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# Tropical birds have a slow pace of life

Popko Wiersma, Agusti Muñoz-Garcia, Amy Walker, and Joseph B. Williams*

Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 290 Aronoff Laboratory, 318 West 12th Avenue, Columbus, OH 43210

Tropical birds are relatively long-lived and produce few offspring, which develop slowly and mature relatively late in life, the slow end of the life-history axis, whereas temperate birds lie at the opposite end of this continuum. We tested the hypothesis that tropical birds have evolved a reduced basal metabolic rate (BMR). We measured BMR of 69 species of tropical birds, the largest data set amassed on metabolic rates of tropical birds, and compared these measurements with 59 estimates of BMR for temperate birds. Our analyses included conventional least squares regression, regressions based on phylogenetic independent contrasts, and a comparison of BMR of 13 phylogenetically matched pairs, one species from the tropics and one from northerly temperate areas. Our triptych showed that tropical birds had a reduced BMR, compelling evidence for a connection between the life history of tropical birds and a slow pace of life. Further, tropical migrants breeding in temperate habitats had a lower BMR than did temperate residents, suggesting that these migrants have physiological traits consistent with a slow pace of life. In addition, we determined that tropical birds had a lower cold-induced peak metabolic rate and thermogenic metabolic scope than temperate species, a finding that is consistent with the hypothesis that their environment has not selected for high levels of thermogenesis, or alternatively, that a slow pace of life may be incompatible with high thermogenic capacity. We conclude that physiological function correlates with the suite of life-history traits.

basal metabolic rate | life history | peak metabolic rate | tropics | migration

Life-history traits, such as clutch size, age at maturity, rate of growth of offspring, and longevity tend to cluster in ecological space such that species with long lives produce small numbers of offspring that develop slowly and mature relatively late in life (1–3). At the opposite end of this "slow–fast" continuum, organisms have low survival rates coupled with large numbers of offspring that develop rapidly and reach sexual maturity at an early age. Among some species, life-history traits also covary with rate of energy expenditure, the pace of life, such that animals with high rates of reproduction have high energy expenditure, and vice versa (4, 5). Support for the connectivity between life history, especially survivorship, and rate of living comes from studies on fruit flies *Drosophila* (6), houseflies *Musca domestica* (7), and nematode worms *Caenorhabditis elegans* (8), as well as meta-analyses on mammals (2, 9, 10). Although less attention has been given to relationships between life history and metabolism in birds, Trevelyan *et al*. (11) did show an association between resting metabolic rate in birds and their maximum life span.

With small clutches (12–14), slower growth as nestlings (15), long periods when fledglings are dependent on parents (16, 17), and higher rates of adult survival than temperate counterparts (15, 18–20), tropical birds fall along the slow end of the life-history continuum, but physiological correlates with these disparities, if present, remain elusive. Understanding physiological differences between tropical and temperate birds may provide insights into the evolution of these fundamental differences in life histories (3, 21, 22).

Even though tropical birds possess life-history traits that are indicative of a slow rate of living, there is little evidence that tropical birds have a reduced rate of metabolism (23, 24). Scholander *et al*. (25) and later Vleck and Vleck (26) concluded that tropical birds had a similar level of metabolism compared with temperate species. In a literature study, Weathers (27) reported that metabolic rates of lowland tropical birds that foraged in the forest were similar to allometric predictions for temperate species. However, he did find a lower standard metabolic rate among 6 species of low latitude birds that foraged in the sun. For 12 species of resident passerines from the Malay Peninsula, Hails (28) reported a reduction in basal metabolic rate (BMR), but his manometric based measurements of oxygen consumption are fraught with methodological uncertainties that could have compromised results. Recent broad-scale analyses that have incorporated phylogenetically adjusted statistics suggested that temperate and tropical birds have similar rates of metabolism (24). Despite lack of evidence, the notion that tropical birds have a slow pace of life seems broadly accepted, a consequence apparently of philosophical reasoning rather than empirical observation.

