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RESEARCH ARTICLE

Small organ size contributes to the slow pace of life in tropical birds

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SUMMARY

Attributes of an animal's life history, such as reproductive rate or longevity, typically fall along a 'slow-fast' continuum. Animals at the fast end of this continuum, such as temperate birds, are thought to experience high rates of mortality and invest more resources in reproduction, whereas animals at the slow end, such as tropical birds, live longer, have fewer offspring and invest more resources in self-maintenance. We have previously shown that tropical birds, compared with temperate species, have a reduced basal (BMR) and peak metabolic rate (PMR), patterns consistent with a slow pace of life. Here, we elucidate a fundamental linkage between the smaller mass of central organs of tropical species and their reduced BMR, and between their smaller flight muscles and reduced PMR. Analyses of up to 408 species from the literature showed that the heart, flight muscles, liver, pancreas and kidneys were smaller in tropical species. Direct measurements on 49 species showed smaller heart, lungs, flight muscles, liver, kidneys, ovaries and testes in tropical species, as well as lower feather mass. In combination, our results indicate that the benign tropical environment imposes a relaxed selection pressure on high levels of sustained metabolic performance, permitting species to reduce the mass of organs that are energetically costly to maintain. Brain, gizzard and intestine were exceptions, even though energy turnover of brain and intestine are high. Feather mass was 37% lower in tropical species compared with similar-sized temperate birds, supporting the idea that temperate birds require more insulation for thermoregulation.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/215/10/1662/DC1>

Key words: body composition, organ mass, feather mass, tropical birds, pace of life, basal metabolic rate.

INTRODUCTION

Life-history theory postulates that many physiological traits and behaviour patterns may be understood in terms of key maturational and reproductive characteristics over an organism's life span (Roff, 1992; Stearns, 1992). Variation in these characteristics is thought to reflect different allocation patterns of resources, time and/or energy, to competing life functions, especially growth, body maintenance and reproduction (Charnov, 1993; Ghalambor and Martin, 2001; Williams, 1957). The costs of reproduction are viewed as energy diverted away from bodily maintenance or immunological competence in support of energy allocation for reproduction (Kirkwood, 1977; Sheldon and Verhulst, 1996; Wiersma et al., 2004). Although it is widely acknowledged that physiological processes are the basis of life-history trade-offs, the mechanisms underlying the diversification of life histories remain elusive (Else et al., 2004; Ricklefs and Wikelski, 2002; Speakman, 2008; Stearns, 1992).

Because the rate of metabolism of an organism integrates numerous aspects of its physiology and links those internal systems with its ecology and life history, investigations into functional linkages between metabolism, at the organ, cellular and molecular level, and key attributes of life history hold considerable promise in advancing our understanding of the connections between metabolic rate and life history (Ricklefs and Wikelski, 2002). Some recent studies challenge the idea of a direct causal link between the rate of metabolism and longevity – the rate of living theory (Pearl, 1928; Speakman, 2005; Rottenberg, 2007). However, linkages

among metabolism, free radical production and longevity remain a fundamental assumption in the free radical theory of ageing, a commonly accepted theory amongst many gerontologists, although it is clear that these linkages operate in complex and yet unresolved ways (Rottenberg, 2007; Austad, 2010; Speakman, 2005; Speakman and Selman, 2011).

Across species, body size is the major determinant of the rate of whole-organism metabolism (McNab, 2008; McNab, 2009), often measured as basal metabolic rate (BMR) (McNab, 1997). Peak metabolic rate (PMR), the maximum rate of oxygen consumption, is measured by forcing the animal to exercise, run or fly (PMR_E) (Chappell et al., 1999), or by exposing them to cold (PMR_C) (Swanson and Liknes, 2006). PMR is assumed to be related to fitness because enhanced performance, as measured by locomotor speed, flying endurance or cold tolerance, should increase survival (Burns and Ydenberg, 2002; Husak et al., 2006; Jayne and Bennett, 1990). PMR_E usually exceeds PMR_C in birds (Hinds et al., 1993), suggesting that different physiological mechanisms may be involved when these two variables are measured.

