot deserts or open grasslands (Weathers 1979).

One other finding merits comment. Early analyses of avian BMR reported higher BMR in passerines than in non-passerines (e.g. Lasiewski & Dawson 1967), but recent studies using phylogenetically informed statistics generally found no difference (e.g. Reynolds & Lee 1996; McKechnie & Wolf 2004). Both OLS and PGLS analysis of our data set revealed higher BMR in passerines than in non-passerines, although by only 12% compared to the 50–60% difference reported by Lasiewski & Dawson. Additional

clade comparisons were hampered by small sample sizes in most orders, but BMR differed between the best-represented non-passerine order (Apodiformes) and both passerines and other non-passerines. Larger sample size and a more recent and robust phylogenetic tree (Hackett *et al.* 2008) may explain why we found differences while earlier phylogenetic analyses did not. Interestingly, non-passerines tend to form a larger proportion of bird communities in tropical habitats than in temperate regions and also tend to be better represented on islands than on the mainland (Faaborg 1977). Perhaps their lower metabolic rates give them an advantage on islands, which are often relatively free of predators, and in the tropics where a slow life history seems to be favoured by selection.

Our data expand upon previous reports of low BMR in tropical birds. We found no effect of environmental temperature on BMR in Peruvian forest birds, consistent with the view that low BMR in tropical birds is mainly 'driven' by slow life history. Nevertheless, we urge due caution in interpreting these findings. Considerable variation in avian life history (clutch and egg size, incubation and nestling periods, mating systems) occurs in both temperate and tropical regions (Skutch 1985; Martin 1996; Robinson *et al.* 2010; G.A. Londoño, unpublished data). This spectrum of life histories probably explains some of the substantial BMR variation remaining after correction for mass, both within regions (Figs 2–3) and across broad geographical contrasts (Fig. 4). Therefore, in addition to inferring physiological consequences of life history from large-scale comparisons as we have done here, a promising approach for testing links between life history, physiology and ecology might be to examine these variables in detail at a species-by-species level (e.g. Tieleman *et al.* 2006). We also note that daily energy consumption, such as is measured with the doubly-labelled water technique, is a more comprehensive and relevant index of metabolic intensity than BMR, and its use should be encouraged in future studies of relationships between life history and energy metabolism.



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## Data accessibility

BMR data for this paper are deposited Dryad Digital Repository: <http://doi:10.5061/dryad.vg313> (Londoño *et al.* 2015).