Part of the challenge of comparing the pace of life of temperate and tropical species is identifying an appropriate index of energy metabolism. Common measures include BMR and field metabolic rate (FMR). The latter may have the greatest ecological relevance because it is the average daily rate of energy expenditure in free-living individuals, and hence is a direct estimate of the pace of life. More rarely, maximal, or peak metabolic rate (PMR) during exercise or severe cold exposure has been determined (29). Of these measures, by far the most common index of metabolic rate is BMR, the minimum metabolic rate of a quiescent, postabsorptive animal, in its thermal neutral zone and rest phase (30). Because BMR makes up 25–40% of a bird's FMR (31), and often correlates with FMR (10, 32), it can be used as a proxy for the pace of life, although admittedly much residual variation remains. For 619 species of mammals, BMR was significantly correlated with PMR, FMR, and life-history parameters such as life span, litter size, and population density (10). In an analysis of 133 species of birds, FMR was positively related to latitude, supporting the idea that the pace of life is reduced in tropical species (33).

Some species over-winter in the tropics but migrate each spring to temperate areas to breed, a journey that requires considerable energy expenditure. If powered flight is an integral part of a species' lifestyle, and if BMR reflects these demands, then one should not expect differences in BMR between migrant and temperate resident groups. Alternatively, because tropical

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**Table 1. Coefficients from general linear model analyses**

| Equation no. | Dependent variable | Group | Constant | Log $M_b$ (g) | Climate[†] | Clade[‡] | Migratory behavior[§] | F | $r^2$ | n |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | BMR | All birds | −1.431*** (0.046) | 0.672*** (0.024) | −0.061*** (0.013) | 0.072*** (0.021) | | 346*** | 0.90 | 124 |
| 2 | BMR | Breeding in tropics | −1.449*** (0.065) | 0.644*** (0.034) | | 0.069* (0.028) | | 228*** | 0.93 | 65 |
| 3 | BMR | Breeding in temperate area | −1.416*** (0.065) | 0.682*** (0.032) | | 0.065* (0.030) | −0.048* (0.017) | 226*** | 0.88 | 59 |
| 4 | PIC BMR[¶] | All birds | | 0.649*** (0.029) | −0.046** (0.016) | 0.029‖ (0.036) | | 169*** | | 123 |
| 5 | PMR | All birds | 0.721*** (0.075) | 0.751*** (0.056) | −0.177*** (0.028) | | | 101*** | 0.85 | 40 |
| 6 | PIC PMR[¶] | All birds | | 0.702*** (0.060) | −0.115*** (0.027) | | | 69.0*** | 0.79 | 39 |

Equations have the form log $BMR$ (W) = a + [$b_x$ × categorical variables] + $b_n$ × log $M_b$ (g). Climate, clade, and migratory behavior were categorical variables, either 0 or 1 for each species. Numbers in parentheses equal ±1 SE. There were no statistically significant interaction terms (all $P > 0.25$). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
[†]Climate = tropical; 0 for Climate = temperate.
[‡]Clade = passerine; 0 for Clade = non-passerine.
[§]Migratory behavior = resident/short-distance migrant; 0 for tropical migrant.
[¶]Equation using standardized phylogenetic independent contrasts of dependent and independent variables.
‖Nonsignificant.

migrants developed the migratory habit in recent geological history (34–38), and because they breed in a benign thermal environment, one might predict that their pace of life is more similar to tropical birds. Some authors have suggested that Neotropical migrants have lower fecundity and higher survival than do temperate residents, patterns consistent with a low rate of energy expenditure (35). Therefore, tropical migrants breeding in temperate regions may have physiological attributes consistent with a slow pace of life.

