

Cold- and exercise-induced peak metabolic rates in tropical birds

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Compared with temperate birds, tropical birds have low reproductive rates, slow development as nestlings, and long lifespans. These “slow” life history traits are thought to be associated with reduced energy expenditure, or a slow “pace of life.” To test predictions from this hypothesis, we measured exercise-induced peak metabolic rates (PMR_E) in 45 species of tropical lowland forest birds and compared these data with PMR_E for three temperate species. We also compared cold-induced PMR (PMR_C) with PMR_E in the same individuals of 19 tropical species. Tropical birds had a 39% lower PMR_E than did the temperate species. In tropical birds, PMR_C and PMR_E scaled similarly with body mass (M_b), but PMR_E was 47% higher than PMR_C. PMR_E averaged $6.44 \times$ basal metabolic rate (BMR) and PMR_C averaged $4.52 \times$ BMR. The slope of the equation relating PMR_E to M_b exceeded the slope for the equation for BMR vs. M_b , whereas slopes for the equations of PMR_C and BMR vs. M_b did not differ. M_b -adjusted residuals of PMR_E were positively correlated with residual BMR, whereas residual PMR_C and residual BMR were not correlated. PMR_E and PMR_C were not correlated after we corrected for M_b . Temperate birds maintained their body temperature at an 8.6°C lower average air temperature than did tropical species. The lower PMR_E values in tropical species suggest that their suite of life history traits on the slow end of the life history continuum are associated with reduced metabolic rates.

maximum metabolic rate | summit metabolism | metabolic scope |
pace of life | cold tolerance

Ecological physiologists have devoted considerable effort to examining the upper limits of physiological performance, especially locomotor performance and metabolic power production during cold exposure. An implicit or explicit hypothesis in this work is that individual variation in performance is correlated with fitness: higher performance such as faster running or greater metabolic power output leads to increased survival and/or reproductive success. In the past few decades, a variety of performance indices have been measured in numerous species, and analyses have examined performance in mechanistic, phylogenetic, ecological, and evolutionary contexts.

In birds, sustained high aerobic metabolism is a salient feature of their physiological performance and is fundamental to their capacity for powered flight and their tolerance of extreme cold (1). The most-studied aerobic index in birds is basal metabolic rate (BMR), the lower limit to aerobic power production (see refs. 2–4). However, it is questionable whether BMR *per se*, rather than other physiological parameters that may correlate with BMR, is ever a “target” for direct selection except when the requirement for reducing heat load or water loss is critical to survival, as might be the case in hot deserts (5). Moreover, BMR is not directly responsible for the remarkable flight capacity or temperature tolerance of birds. Instead, it is the upper limit to aerobic power output (peak metabolic rate; PMR) that forms the metabolic foundation of the high-intensity avian way of life. Intuitively, PMR can be linked to fitness in numerous contexts, such as survival during migration, predator avoidance, or survival during extreme cold.

A complication in analyses of maximum aerobic limits is that several approaches have been used to elicit PMR. Some investigators have used maximal metabolism during exercise (PMR_E) and others maximum rates of metabolism during cold-induced thermogenesis (PMR_C; sometimes called “summit metabolism”). Typically, PMR_C is measured during brief exposure to low ambient temperatures (T_a) (e.g., ref. 6), often in a helium-oxygen (heliox) atmosphere to increase conductance (7). Although measuring PMR_E is a technical challenge, it has been quantified in birds trained to fly in wind tunnels (e.g., ref. 8) or run on treadmills (e.g., refs. 9 and 10) or by using related methodologies such as “flight wheels” (11–13). Most data on avian PMR have been obtained during cold challenge, even though exercise often elicits higher rates of energy expenditure (e.g., ref. 14). The fact that these two measurements differ presents a problem in interpretation. To understand the relationship between PMR_E and PMR_C, it would be of value to measure both parameters on the same individuals, but such data are currently unavailable. Another interpretive bias concerning PMR stems from the fact that most species studied are native to temperate climates. No data exist on PMR for tropical birds. Although the tropics comprise many different habitats, we use the term “tropical” here to refer specifically to tropical lowland forest.