## References

- Anderson, K.J. & Jetz, W. (2005) The broad-scale ecology of energy expenditure of endotherms. *Ecology Letters*, **8**, 310–318.
- Bennett, P.M. & Harvey, P.H. (1987) Active and resting metabolism in birds: allometry, phylogeny and ecology. *Journal of Zoology*, **213**, 327–363.
- Blomberg, S.P., Garland, T. Jr & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Chappell, M.A., Bech, C. & Buttemer, W.A. (1999) The relationship of central and peripheral organ masses to aerobic performance variation in House Sparrows. *Journal of Experimental Biology*, **202**, 2269–2279.
- Cooper, S.J. & Swanson, D.L. (1994) Seasonal acclimatization of thermoregulation in the black-capped chickadee. *Condor*, **96**, 638–646.
- Daan, S., Masman, D. & Groenewold, G. (1990) Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *American Journal of Physiology*, **259**, R333–R340.
- Daan, S., Masman, D., Srijijkstra, A.M. & Kenagy, G.J. (1991) Daily energy turnover during reproduction in birds and mammals: its relationship to basal metabolic rate. *Acta XX Congressus Internationalis Ornithologici* (ed B.N. Bell), pp. 1976–1987. Ornithological Trust Board, Wellington, New Zealand.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.
- Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.
- Dutenhoffer, M.S. & Swanson, D.L. (1996) Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology*, **69**, 1232–1254.
- Faaborg, J. (1977) Metabolic rates, resources, and the occurrence of non-passerines in terrestrial avian communities. *American Naturalist*, **111**, 903–916.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist*, **125**, 1–15.
- Fogden, M.P.L. (1972) The seasonality and population dynamics of equatorial forest birds in Sarawak. *Ibis*, **114**, 307–343.
- Francis, C.M., Terborgh, J.S. & Fitzpatrick, J.W. (1999) Survival rates of understory birds in Peru. *Proceedings of the 22nd International Ornithological Congress, Durban* (eds N.J. Adams & R.H. Slotow), pp. 326–335. BirdLife South Africa, Johannesburg, South Africa.
- Garland, T. Jr, Harvey, P.H. & Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology*, **41**, 18–32.
- Gessaman, J.A. & Nagy, K.A. (1988) Energy metabolism: errors in gas-exchange conversion factors. *Physiological Zoology*, **61**, 507–513.
- Gill, S.A. & Haggerty, T.M. (2012) A comparison of life-history and parental care in temperate and tropical wrens. *Journal of Avian Biology*, **43**, 461–471.
- Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **326**, 119–157.
- Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J. *et al.* (2008) Phylogenomic study of birds reveals their evolutionary history. *Science*, **320**, 1763–1768.
- Hails, C.J. (1983) The metabolic rate of tropical birds. *Condor*, **85**, 61–65.
- Hammond, K.A., Chappell, M.A., Cardullo, R.A., Lin, R. & Johnsen, T.S. (2000) The mechanistic basis of aerobic performance variation in red junglefowl. *Journal of Experimental Biology*, **203**, 2053–2064.
- Jankowski, J.E., Merkord, C.L., Rios, W.F., Cabrera, K.C., Salinas, R.N. & Silman, M.R. (2013) The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, **40**, 950–962.
- Jetz, W., Freckleton, R.P. & McKechnie, A.E. (2008) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS One*, **3**, e3261.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.
- Jimenez, A.G., Cooper-Mullin, C., Calhoun, E.A. & Williams, J.B. (2014) Physiological underpinnings associated with differences in pace of life and metabolic rate in north temperate and neotropical birds. *Journal of Comparative Physiology B*, **184**, 545–561.
- Karasov, W.H., Phan, D., Diamond, J.M. & Carpenter, F.L. (1986) Food passage and intestinal nutrient absorption in hummingbirds. *Auk*, **103**, 453–464.
- Kersten, M. & Piersma, T. (1987) High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea*, **75**, 175–187.
- Kulesza, G. (1990) An analysis of clutch size in New World passerine birds. *Ibis*, **132**, 407–422.
- Kvist, A. & Lindstrom, A. (2001) Basal metabolic rate in migratory waders: intra-individual, intraspecific, interspecific and seasonal variation. *Functional Ecology*, **15**, 46–473.
- Lasiewski, R.C. & Dawson, W.R. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*, **69**, 13–23.
- Liknes, E.T., Scott, S.M. & Swanson, D.L. (2002) Seasonal acclimatization in the American goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor*, **104**, 548–557.
- Londoño, G.A., Chappell, M.A., Castañeda, M.D., Jankowski, J.E. & Robinson, S.K. (2015) Data from: basal metabolism in tropical birds: latitude, altitude, and the “pace of life”. *Dryad Digital Repository*: <http://doi:10.5061/dryad.vg313>.
- Martin, T.E. (1996) Life history evolution in tropical and south temperate birds: what do we really know? *Journal of Avian Biology*, **27**, 263–272.
- Martin, T.E., Lloyd, P., Bosque, C., Barton, D.C., Bianucci, A.L., Cheng, Y.-R. *et al.* (2011) Growth rate variation among passerine species in tropical and temperate sites: an antagonistic interaction between parental food provisioning and nest predation risk. *Evolution*, **65**, 1607–1622.
- Martins, E.P. & Hansen, T.F. (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist*, **149**, 646–667.
- McKechnie, A.E. (2008) Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. *Journal of Comparative Physiology B*, **178**, 235–247.
- McKechnie, A.E. & Swanson, D.L. (2010) Sources and significance of variation in basal, summit and maximal metabolic rates in birds. *Current Zoology*, **56**, 1–31.
- McKechnie, A.E. & Wolf, B.O. (2004) The allometry of avian basal metabolic rate: good predictions need good data. *Physiological and Biochemical Zoology*, **77**, 502–521.
- Moreau, R.E. (1944) Clutch-size: a comparative study with special reference to African birds. *Ibis*, **86**, 286–342.
- Pagel, M. (1999) Inferring the historical patterns of biological evolution. *Nature*, **401**, 877–884.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.
- Pearl, R. (1928) *The Rate of Living: Being an Account of Some Experimental Studies on the Biology of Life Duration*. A.A. Knopf, New York.



- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., Van der Meer, J. & Wiersma, P. (1996) Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiological Zoology*, **69**, 191–217.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Development Core Team (2013) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-113.
- R Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Revell, L.J. (2010) Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, **1**, 319–329.
- Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- Reynolds, P.S. & Lee, R.M. III (1996) Phylogenetic analysis of avian energetics: passerines and nonpasserines do not differ. *American Naturalist*, **147**, 735–759.
- Reznick, D. (2014) Evolution of life histories. *The Princeton Guide to Evolution*. (eds J.B. Losos, D.A. Baum, D.J. Futuyma, H.E. Hoeksstra, R.E. Lenski, A.J. Moore, C.L. Peichel, D. Schluter & M.C. Whitlock), pp. 268–275. Princeton University Press, Princeton, New Jersey.
- Ricklefs, R.E. (1976) Growth rates of birds in the humid New World tropics. *Ibis*, **118**, 179–207.
- Ricklefs, R.E., Konarzewski, M. & Daan, S. (1996) The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *American Naturalist*, **147**, 1047–1071.
- Ricklefs, R.E. & Wikelski, M. (2002) The physiology/life history nexus. *Trends in Ecology and Evolution*, **17**, 462–468.
- Ritz, C. & Spiess, A.N. (2008) qpcR: an R package for sigmoidal model selection in quantitative real-time polymerase chain reaction analysis. *Bioinformatics*, **24**, 1549–1551.
- Robinson, W.D., Hau, M., Klasing, K.C., Wikelski, M., Brawn, J.D., Austin, S.H. et al. (2010) Diversification of life histories in New World birds. *Auk*, **127**, 1–10.
- Roff, D. (1992) *The Evolution of Life Histories: Theory and Analysis*. Chapman & Hall, New York.
- Russell, E.M., Yom-Tov, Y. & Geffen, E. (2004) Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology*, **15**, 831–838.
- Schaefer, H.C., Eshiamwata, G.W., Munyekenye, F.B. & Bohning-Gaese, K. (2004) Life-history of two African *Sylvia* warblers: low annual fecundity and long post-fledging care. *Ibis*, **146**, 427–437.
- Scholander, P.F., Hock, R., Walters, V. & Irving, L. (1950) Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biological Bulletin*, **99**, 259–271.
- Sibley, C.G., Ahlquist, J.E. & Monroe, B.L. (1988) A classification of the living birds of the world based on DNA–DNA hybridization studies. *Auk*, **105**, 409–423.
- Skutch, A.F. (1985) Clutch size, nesting success, and predation on nests of Neotropical birds, reviewed. *Neotropical Ornithology, Ornithological Monographs*, **36** (eds P.A. Buckley, M.S. Foster, E.S. Morton, R.S. Ridgely & F.G. Buckley), pp. 575–603. University of California Press, Washington, DC.
- Snow, D.W. & Lill, A. (1974) Longevity records for some Neotropical land birds. *Condor*, **76**, 262–267.
- Speakman, J.R., Selman, C., McLaren, J.S. & Harper, E.J. (2002) Living fast, dying when? The link between aging and energetics. *Journal of Nutrition*, **132**, 1583S–1597S.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
- Stromme, S.B. & Hammel, H.T. (1968) A simple method for calibration of gas meters. *Journal of Applied Physiology*, **25**, 184–185.
- Tieleman, B.I. (2007) Differences in physiological responses to temperature among stonechats from three populations reared in a common environment. *Comparative Biochemistry and Physiology A*, **146**, 194–199.
- Tieleman, B.I., Dijkstra, T.H., Lasky, J.R., Mauk, R.A., Visser, G.H. & Williams, J.B. (2006) Physiological and behavioural correlates of life-history variation: a comparison between tropical and temperate House Wrens. *Functional Ecology*, **20**, 491–499.
- Van Voorheis, W.A. & Ward, S. (1999) Genetic and environmental conditions that increase longevity in *Caenorhabditis elegans* decrease metabolic rate. *Proceedings of the National Academy of Sciences of the United States of America*, **96**, 11399–11403.
- Vleck, C.M. & Vleck, D. (1979) Metabolic rate in five tropical birds species. *Condor*, **81**, 89–91.
- Weathers, W.W. (1979) Climatic adaptation in avian standard metabolic rate. *Oecologia*, **42**, 81–89.
- White, C.R. & Seymour, R.S. (2004) Does basal metabolic rate contain a useful signal? Mammalian BMR allometry and correlations with a selection of physiological, and life-history variables. *Physiological and Biochemical Zoology*, **77**, 929–941.
- White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation and not primary productivity. *Proceedings of the Royal Society of London Series B*, **274**, 287–293.
- Wiersma, P., Chappell, M.A. & Williams, J.B. (2007) Cold- and exercise-induced peak metabolic rates in tropical birds. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 20866–20871.
- Wiersma, P., Nowak, B. & Williams, J.B. (2012) Small organ size contributes to the slow pace of life in tropical birds. *Journal of Experimental Biology*, **215**, 1662–1669.
- Wiersma, P., Muñoz-García, A., Walker, A. & Williams, J.B. (2007) Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 9340–9345.
- Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E. (2003) Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London Series B*, **270**, 2383–2388.
- Williams, J.B., Miller, R.A., Harper, J.M. & Wiersma, P. (2010) Functional linkages for the pace of life, life-history, and environment in birds. *Integrative and Comparative Biology*, **50**, 855–868.

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## Supporting Information

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

**Table S1.** Monthly air temperature ( $T_a$ ; °C) and precipitation (mm) for the three field sites.

**Table S2.** Mean, 95% confidence interval (CI), and range (Min–Max) values of phylogenetic signal of body mass (g) and Basal Metabolic Rate (BMR; watts) estimated using Pagel's lambda ( $\lambda$ ; Pagel 1999) on 5000 random trees including 489 species (our largest dataset) from the Global Phylogeny of Birds (<http://birdtree.org/>; Hackett backbone, 'genetic data only' tree distribution; Jetz et al. 2012, Hackett et al. 2008).

**Table S3.** Mean, 95% confidence interval (CI), and range (Min–Max) of  $r$  and  $P$  values from correlations between body mass and Basal Metabolic Rate using Phylogenetic Independent Contrasts.

**Table S4.** Mean mass (g) and mean Basal Metabolic Rate (BMR), and breeding habitat data from our 3-year field study in Peru, previously unpublished data from M.A. Chappell's lab (UCR), and literature sources (McKechnie & Wolf 2004; White et al. 2007; Wiersma et al. 2007).

**Table S5.** Akaike Information Criterion (AIC) and delta AIC ( $\Delta$ AIC) values used to compare alternative models of evolution for the correlation structure in PGLS analyses.