PMR, the maximum rate of energy expenditure, is typically achieved by forcing animals to exercise, or by exposing them to cold in metabolism chambers (39). Cold-induced PMR defines the maximum heat generating capacity of an endotherm and correlates positively with endurance to cold (40, 41). Unlike the rate of energy expenditure in basal conditions, which in mammals is influenced not only by muscle tissue, but also by tissues of digestive organs, heart, and brain (42), in birds, heat generation during cold exposure relies almost exclusively on shivering by skeletal muscles (43, 44). Although BMR and PMR often show a positive correlation independent of mass (45), some studies have shown that these two variables are unrelated (46, 47). If animals experience cold temperatures, such as temperate birds during winter, they likely have evolved metabolic machinery with high thermogenic capacity, which may mandate a high BMR to support these tissues. Because lowland tropical birds do not experience low ambient temperatures ($T_a$), it could be that they have a lower PMR than would resident temperate species.

Here, we test the hypothesis that tropical birds, with their low rate of reproduction and increased survival, have evolved a reduced BMR. We measured BMR of 69 species of tropical birds from 29 families, the largest data set amassed on metabolic rates of tropical birds, and compared these measurements with 59 estimates of BMR for temperate birds from 17 families. Our analyses included both conventional least squares regression (CLSR), and regressions based on phylogenetic independent contrasts (PIC) (48, 49). We further tested the hypothesis by measuring BMR of 13 phylogenetically matched pairs, one species of each pair from the tropics and the other from northerly temperate areas. Our tripartite comparison, CLSR, PIC, and paired comparisons, showed that tropical birds had a reduced BMR, compelling evidence for a connection between the life-history of birds and pace of life. Further, tropical migrants

breeding in temperate habitats had a lower BMR than did temperate residents, suggesting that these migrants have physiological traits consistent with a slow pace of life. In addition, we have measured cold-induced PMR of 19 species of tropical birds, data not gathered for birds from this climate before. We determined that tropical birds had a reduced PMR consistent with the hypothesis that their environment has not selected for high levels of thermogenesis, or alternatively, that a slow pace of life may be incompatible with high thermogenic capacity.

## Results

**BMR of Tropical and Temperate Birds.** When we used conventional statistics and included climate and clade as fixed effects in our model, and mass as a covariate, tropical birds had a significantly lower BMR than temperate birds ($P < 0.001$), a reduction that equaled 17.8% (Table 1, equation 1; Fig. 1). Passerines had a significantly higher BMR than did birds belonging to other orders, both within tropical species and within temperate species (Table 1, equations 2 and 3). We detected no significant inter-
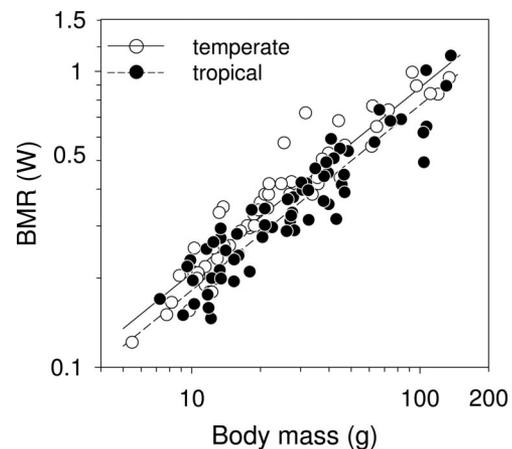