Tropical and temperate birds lie at opposite ends of a life history continuum, with tropical species falling at the “slow” end; they show lower mortality, longer lifespan, and reduced reproductive effort (15–19). A reasonable deduction from these differences in climate and life history is that selection on the upper limits of physiological performance—especially aerobic metabolism—may be relaxed in tropical species. Because thermal conditions in their habitats are warm and stable, tropical birds do not experience selection for high PMR_C. This is consistent with measurements of lower PMR_C in tropical birds than in temperate birds (20). Predictions for differences between tropical and temperate birds in PMR_E are less intuitive. Aerodynamic power requirements for flight are unaffected by latitude, so on that basis there is no reason to expect divergence of PMR_E between temperate and tropical species. Nevertheless, the lack of long-distance migration in lowland tropical species, potentially shorter flight durations in dense forests, and lower brood-care requirements in most tropical birds make it plausible to expect reduced emphasis on high-endurance sustained flight and hence lower PMR_E. Also, some data (e.g., refs. 21 and 22) suggest that PMR and BMR are functionally coupled and, therefore, should show positive correlations within and among

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Table 2. Pearson correlation coefficients of residuals of BMR, PMR_C, and PMR_E from regressions with logM_b

Residuals of	Residual logBMR	Residual logPMR _C	Residual logBMR ^{PIC}	Residual logPMR _C ^{PIC}
logPMR _E	0.387* (31)	0.119 (16)	—	—
logPMR _C	0.132 (19)	—	—	—
logPMR _E ^{PIC}	—	—	0.406* (30)	0.00 (15)
logPMR _C ^{PIC}	—	—	−0.174 (18)	—

Standard errors are given in parentheses. Variables marked PIC were transformed to phylogenetic independent contrasts. *, $P < 0.05$.

factorial scope is also considerably higher than our estimate for tropical species.

Lower Limit of Cold Tolerance. We compared the temperature at cold limit (T_{CL}) values of tropical birds with those of 21 summer-acclimatized temperate species (6), using general linear models (GLMs) on log₁₀-transformed data with M_b and Climate as independent variables. Temperate birds could maintain their PMR at a lower T_{CL} than tropical birds. In tropical species, T_{CL} was 8.6°C higher than in temperate species ($F_{1,37} = 53.1$, $P < 0.001$). We found no interaction between Climate and M_b ($F_{1,36} = 0.87$, $P = 0.36$).

Log T_{CL} was negatively associated with log M_b (Table 1). The relationship with M_b remained significant when PICs were used (log T_{CL}^{PIC} in Table 1). T_{CL} on average decreased from 17.4°C to −0.6°C with increasing M_b from 9.6 to 71.0 g.

Discussion

We have presented measurements of PMR_C and PMR_E in birds from tropical lowland forests and compared these two variables in the same species. In combination with BMR data for the same species (20), our results enable us to examine several aspects of avian aerobic performance with relatively few confounding factors related to methodology, phylogeny, or seasonality.

One of our goals was to compare peak aerobic metabolism during exercise with that elicited by intense cold exposure in tropical birds. We found a 47% higher PMR_E than PMR_C in tropical birds (Fig. 2). In warm-acclimated small mammals, PMR_E and PMR_C are often similar (24, 26), but in many species, cold acclimation induces hypertrophy of brown adipose tissue, which augments shivering thermogenesis (27). As a result, PMR_C is often considerably greater than PMR_E in small mammals after seasonal or laboratory acclimation to low temperature (e.g., refs. 26 and 28). In large mammals, PMR_E seems to consistently exceed PMR_C (14, 29), but that may be a reflection of the difficulty in eliciting PMR_C in large, well insulated endotherms.

Birds lack tissues specialized for heat production (30, 31). Therefore, regulated power production in both exercise and thermogenesis relies on skeletal muscle (32). Most studies of avian PMR have focused on PMR_C in small species because that measurement is technically easier than eliciting maximal exercise metabolism and because of the challenge of attaining PMR_C in large birds. In tropical species, forced exercise in our flight wheel elicited a higher PMR than cold exposure. There are no data for temperate birds where both PMR_E and PMR_C were measured in the same species. However, an assortment of interspecific measurements of cold-induced and exercise-induced PMR in temperate species shows the same trend: PMR is higher in exercise than in thermogenesis (14). On average, PMR_C in temperate birds is 5–6 × BMR (1, 22), occasionally reaching 8 × BMR [e.g., in winter-acclimated black-capped chickadees, *Poecile atricapillus* (6)]. In contrast, PMR_E obtained in flight wheels or treadmills is ≈7–12 × BMR (9–13).

Differences between PMR_E and PMR_C may be due to the way the flight musculature is used. In flapping flight, the pectoralis-

supracoracoideus complex can operate at maximum intensity. In contrast, effective shivering requires isotonic, simultaneous antagonistic contractions, which limits force generation by the large downstroke muscles and thus constrains total power output (32). Among tropical species, the mangrove swallow, *Tachycineta albilinea*, had the highest PMR_C. Because this species is an active aerial forager, this raises the question of whether rate of heat production can be a byproduct of adaptations to an active aerial lifestyle (see ref. 33).

There is an apparent difference between the PMR_E of birds measured during long-duration steady flight vs. forced exercise in flight wheels or treadmills. We found a lower PMR_E in flight wheel tests than the average value of 16 × BMR for birds in long-duration steady flights (e.g., refs. 8, 14, 34, and 35). We tentatively conclude that PMR_E measured in a flight wheel is lower than PMR measured in flight.