Recently, we demonstrated that tropical birds have an 18% lower BMR, 34% lower PMR_C and 39% lower PMR_E compared with temperate species (Wiersma et al., 2007a; Wiersma et al., 2007b). Along with a reduced metabolism, tropical birds tend to have a smaller clutch size than their temperate counterparts (Cardillo, 2002; Kulesza, 1990), have protracted nestling and fledgling periods (Russell et al., 2004; Schaefer et al., 2004; Tarwater and Brawn, 2010), and tend to live longer than temperate species (Fogden, 1972;

Francis et al., 1999; Johnston et al., 1997; Ricklefs, 1997; Snow and Lill, 1974). This suite of physiological and life-history characteristics is often embodied in the phrase 'slow pace of life' (Promislow and Harvey, 1990; Ricklefs and Wikelski, 2002).

Progress in understanding the evolution of metabolic rates requires knowledge of the physiological mechanisms acted upon by natural selection that produce variation in metabolism (Williams et al., 2010). Metabolic intensity of tissues may vary because of differences in mitochondria (Else and Hulbert, 1985; Moyes, 2003; Porter, 2001; Suarez, 1996), concentrations of metabolic enzymes (Garrido et al., 1996; Marsh and Dawson, 1982; Vézina and Williams, 2005; Weber and Piersma, 1996), activity of the membrane sodium pump (Wu et al., 2001) and fatty acid composition of cell membranes (Brzek et al., 2007; Hulbert and Else, 2005). Variation in BMR between lowland tropical birds and their temperate counterparts could arise if the relative size of some or all of the central organs in tropical species were smaller (Piersma et al., 1996). In a study that employed data on human organ masses and organ-specific metabolism, about 60% of resting oxygen consumption could be attributed to the liver, brain, heart and kidneys, but these organs together accounted for only 5% of body mass (Gallagher et al., 1998). Mass-specific oxygen consumption, or metabolic intensity, of these tissues exceeds that of tissues from the gastro-intestinal tract, lungs and muscle by 2–5 times (Elia, 1992; Krebs, 1950). Studies within species have shown correlations between BMR and masses of central organs (Brzek et al., 2007; Chappell et al., 1999; Even et al., 2001; Piersma et al., 1996), but other studies have failed to find correlations between BMR and sizes of central organs within species (Geluso and Hayes, 1999; Russell and Chappell, 2007). In some interspecific comparisons, authors have elucidated positive correlations between BMR and sizes of some organs (Daan et al., 1990; Raichlen et al., 2010), but other studies have failed to find such an association (Tieleman et al., 2003).

During exercise, oxygen consumption of skeletal muscles increases to more than 90% of the total, requiring blood flow to be routed away from central organs to muscles (Taylor et al., 1981). Because cold- and exercise-induced PMR is lower in tropical compared with temperate birds (Wiersma et al., 2007a; Wiersma et al., 2007b), one might predict that skeletal muscles are smaller in tropical species.

In this paper, we identify a functional linkage between the low rate of basal metabolism in tropical birds and the small size of their central organs. Further, we offer compelling evidence that the low PMR of tropical birds can be explained, at least in part, by a reduction in skeletal muscle mass. Our approach included collation of a large data set on organ sizes of birds from the literature and direct measurement of organ sizes of lowland tropical species and species from Ohio. The results from literature data and our direct measurements offer unequivocal evidence that tropical birds have smaller heart, lungs, liver, pancreas, kidneys, ovaries and testes than do temperate species of the same body size, which accounts for, at least in part, their lower rate of basal metabolism. Moreover, we found that flight muscles of tropical birds were 18% smaller than those of temperate species. This suggests that natural selection has adjusted organ size to fit the ecological needs of a species, and this affects their overall rate of metabolism.