**Fig. 1.** BMR (W) as a function of body mass (g) in tropical and temperate birds. Open circles, temperate species; filled circles, tropical species; solid and dashed line, result of a general linear model for, respectively, temperate and tropical species.
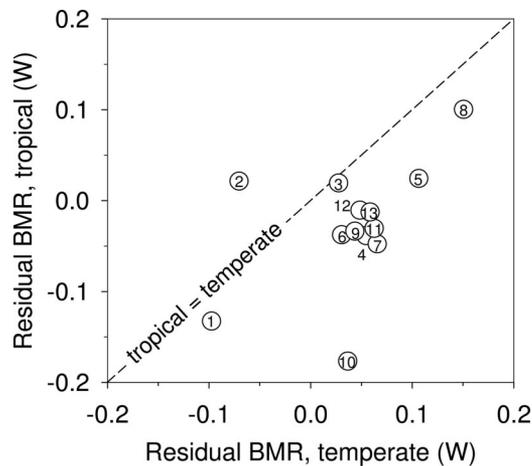
**Fig. 2.** Residual basal metabolic rate of temperate birds plotted as a function of residual basal metabolic rate of tropical birds. The line of equality is represented by a dashed line. Numbers within circles signify pairs of species as follows: 1, *Zenaida macroura, Columbina talpacoti*; 2, *Vireo olivaceus, V. flavoviridis*; 3, *Tachycineta bicolor, Progne chalybea*; 4, *Turdus migratorius, T. grayi*; 5, *Mimus polyglottos, M. gilvus*; 6, *Troglodytes aedon aedon, T. a. musculus*; 7, *Thryothorus ludovicianus, T. rufalbus*; 8, *Carduelis tristis, Euphonia laniirostris*; 9. *Melospiza melodia, Arremonops conirostris*; 10, *Dendroica petechia petechia, D. p. erithachorides*; 11, *Agelaius phoeniceus, Sturnella militaris*; 12, *Quiscalus quiscula, Q. mexicanus*; 13, *Cardinalis cardinalis, Cyanocompsa cyanoides*.

action terms, suggesting that slopes did not differ between passerines and non-passerines, or between tropical and temperate birds. The slope of the model for all birds that included both climate and clade was 0.672.

Tropical and temperate birds also differed significantly in BMR when we used independent contrasts in our model (Table 1, equation 4). This analysis revealed that BMR of tropical birds was 9.8% lower than that of temperate species, but the difference between passerines and non-passerines was not significant.

**BMR Comparisons Within Species Pairs.** For tropical-temperate paired comparisons of BMR, we first regressed log BMR against log $M_b$ for these 26 species: log $BMR$ (W) $= -1.349 + 0.655 \times$ log $M_b$ (g) ($F = 216.0, r^2 = 0.90, P < 0.0001$). Then we used this equation to calculate residuals, which averaged $0.0402 \pm 0.018$ W in temperate species and $-0.0278 \pm 0.019$ W in tropical species (Fig. 2). Residuals for tropical species were 13% lower than residuals for temperate species (Wilcoxon signed ranks test, $Z = -2.41, P < 0.02$). Body masses of temperate and tropical birds did not differ statistically (paired *t* test: $t = -0.30, P > 0.7$). Within our paired comparisons, body temperature just before entry into the metabolism chamber did not differ significantly between tropical and temperate species (paired *t* test, $t = 0.11, P > 0.8$). Body temperature averaged 40.45°C ($n = 26$).

**BMR of Migrant Species.** When on their temperate breeding grounds, tropical migrants had a significantly lower BMR than did temperate year-round residents ($P < 0.05$; Table 1, equation 3). BMR estimates of marginal means (50), controlling for body mass and clade in a general linear model, were $0.304 \pm 0.008$ W in tropical birds, $0.329 \pm 0.01$ W for tropical migrants breeding in temperate areas, and $0.368 \pm 0.009$ W for temperate residents. Tropical migrants breeding in temperate areas had a lower mean BMR than did temperate residents breeding in the same region (general linear model contrasts test, $P < 0.01$), but a significantly higher BMR than tropical residents (contrasts test, $P < 0.01$).

**PMRs.** PMR of 19 species of tropical birds was described as follows: log $PMR$ (W) $= -0.975 + 0.814 \times$ log $M_b$ (g) ($F = 58.9$,
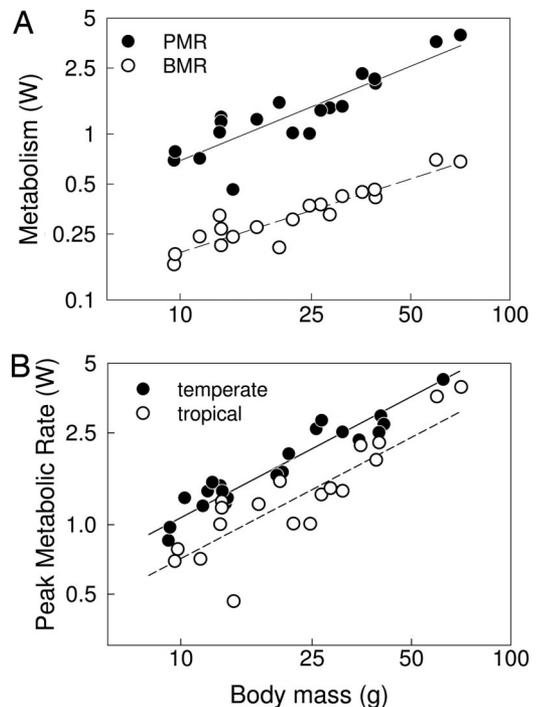