Another goal of our study was to compare aerobic limits in temperate and tropical birds, and we found considerably lower PMR_E in tropical species than in the small number of temperate birds tested with similar methods. The difference is puzzling, but analyses of performance traits associated with contrasting environmental regimes might provide useful insight into proximate and ultimate causes of physiological diversity (36). Several aspects of climate and life history suggest that temperate and tropical bird species might show metabolic divergence. First, tropical lowland forest environments are considerably warmer and have less daily and seasonal T_a variation than is typical of temperate habitats; in particular, tropical lowlands lack the prolonged periods of cold characteristic of temperate-zone winters. Therefore, unlike temperate residents, tropical birds are presumably not under strong selection for high thermogenic capacity and cold tolerance. This hypothesis is supported by data on 57 rodent species that show a negative correlation between PMR_C and mean minimum annual T_a (37). Hence, one might predict a lower PMR_C in tropical birds. Second, compared with temperate birds, tropical lowland birds generally lie at the slow end of the life history continuum (15, 16). In combination with low thermoregulatory costs, these life history differences might be expected to result in a lower average daily rate of energy expenditure (a syndrome of characteristics sometimes referred to as the “slow pace of life”) in tropical species (20). Both theory (38) and, for several taxa, data (39, 40) suggest negative correlations between the pace of life and both reproductive rate and survival.

Although it is intuitive to predict lower thermoregulatory capacity in tropical species, it is less clear how differences in life history and pace of life might affect the limits to aerobic exercise capacity. On the one hand, the highest power output in volant species presumably occurs during flapping flight. Other factors (altitude, temperature, etc.) being equal, air density and viscosity are quite similar in tropical and temperate regions. Accordingly, the aerodynamic forces required to support flapping flight are largely independent of latitude. Therefore, the metabolic power requirements for flight should be the same at all latitudes, so if the energy demands of flight drive the upper limit to aerobic

trial. Body temperature (T_b , °C) was measured at the start and end of each cold-exposure trial, using a 36-gauge thermocouple inserted into the cloaca. Thermocouples were read to $\pm 0.1^\circ\text{C}$ by a Bailey Bat-12 thermocouple reader.

All procedures were approved by the Institutional Animal Care and Use Committee of Ohio State University (protocol IACUC2004A0093). Catching of birds was permitted by Panamanian Autoridad Nacional del Ambiente (permit no. SE/A-36-06) and Autoridad del Canal de Panamá.

Measurements of PMR_C and T_{CL} . The methods used for our measurements of PMR_C in tropical birds are given in Wiersma *et al.* (20). Briefly, we used heliox in a flow-through respirometry system, with a bird placed in a metabolism chamber that was in a temperature-controlled freezer. Inlet and outlet O_2 concentration and chamber T_a were recorded at 1-sec intervals. Instantaneous $\dot{V}\text{O}_2$ ($\dot{V}\text{O}_{2\text{inst}}$) was calculated by using equations from Bartholomew *et al.* (59) and equation 4 of Hill (60), based on 5-min running averages of O_2 concentrations. The effective volume of the system was estimated as 5,397 ml from washout curves. We used 20.08 J/ml O_2 to convert $\dot{V}\text{O}_{2\text{inst}}$ to heat production in watts (61).

We estimated cold tolerance by measuring the lowest T_a at which a bird could maintain its PMR (the T_{CL} ; °C) (see ref. 6; *sensu* ref. 62). T_{CL} was converted to °K and \log_{10} -transformed before statistical analyses.

Measurements of PMR_E . We used a metabolic flight wheel to measure PMR_E (11). Dry air was supplied under positive pressure from a cylinder of compressed air, regulated at 5 liters/min (at standard temperature and pressure) with a Tylan mass flow controller calibrated before and after the field season against a DTM-113 dry volume meter (Singer American Meter Division). Excurrent air was subsampled at ≈ 100 ml/min, dried with Drierite, scrubbed of CO_2 by using soda lime, redried, and routed through a Sable Systems Oxilla dual-channel O_2 analyzer. Reference air for the differential reading came from the compressed air cylinder. Flow rate, wheel rotation speed, and O_2 concentration were recorded every 1.0 sec with a Macintosh laptop computer and Sable Systems UI-2 AD converter running Warthog LabHelper software (<http://warthog.ucr.edu>).