MATERIALS AND METHODS

We obtained organ masses for 408 species from the literature (supplementary material Table S1). Origins of birds collected by Hartman (Hartman, 1961) were corroborated using original data provided by J. Condit, Museum of Biological Diversity, Columbus,

OH, USA, and by G. Ludwig, National Museum of Natural History, Washington, DC, USA. Data for organs from birds that were collected from the southern USA were excluded from analyses. Based on information on habitat and distribution, tropical birds collected by Hartman ($N=295$) (Hartman, 1955; Hartman, 1961) originated mainly from lowland Panama, but a few specimens apparently came from altitudes of 1000–2000 m. Crile and Quiring (Crile and Quiring, 1940) collected birds in eastern Africa, mainly Lake Manyara, Tanzania ($N=16$), and from lowland Guatemala ($N=1$), whereas Rensch and Rensch (Rensch and Rensch, 1956) gathered data on tropical birds near Mysore, India, elevation *ca.* 770 m ($N=9$). We assigned a species as temperate when they were collected at latitudes between 35°N and 67°N or S, and as tropical when they were collected between 23°N and 23°S. We excluded organ masses of long-distance migrants. Where individual or sex-specific values were given for the mass of organs, we calculated the mean. We used organ dry mass in our analyses. Because all authors reported wet organ mass, we estimated organ dry mass based on measurements of water content that we had made. Conclusions did not vary when we used wet or dry organ mass in our analyses. Body masses of all birds were obtained from original sources.

We directly measured organ sizes of 32 species of lowland tropical birds, captured with mist nets in and around Gamboa, Panama (9°7'N, 79°42'W) in March–June, 2006 and 2007, and of 17 species of temperate birds, collected with mist nets during the breeding season in Ohio in 2006 and 2007 (supplementary material Table S2). Birds were killed by cervical dislocation; all feathers were removed and the brain (including brainstem), gonads (including oviduct for females), stomach, intestines (excluding pancreas), liver, kidneys, heart, lungs, flight muscles (pectoralis and supracoracoideus), leg muscles, spleen and gallbladder excised. Intestines and gizzard were opened and the contents removed by washing. We removed visible fat from body components prior to weighing. We counted all remaining tissue including the skeleton and excluding skin in the category 'carcass'. Organs were placed in preweighed aluminium trays and feathers in previously dried paper bags. We dried both to constant mass for a minimum of 3 days in an oven at 70°C. Dried organs and feathers were weighed to the nearest 0.1 mg using a Mettler analytical balance.

All procedures were approved by the Institutional Animal Care and Use Committee of The Ohio State University (protocol IACUC2004A0093) and capture of birds in Panama was accomplished under permit from Panamanian Autoridad Nacional del Ambiente (No. SE/A-36-06) and Autoridad del Canal de Panamá.

Statistics

We used phylogenetic generalized least squares (PGLS) analyses to test for the effect of climate (tropical or temperate) on dry mass of tissues. For data from the literature, dry masses of organs were regressed against climate and fresh body mass, from which the mass of the focal organ had been subtracted to ensure independence of data (Christians, 1999). In addition, the source of data was added as an independent variable to control for methodological differences among investigators. In analyses of our direct measurements of organ size, we controlled for sex, diet and migratory behaviour (see supplementary material Table S2). To control for size we used dry carcass mass instead of body mass. Carcass mass, which included the skeleton, was the remainder of tissues after all major organs had been removed. Because body mass includes the mass of the focal organ, it is not an independent variable. Subtracting the mass of the

focal organ from body mass would in most cases not solve the problem because the sizes of other organs often covary with the mass of the focal organ.

We used PGLS because this method is an improvement over previous methods of incorporating phylogeny into statistical models, such as phylogenetic independent contrasts (PIC), because it can test and modify assumptions within these earlier models, and provide information on how traits have evolved by selecting the most appropriate evolutionary model. PGLS is a regression model where the structure of the error term incorporates the phylogeny of the species by adjusting the variance–covariance matrix, thus taking into account the independence of data points as a result of phylogenetic history (Paradis, 2006; Rohlf, 2001). Covariances can be manipulated to conform to different models of trait evolution and to incorporate varying degrees of phylogenetic signal. Three models of trait evolution were evaluated and the best model was selected on the basis of corrected Akaike information criteria (AIC_C) (Burnham and Anderson, 2002). Pagel's model modifies covariances between species by multiplying with a constant, λ , as estimated by the model. When species traits are phylogenetically uncorrelated, $\lambda=0$, and when there is a strong phylogenetic signal within the data, $\lambda=1$. For the latter trait, evolution follows Brownian motion where differences in traits between species are proportional to the time since divergence (Felsenstein, 1985). The second model that was evaluated incorporated stabilizing selection, where trait covariances decrease exponentially with increasing time since divergence and where the strength of the directional selective force is controlled by parameter α (Martins and Hansen, 1997). The model allows trait evolution to vary between non-directional Brownian motion ($\alpha=0$) and strong directional selection ($\alpha=1$). Grafen's model first calculates branch lengths based on number of descendants, thereby discarding information on branch lengths (Grafen, 1989). The tree is scaled so that the root has depth 1, and branch lengths are raised to the power ρ . When $\rho=1$, a strong phylogenetic signal is implied.