**Fig. 3.** Cold-induced peak metabolic rates in tropical and temperate birds. (*A*) PMR (filled circles) and BMR (open circles) as a function of body mass for 19 species of tropical birds. Solid line, regression for PMR; dashed line, regression for BMR. (*B*) PMR of temperate (open circles) and tropical (filled circles) birds. Solid line, regression for temperate species; dashed line, regression for tropical species.

$r^2 = 0.78, P < 0.0001$), whereas BMR of these same species was described as log $BMR = -1.349 + 0.635 \times$ log $M_b$ ($F = 112.5, r^2 = 0.86, P < 0.0001$) (Fig. 3*A*). In an ANCOVA with log BMR as the dependent variable, type of metabolic rate, either PMR or BMR, as a fixed effect, and log $M_b$ as a covariate, the interaction term was insignificant indicating that slopes of these equations did not differ statistically ($F = 2.6, P = 0.11$).

Using CLSR, we compared values of PMR in tropical birds with published values for 21 summer-acclimatized temperate passerines (41) and found that tropical birds had a lower PMR than did temperate birds (Table 1, equation 5). The equation that described the relationship between PMR and body mass for temperate birds was log $PMR = -0.654 + 0.699 \times$ log $M_b$ ($F = 200, n = 21, P < 0.001$) (Fig. 3*B*). Average PMR was $1.23 \pm 0.06$ W in tropical birds and $1.86 \pm 0.08$ W in temperate birds, a reduction of 34% in tropical species. Average body mass did not differ between tropical and temperate birds ($t = 0.68, P = 0.50$). Excluding data from the single non-passerine species did not alter conclusions. Metabolic scope (PMR/BMR) averaged $4.27 \pm 0.2$ in tropical birds ($n = 19$) and $5.49 \pm 0.3$ in temperate birds ($n = 9$), values that were significantly different ($t = 2.63, P < 0.02$).

When we compared PMR of tropical and temperate birds using PIC, we found the same trends as we did with CLSR (Table 1, equation 6). The coefficient for contrasts of climate was significant ($t = -4.4, P < 0.001$).

**Discussion**

In this article, we have attempted to map physiology of tropical and temperate birds onto their environment and demography. We hypothesized that tropical birds have a reduced BMR compared with temperate species because tropical birds have life-history traits consistent with a slow pace of life. We present

compelling evidence that tropical birds have a slow pace of life, reflected in their reduced BMR. Analyses using CLSR, PIC, and paired comparisons, all confirm that BMR is lower in tropical species. Thus, we have demonstrated that the suite of life-history characters possessed by tropical birds is correlated with a reduced rate of metabolism.

What proximate mechanisms bring about a reduced BMR in tropical birds? Physiological differences at the subcellular level, such as mitochondrial density and/or efficiency, or degree of unsaturation of lipids in membranes, have been proposed to influence BMR (51, 52). In addition, relative sizes of organs, such as liver, kidney, heart, and intestine explain some variation in BMR in mammals and birds (53). However, in a study on larks, no support was found for the idea that differences in organ masses contribute to differences in BMR, which varied 2-fold among species (54). In laboratory selection experiments, and within a species, individuals with higher BMR often have relatively larger organ masses (55), but it is not clear how these results apply across species.