Measurements of PMR_E were made during the day at T_a of $23 \pm 0.5^\circ\text{C}$. After weighing birds, we placed them inside the wheel, sealed it, and obtained an initial baseline reading of O_2 concentration. After 1–2 min, we began rotating the wheel slowly (≈ 0.3 m/sec at the rim), increasing speed as birds became oriented to the direction of movement. We exercised birds at increasing intensity until they showed signs of exhaustion (panting and gaping; refusal to run or fly despite wheel rotation) and O_2 consumption reached a plateau, whereupon the wheel was stopped and a second baseline reading was obtained. Typical tests lasted <15 min. This method has been used to elicit maximum $\dot{V}\text{O}_2$ in birds (11, 12) with high repeatability (63). Some individuals refused to run or flap in the wheel chamber, and we excluded these from our analyses.

For wheel measurements, we also used calculations of $\dot{V}\text{O}_{2\text{inst}}$ (59). The effective volume of the wheel, estimated from washout curves, was 8,300 ml. Calculations of effective volume, baseline adjustment, smoothing to eliminate electrical noise, and computation of $\dot{V}\text{O}_{2\text{inst}}$ were performed with Warthog LabAnalyst. Because the flowmeter was upstream of the chamber and excurrent CO_2 was absorbed, metabolism was calculated as $\dot{V}\text{O}_{2\text{inst}} = \dot{V} \cdot [F_i\text{O}_2 - F_e\text{O}_2] / [1 - F_e\text{O}_2]$, where \dot{V} is flow rate and $F_i\text{O}_2$ and $F_e\text{O}_2$ are incurrent and instantaneous excurrent O_2 concentrations, respectively ($F_i\text{O}_2$ was 0.2095). PMR_E was computed as the highest continuous 1-min average of $\dot{V}\text{O}_{2\text{inst}}$ (11) and converted to watts, as described for PMR_C .

Data for Tropical–Temperate Comparisons. We compared our PMR_E measurements with data from the literature for three temperate species that were measured by using a flight wheel. We used mean values for adults of house sparrows ($n = 36$; ref. 11) from Australia, red-eyed vireos ($n = 10$; ref. 13) from North America, and satin bowerbirds from northeast New South Wales, Australia ($M_b = 216.2 \pm 1.7$ g, $\text{PMR}_E = 14.1 \pm 0.23$ W, $n = 36$; J. Savard, J. Siani, M.A.C., and G. Borgia, unpublished data). Satin bowerbirds and house sparrows were caught and measured during the breeding season: the same period during which we made measurements on tropical species. Red-eyed vireos were caught during fall migration and kept in small cages for 1–2 months before measuring. It is not known whether this management may have affected their PMR , but a decrease in maximum muscle output in the red-eyed vireos might be expected because they were constrained to small cages, inhibiting muscle usage. Species-specific averages of BMR from Wiersma *et al.* (20) were used to calculate fASs [fAS_C and fAS_E (= PMR/BMR)].

Statistical Analyses. We tested for statistical significance by using *t* tests and GLMs. To compare PMR_E of tropical and temperate species, we tested for a significant effect of climate (tropical or temperate) in a GLM. Because M_b of satin bowerbirds substantially exceeded M_b of our tropical species (see Fig. 1), we also analyzed PMR_E of house sparrows and red-eyed vireos separately, using *t* tests. For these *t* tests, we first regressed \log_{10} -transformed PMR_E against $\log M_b$ for the tropical species and compared each average temperate species' PMR_E with the predicted tropical PMR_E . To obtain the correct standard error of the predicted tropical PMR_E , we fitted the regression line with a constant equaling M_b of the focal temperate species, instead of $x = 0$.

We calculated M_b -independent residual metabolic rates from regressions of species-average $\log \text{PMR}$ or $\log \text{BMR}$ on $\log M_b$. Where variables could covary, such as PMR and BMR , we tested for associations by using Pearson's correlation coefficient. To test for differences between slopes of the allometric relationships, we rearranged data of the variables PMR_C , PMR_E , fAS_C, fAS_E, and BMR into a single variable, while adding a variable coding for the different metabolism measurement types. The M_b s associated with the different metabolism variables were likewise reorganized. This procedure allowed us to then test for differences in $\log M_b$ slopes by testing the interaction term of $\log M_b$ and the "measurement type variable" in a GLM, along with $\log M_b$ and the measurement type variable.

Because species are phylogenetically related to varying degrees, associations between traits of species may be differentially affected by common ancestry. Accordingly, we transformed our measurements to PICs (64, 65) to reduce phylogenetic effects in analyses. The use of PICs relies on assumptions about trait evolution that are sometimes difficult or impossible to verify, so we used both conventional and PIC analyses when interpreting results (66–68). We constructed a phylogenetic tree (see SI Fig. 3) primarily based on Sibley and Ahlquist (69) and calculated PICs by using PDTREE (70). Details on PIC analysis and tree construction are given in Wiersma *et al.* (20).

Statistical tests were performed using SPSS version 14.0, with $\alpha = 0.05$. Values are shown as mean ± 1 standard error.

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