PGLS statistics were performed in R v.2.12 (R Development Core Team, 2011) using the package *ape* v.2.6 (Paradis et al., 2004) to calculate phylogenetic correlation structures, package *nlme* v.3.1 (Pinheiro et al., 2011) for PGLS analyses and package *AICcmodavg* v.1.14 (Mazerolle, 2011) for calculating AIC_C .

Because potential errors in phylogeny could affect the outcome of statistical tests, we also compared organ masses within phylogenetically closely related pairs of tropical–temperate species (supplementary material Table S3). Differences between sister species from separate environments are not likely to be the result of phylogenetic distance. Pair-wise analysis uses less phylogenetic information but also restricts the number of data points to species with recent common ancestors. Analyses were performed using linear mixed models with species pair and intercept entered as random effects. We entered 'carcass mass', 'climate', 'sex', 'diet' and 'migratory behaviour' as independent variables. Mixed models were performed using SPSS v. 19 (SPSS Inc., Chicago, IL, USA).

Phylogenies

For the large number of species in our data set from the literature, we used a family-level tree and included species of the same family as polytomies. We used the family tree of Sibley and Ahlquist (Sibley and Ahlquist, 1990), which was obtained from the R-package 'ape'.

The phylogenetic relationships for species that we directly measured were based on information assembled by Boyd (Boyd,

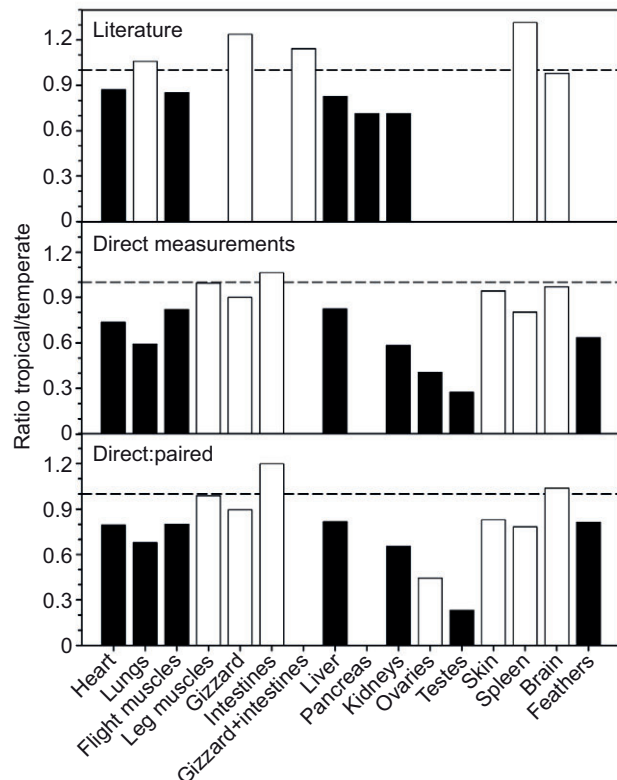


Fig. 1. Ratios of the difference in dry mass between organs of tropical and temperate species. Because models were linear and, except for feather mass, contained no interactions, the results are not affected by body size, sex, migratory strategy or diet. Filled bars represent a significant difference between tropical and temperate species.

2011) (supplementary material Fig. S1). Branch lengths were derived from Sibley and Ahlquist (Sibley and Ahlquist, 1990). When a species' phylogeny was not resolved, we introduced a polytomy. Individuals of one species were incorporated into the tree as polytomies at the tips with zero branch lengths. Trees were manipulated using TreeGraph 2 (Stöver and Müller, 2010) and Mesquite (Maddison and Maddison, 2010).