If organ masses influence BMR, then tropical birds might be expected to have smaller organs relative to their body mass than temperate counterparts do. Although data do not exist to directly test this assertion, in an early study, Rensch and Rensch (56) presented data on wet mass of liver, kidney, heart, spleen, pancreas, stomach, and intestine of 15 species of temperate birds from Europe and 12 species of subtropical birds from India. We reanalyzed their data to test whether organ mass varied with latitude. In ANCOVAs that incorporated a modified Bonferroni correction (57), we found that heart mass was significantly smaller in subtropical birds than for temperate birds ($F = 8.9$, $P < 0.05$), but wet masses of other organs were not significantly different. The data of Rensch and Rensch (56) offer only weak support for the idea that tropical birds have smaller organs, which suggests that intracellular processes are more important in explaining differences in BMR between tropical and temperate birds.

A number of birds have evolved in the tropics, and live there in the winter, but migrate to temperate areas to breed in spring. These migrants have an expensive lifestyle during migration because of energy demands of long-distance flight. During the nonbreeding period, migrants avoid low $T_a$s, which would demand heat production for thermoregulation, and they avoid inclement weather during winter that may increase mortality (58, 59). Furthermore, life histories of long-distance migrants differ from those of temperate residents. In an analysis of 373 North American and 252 European bird species, long-distance migrants were shown to have smaller clutches, fewer broods and lower annual fecundity than did short-distance migrants and residents (60). In addition, long-distance migrants in some studies had higher survival rates than resident species (59, 61). Because these attributes are consistent with a slower pace of life, we hypothesized that tropical migrants breeding in temperate regions would have lower BMR than temperate residents. We showed that BMR of tropical migrants was lower than temperate resident birds when both were breeding in the same environment, but tropical migrants had an elevated BMR when compared with tropical residents. Differences between these groups cannot be attributed to acclimatization because they were experiencing the same environment. Therefore, we demonstrate in our study an association between physiology of Neotropical migrants and their life-history.

PMR in birds, as estimated by cold exposure, represents maximum oxidative phosphorylation during shivering, and thus defines the capacity for thermogenic heat production. There is no *a priori* reason to suspect that PMR and BMR scale in the same way, because they represent different physiological processes (62). Although slopes of PMR and BMR scaled differently (Table 1), differences were not significant. However, tropical birds had a PMR that was 34% lower, and a thermogenic metabolic scope that was 22% lower than temperate species. Therefore, compared with temperate species, tropical birds had a lower BMR, and this reduction was associated with a reduced PMR.

Physiological change can be the result of acclimatization, adaptation, or a combination of both. One might argue that the differences in physiology between tropical and temperate birds could be a result of acclimatization, physiological adjustments within an individual in response to alteration in environment (63). Whereas changes in BMR may result from acclimatization to environmental variation between seasons (64–66), we have designed our pairwise comparisons of tropical and temperate birds explicitly to minimize differences in BMR attributable to acclimatization. We have measured BMR of species from both the tropics and temperate regions during the breeding season when differences in $T_a$ are relatively small. Based on long-term meteorological data, average air temperature was 23°C in Columbus, Ohio, and 27°C in Gamboa, Panama.

We think that differences in metabolic rate between tropical and temperate birds are, at least in part, the result of natural selection acting on the physiological phenotype, which is optimized to the environment. Our assertion that natural selection is responsible for differences in metabolism between these two groups requires that BMR is heritable, an idea with some support (67–69). Life-history theory suggests that lower extrinsic mortality in the tropics results in a suite of changes in reproductive variables among species that live there, generally described as low reproductive effort (70–72), and that adults allocate more energy to self-maintenance (73), thereby increasing survival rate. When feeding nestlings, tropical house wrens *Troglodytes aedon* had a lower field metabolic rate, made fewer feeding trips to the nest, and raised fewer chicks per brood than did temperate house wrens (74), a finding consistent with theory. We think that part of the increased self-maintenance in tropical birds manifests itself in a reduced pace of life, reflected in a decreased BMR, which correlates with an increase in survival. When ancestral birds that lived in a tropical environment invaded more temperate regions, their reproductive effort increased to compensate for increased extrinsic mortality, and elevated reproductive effort required increased metabolism. Also, as part of this assemblage of traits to increase survival in the tropics, organisms ought to invest more resources in their immune system to thwart disease and increase their probability of survival. This hypothesis suggests the counter intuitive idea that organisms with a decreased BMR might have a higher level of immune function. Tieleman *et al.* (74) found that, in tropical birds, bactericidal activity of whole blood was negatively correlated with mass-adjusted BMR, indicating that species with a slower pace of life have evolved a more robust constitutive innate immune capability.