RESULTS

Based on literature data, heart, flight muscles, liver, pancreas and kidneys were 13–29% smaller in tropical species (Fig. 1, Table 1). Direct measurement of organ masses showed that heart, lungs, flight muscles, liver, kidneys, ovaries, testes and feathers were significantly lighter in tropical species (Fig. 1, Table 2). These differences ranged from –18% for the flight muscles and liver to –72% in reproductive organs. Leg muscles, gizzard, intestine and skin did not statistically differ between climates. Fresh mass of all organs summed was 14.8% lower in tropical than in temperate birds with equal carcass mass. Masses of several organs were correlated with sex, migratory behaviour and diet (Table 2). Lungs were smaller in our direct measurements but not in data from the literature. Gizzard, intestine and brain were not significantly different in either data set. In our direct measurements, feather mass was significantly lower in tropical birds. The slope of the relationship between feather mass and body mass was shallower in temperate species, indicating that small temperate species had relatively more feathers (Fig. 2).

When we compared organs from phylogenetically paired comparisons, we found significantly reduced sizes of heart, lungs,

Table 1. Results of phylogenetic generalized least squares (PGLS) models describing dry tissue mass as a function of body mass minus fresh focal tissue mass, tropical or temperate climate

	Gizzard+									
	Heart	Lungs	Flight muscles	intestines	Gizzard	Liver	Pancreas	Kidneys	Spleen	Brain
Intercept	-1.718±0.067***	-1.554±0.126***	-0.603±0.068***	-0.835±0.226**	-1.808±0.350***	-1.096±0.083***	-2.837±0.339***	-1.715±0.086***	-2.870±0.646***	-0.952±0.080***
log ₁₀ body mass [†]	0.901±0.014***	0.911±0.044***	1.010±0.015***	0.933±0.086***	1.140±0.142***	0.850±0.029***	1.106±0.028***	0.914±0.030***	1.040±0.252***	0.607±0.018***
Climate (=tropical)	-0.0602±0.0135***	0.0244±0.0579	-0.0700±0.0334*	0.0580±0.1318	-0.154±0.113	-0.0831±0.0387*	-0.147±0.001***	-0.147±0.036***	0.119±0.354	-0.00877±0.0179
Source=1	0	0		0		0		0	0	0
Source=2										-0.0445±0.0202*
Source=3										-0.0881±0.0527
Source=4	-0.135±0.025***		0							
Source=5						-0.141±0.136			-0.233±0.737	
Source=6	-0.143±0.039***				0	-0.148±0.056*	0	-0.0175±0.0553	-0.0901±0.4345	
d.f. (residual, total)	403, 408	29, 32	285, 288	9, 12	9, 12	45, 50	5, 8	41, 45	15, 20	134, 139
AIC _c Pagel	-627.3 (λ=0.736)	-7.6 (λ=0.409)	-536.9 (λ=0.793)	13.7 (λ=0.007)	-58.5 (λ=1.000)	-31.7 (λ=0.000)	35.5 (λ=1.000)	-35.0 (λ=0.045)	59.1 (λ=-0.077)	-218.2 (λ=0.867)
AIC _c Grafen	-536.6 (p=0.169)	-6.1 (p=0.174)	-479.8 (p=0.287)	13.5 (p=0.063)	18.7 (p=0.000)	-29.0 (p=0.000)	32.6 (p=7.676)	-35.8 (p=0.108)	59.1 (p=0.000)	-189.2 (p=0.403)
AIC _c Martins	-490.3 (α=1.000)	-4.1 (α=1.000)	-452.4 (α=1.000)	19.9 (α=1.000)	19.4 (α=1.000)	-7.3 (α=1.000)	37.4 (α=1.000)	-16.6 (α=1.000)	68.4 (α=1.000)	-161.0 (α=1.000)

Data are log₁₀ tissue or organ mass and were collected from literature sources.

The phylogeny was revolved down to family level. Shown are parameter estimates with standard errors and *P*-value categories, as well as degrees of freedom (total=number of species), evolutionary model parameter estimates and corrected Akaike information criteria (AIC_c) values of final model.

Significant variables are shaded grey as is the model with the lowest AIC_c.

P*<0.05; *P*<0.01; ****P*<0.001.

[†]Excluding mass of focal tissue.

Source=0 for reference category or indicating the single data source. Source 1 (Crile and Quiring, 1940), 2 (Garamszegi et al., 2002), 3 (Graber and Graber, 1965), 4 (Hartman, 1955; Hartman, 1961), 5 (Oakeson, 1956), 6 (Rensch and Rensch, 1956).

flight muscles, liver, kidneys, testes and feathers in tropical birds, in support of our previous findings (Table 3).

We examined scaling exponents for each organ to evaluate whether organs scaled differently between tropical and temperate birds and whether masses increased in proportion with body size. Most organs scaled in proportion to body size except for the heart, liver and kidneys, with lower slopes of around 0.88, and brain which had a slope of 0.555 (*t*-tests, *P*<0.05; Table 2). Slopes did not differ between tropical and temperate species for any organ (PGLS, testing for interaction between carcass mass and climate, all *P*>0.05). The slope for feather mass was higher in tropical species (Fig. 2).

DISCUSSION

We have demonstrated a strong link between a slow pace of life in tropical birds and smaller organ sizes. Our results indicate that the heart, liver, pancreas, lungs, flight muscles, kidneys, ovaries and testes were reduced in mass in tropical species, which will contribute significantly to the birds' reduced BMR. Moreover, we found that muscles that power flight are significantly reduced in tropical species, which would contribute to the reduced PMR (see Vézina et al., 2006). Feather mass was greater in temperate species, a likely requirement for their larger thermoregulatory demand. Despite its high energy turnover and diversification in size among bird taxa (Nealen and Ricklefs, 2001), brain size was similar in tropical and temperate birds.

Model estimates inform about phylogenetic signal and the evolutionary trajectory that best fits that data. The method of PIC (Felsenstein, 1985) depends on a model with maximum phylogenetic correlation as predicted by Brownian motion. Although the extent of the phylogenetic signal in literature data and our direct measurements varied considerably, in most cases controlling for phylogeny was warranted (Pagel's λ in Tables 1 and 2), but estimates of model parameters, in particular λ and ρ , showed that the optimal

models for organ masses were, in general, intermediate between a star phylogeny and our structured phylogeny based on DNA hybridization.

BMR depends on the mass of organs and tissues and on the metabolic intensities of their cells. Krebs (Krebs, 1950) showed that tissue metabolism of mammals scaled allometrically with BMR as body size increased, findings later confirmed by more precise measurements (Savage et al., 2007). We showed earlier that the allometric slope for BMR of birds from the same areas and time of year, and often of the same species as analysed here for organ masses, is close to 0.67 (Wiersma et al., 2007a). Masses of most organs, except brain, spleen, ovaries and testes, varied with body mass, with slopes exceeding 0.67, and only brain, heart, liver and kidneys had slopes lower than 1 (*t*-tests, correcting for body mass for proper comparison with slopes for BMR; supplementary material Table S4). This evidence is consistent with the idea that the metabolic intensity of organ tissues decreases with increasing body mass. Allometric exponents for organ masses did not differ between tropical and temperate species.

We found that tropical birds have a smaller feather mass than temperate species. When birds live in conditions like the lowland tropics where the air temperature rarely falls below the lower critical temperature, and where high air temperatures may be more problematic, possessing a plumage with low insulation may be advantageous. It reduces energy expenditure at high temperatures and reduces costs of growth and maintenance of feathers. Indeed, feather mass was on average 37% lower in tropical species (Fig. 1). Scholander et al. (Scholander et al., 1950) showed that the insulative properties of arctic mammal fur were higher than those of tropical mammals, and speculated that birds showed the same pattern. Our results lend support to Scholander's idea. Moreover, we showed that slopes for feather mass were higher in tropical than in temperate species (1.10 versus 0.95; *P*<0.01): small tropical birds have lower

Table 2. Results of PGLS models describing dry tissue mass as a function of dry carcass mass, tropical or temperate climate, sex, migratory strategy and diet