## Materials and Methods

**Capture of Birds.** In Panama, we mist netted birds in and around Gamboa, (9°7′N, 79°42′W), in secondary growth and rainforest, along Pipeline Road, from April 7 to July 3, 2004 and May 5 to June 8, 2005, whereas, in Ohio, birds were mist netted around Columbus (39°57′N, 82°60′W) in April 2005 and May-July 2006. We housed birds in small cages and provided water and food ad libitum. We measured BMR of birds during the night of the day of capture and released them the following morning before sunrise. We kept a few birds for 24 h before measuring their metabolism.

We weighed birds with a previously calibrated Pesola scale at the end of each metabolic trial and measured their body temperature using a 36-gauge thermocouple and Baily Batt-12 thermocouple reader.

**Measurements of Basal Metabolic Rate.** We measured rates of oxygen consumption $\dot{V}O_2$ by standard flow-through respirom-

etry (75). Beginning at 1900 h, we placed birds in one of four stainless steel metabolism chambers that varied in size from 5.3 to 10.3 liters, depending on the size of the bird. Each chamber was equipped with a Lexan lid, sealed with a rubber gasket. The chambers sat in a large insulated box with a Peltier device (Pelt-4; Sable Systems) to control $T_a$ at $30 \pm 0.1°C$. Preliminary trials on an array of tropical birds confirmed that 30°C was within their thermal neutral zone (J.B.W., unpublished data). Birds perched on wire mesh over a layer of mineral oil that trapped excrement to exclude it as a source of water vapor. Compressed air coursed through columns of Drierite to remove water, through previously calibrated (76) Mykrolis mass flow controllers (FC-2900; 2 standard liters per minute) set between 300 and 800 ml/min (standard temperature and pressure), depending on species, and then into each chamber. We used an automated system of solenoids to sample air from each chamber sequentially. Exiting air first passed through an Edgetech Dewprime II dewpoint hygrometer, then through silica gel, Ascarite, and silica gel to remove water and $CO_2$, and then into an Applied Electrochemistry S3A-II oxygen analyzer. A data logger (Campbell Scientific, model CR23X) recorded fractional concentration of oxygen of air exiting from each chamber for 15 min, then switched to the air stream of the next chamber. Reference air was routed directly from the air tank to one channel of the oxygen analyzer. We validated the entire system for measuring $O_2$ consumption, and measurement error was $\pm 2\%$ (74).

After allowing birds to become accustomed to the chamber for 3 h, we recorded $O_2$ concentration and dewpoint of inlet and outlet air, and $T_a$ within the chamber. We selected the lowest 10-min average of oxygen consumption as an estimate of BMR, which usually occurred during the 4th or 5th hour of measurement. Relative humidity of outlet air was always <30%. Oxygen consumption was calculated with equation 4 of Hill (77). We used 20.08 J/ml $O_2$ to convert oxygen consumption to heat production (78). All BMR data are presented in supporting information (SI) Table 2.

**Literature Data for BMR.** We collated values of BMR for temperate birds from the literature for species from North America or Eurasia (79, 80). We included BMR values in which birds were not raised in captivity or confined for an extended period, were postabsorptive, were in their rest phase, were in the dark at a thermoneutral temperature, and were measured during the breeding season. Including the 13 species that we measured for our paired comparisons, we tabulated 59 estimates of BMR for temperate birds from 17 families.