	Heart	Lungs	Flight muscles	Leg muscles	Gizzard	Intestines	Liver
Intercept	-1.442±0.0574***	-1.460±0.055***	-0.312±0.0704***	-1.018±0.090***	-1.460±0.1290***	-1.543±0.126***	-1.015±0.084***
log ₁₀ dry carcass mass	0.872±0.0332***	0.956±0.038***	0.990±0.035***	1.105±0.041***	0.907±0.072***	1.063±0.076***	0.881±0.047***
Climate (=tropical)	-0.133±0.017***	-0.228±0.024***	-0.0855±0.0152***	-0.0022±0.0164	-0.0459±0.0473	0.0267±0.0402	-0.0841±0.0231**
Sex (=male)	0.0317±0.0118**	0.0254±0.0143*	0.00165±0.01036	-0.0167±0.0113	-0.0364±0.0216	-0.107±0.029**	-0.0326±0.0160*
Migrant (=yes)	-0.0666±0.0289*	0.0269±0.0388	0.0148±0.0264	-0.0125±0.0290	-0.215±0.074**	-0.0365±0.0690	-0.0312±0.0395
Diet (=granivorous)	-0.0453±0.0296	-0.0169±0.0379	-0.0268±0.0314	-0.0366±0.0380	0.321±0.078***	-0.189±0.089**	-0.171±0.042***
Diet (=insectivorous)	-0.0588±0.0350	-0.0727±0.0411	-0.0947±0.0395*	-0.0564±0.0482	0.330±0.090**	-0.194±0.0783*	-0.138±0.050**
Diet (=nectivorous)	0.129±0.104	0.0062±0.0874	0.0605±0.1354	-0.218±0.178	-0.298±0.164	-0.0385±0.2257	-0.0811±0.1550
Diet (=omnivorous)	-0.0933±0.0302**	-0.0635±0.0398	-0.0797±0.0338*	0.0469±0.0418	0.248±0.085**	-0.127±0.069	-0.152±0.043**
Diet (=frugivorous)	0	0	0	0	0	0	0
d.f. (residual, total)	175, 184	176, 185	178, 187	178, 187	174, 183	177, 186	177, 186
AIC _C Pagel	-335.5 (λ=0.629)	-269.0 (λ=0.509)	-367.2 (λ=0.858)	-324.4 (λ=0.923)	-72.3 (λ=0.837)	-25.7 (λ=0.520)	-225.6 (λ=0.690)
AIC _C Grafen	-333.5 (p=0.141)	-270.7 (p=0.127)	-364.8 (p=0.373)	-312.0 (p=0.336)	-99.8 (p=0.330)	-21.7 (p=0.096)	-221.8 (p=0.138)
AIC _C Martins	NA	-252.9 (α=0.724)	NA	-314.0 (α=0.075)	NA	-8.6 (α=0.589)	-217.7 (α=0.540)
	Kidneys	Ovaries	Testes	Skin	Spleen	Brain	Feathers
Intercept	-1.401±0.057***	-1.634±0.299***	-1.940±0.333***	-1.042±0.068***	-2.680±0.247***	-1.171±0.057***	-0.375±0.073***
log ₁₀ dry carcass mass	0.894±0.037***	0.845±0.318***	1.132±0.238***	1.056±0.061***	0.925±0.158***	0.599±0.029***	1.035±0.043***
Climate (=tropical)	-0.234±0.024***	-0.390±0.151***	-0.560±0.158***	-0.0256±0.0261	-0.0955±0.0972	-0.0126±0.0133	-0.198±0.021***
Sex (=male)	-0.0264±0.0128*			-0.0475±0.0160**	-0.0988±0.0726	0.0156±0.009	-0.0061±0.0145
Migrant (=yes)	-0.0923±0.0376*	-0.395±0.290	0.202±0.252	-0.0259±0.0420	-0.0749±0.1548	-0.0462±0.0231*	0.0515±0.0346
Diet (=granivorous)	-0.187±0.038***	-0.752±0.289***	-0.276±0.242	0.0095±0.0573	-0.0811±0.180	0.0145±0.0270	0.0569±0.0379
Diet (=insectivorous)	-0.0585±0.0418	-0.411±0.290	-0.215±0.257	0.0006±0.0680	-0.164±0.185	-0.0127±0.0333	-0.0095±0.0476
Diet (=nectivorous)	0.0511±0.0844	-0.239±0.608	-0.683±0.555	-0.0892±0.0623		-0.0751±0.1085	
Diet (=omnivorous)	-0.142±0.040**	-0.341±0.329	-0.0330±0.2479	-1.042±0.068	-0.0724±0.1652	0.0524±0.0284	0.0306±0.0390
Diet (=frugivorous)	0	0	0	0	0	0	0
d.f. (residual, total)	176, 185	50, 58	50, 58	101, 109	112, 120	175, 184	112, 120
AIC _C Pagel	-301.3 (λ=0.651)	117.5 (λ=1.000)	307.7 (λ=1.000)	-137.6 (λ=0.841)	152.1 (λ=0.257)	-412.3 (λ=0.816)	-164.2 (λ=0.686)
AIC _C Grafen	-302.1 (p=0.184)	106.0 (p=0.155)	205.7 (p=0.162)	-131.6 (p=0.233)	152.6 (p=0.031)	-401.5 (p=0.253)	-201.9 (p=0.134)
AIC _C Martins	-272.3 (α=0.709)	100.9 (α=0.260)	201.5 (α=0.156)	-139.1 (α=0.158)	152.4 (α=1.221)	-371.1 (α=0.071)	-200.8 (α=0.444)