**Species for Paired Comparisons.** For our paired comparisons, we chose 13 pairs of closely related species from seven families, one couplet from Columbiformes, and the rest belonging to Passeriformes (SI Fig. 4). In paired comparisons, we measured 162 individuals. For 23 species, we measured five or more individuals, whereas for the remaining 3 species, two to four individuals.

**Measurement of Peak Metabolic Rate.** For measurements of PMR (SI Table 3), we used the same system as for measurement of BMR except that we placed birds in a stainless steel chamber within a freezer outfitted with the Peltier device. At the start of a measurement, we maintained birds in the chamber at 30°C until they became calm as judged from traces of their oxygen consumption. Then, incoming air was switched to heliox, a mixture of 21% oxygen and 79% helium (39). We first flushed air from the chamber by infusing heliox at 2,000 ml/min. Then we lowered flow rate to between 400 and 1,500 ml/min, depending on the species, waited for our system to equilibrate, and switched on the freezer. Temperature within the chamber dropped at a rate of 0.7°C/min. One channel of the oxygen analyzer monitored the heliox mixture directly from the tank, whereas the other channel measured the concentration of oxygen in gases coming from the chamber. We recorded $O_2$ concentration and dewpoint temperature of inlet and outlet air, and $T_a$ within the chamber at 1-s intervals.

To estimate peak $\dot{V}O_2$, we calculated an instantaneous rate of oxygen consumption (41, 81). The effective volume of our system was 5,400 ml as estimated from washout curves of $CO_2$. Before calculations, we smoothed curves of changes in oxygen consumption using 5-min running averages of $O_2$ concentrations.

All measurements were carried out under Institutional Animal Care and Use Committee protocol IACUC2004A0093.

**Statistical Analyses.** We used three comparative methods to understand evolutionary diversification in the physiology of tropical and temperate birds. First, we used conventional least squares regression. Second, we used regressions based on phylogenetic independent contrasts (48, 49). Third, we selected 13 tropic-temperate pairs and measured BMR of each species in the pair using the same system and methods. Statistics based on paired comparisons test for differences between trait values of neighboring species with a common ancestor; any differences are likely to have arisen as a result from selection because of environment. If comparisons based on CLSR, PIC, and paired comparisons all support a hypothesis, then results offer compelling evidence.

For CLSR, we used general linear models to fit relationships of BMR (watt) with body mass ($M_b$, grams), climate (either tropical or temperate), migratory status, and phylogenetic clade (either passerine or non-passerine). We used the model log $BMR$ (W) = a + [$b_x$ × categorical variable] + $b_n$ × log $M_b$ (g). For categorical variables, climate, clade, and migratory behavior, we assigned values of 1 for tropical climate, passerine clade, and tropical migrant, and a value of 0 otherwise. We defined a tropical migrant as one that breeds in temperate regions and migrates to the tropics after the breeding season, whereas temperate short-distance migrants were defined as those species that travel south in the fall, but to areas north of the tropics. None of the tropical species that we measured in Panama were migratory.

We constructed a phylogenetic tree of species based on Sibley and Ahlquist (82) with some modifications within Passeriformes following Barker *et al*. (83), Klicka (84), and Yuri (85) (SI Fig. 5). Branch lengths were based on $\Delta T_{50}H$ values. We assigned arbitrary branch lengths of 1 when species were part of an unresolved polytomy (86). When branch lengths were unknown, we set their value to the average branch length of the two neighboring species. We used subsets of this tree when calculating contrasts for a given assemblage of species.

We calculated standardized PICs using PDTREE (87). We standardized branch lengths using either a log-transformation or an exponential function.

We reduced degrees of freedom by the number of unresolved nodes in a tree in statistical tests (88). In regressions based on PIC, all models were fit through the origin (49). To test for differences in BMR within pairs, we used a Wilcoxon signed ranks test (89). Mean values are shown $\pm 1$ SE. We preformed statistical tests using SPSS 13.0, with $\alpha = 0.05$.

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