Data are log₁₀ tissue or organ mass.

Migratory strategy: long-distance migrants that breed in North America and migrate at least as far as Central America vs sedentary birds and short-distance migrants.

Parameter estimates for alternative variable values are used as reference and equal 0 and are not shown. For diet, frugivory is used as reference category.

Shown are parameter estimates with standard errors and *P*-value categories, as well as degrees of freedom (total=number of specimens), evolutionary model parameter estimates and AIC_C values of final model. Significant variables are shaded grey as is the model with lowest AIC_C. When a model did not converge AIC_C=NA.

P*<0.05; *P*<0.01; ****P*<0.001.

feather mass but these differences diminish as body size increases (Fig. 2). Because the surface to volume ratio increases when body size decreases, we hypothesize that it is more advantageous for temperate birds that are small to have extra insulation than it is for larger birds as a result of the former's high thermoregulatory requirements at low ambient temperatures. In addition, because lower critical temperatures increase with body size, small birds are likely to have greater selection pressure to increase insulation.

Ultimately, evolutionary physiologists seek to identify selection pressures that fashion physiological phenotypes occurring within a given environment. In the tropics, it is plausible that individuals have lower energy needs than their temperate counterparts. Tropical birds have a shorter day length in which they can be active compared with temperate birds during the breeding season, live in an environment that is stable and warm, and are likely to have abundant food resources. Because in a benign environment birds may have lower energy demands, we suggest that selection has down-regulated organ systems responsible for digestion and heat production (Piersma et al., 1996). In colder environments, selection might be expected to favour individuals with a greater capacity for activity and thermoregulation, requiring more energy intake and larger organs to process food (Kersten et al., 1998). Contrary to our expectations, gizzard and intestines were not reduced in tropical

species (Fig. 1), which is remarkable considering the presumed high metabolic costs of intestinal tissue (Aiello and Wheeler, 1995). However, the metabolic intensity of mammalian intestines varies considerably, so we do not know that intestinal tissues of birds have high rates of metabolism (Aiello and Wheeler, 1995). Moreover, the intestinal tract of mammals is considerably larger than that of birds (Isler and van Schaik, 2006). For example, intestines represent 2.1% of fresh body mass in our data and 9.1% in mice of 20 g (Konarzewski and Diamond, 1995). But even if the metabolic costs of the intestines are minimal, the question of why their size does not follow the general pattern of other central organs in tropical and temperate birds remains.

Our data are also consistent with the heat dissipation limit theory, which assumes that maximum rates of heat loss limit reproductive effort, causing the association between life-history variables and body mass (Speakman and Król, 2010). In this view, tropical birds are under selection to minimize energy expenditure and maximize heat loss, which can be achieved by having smaller organs and reduced insulation.

Only a small fraction of total body mass consists of internal organs, in tropical birds 9.5–15.5%, but because these organs have high metabolic intensities, they contribute towards a significant part of BMR (Elia, 1992). Rather than operating directly on BMR, we

Table 3. Results of pair-wise comparisons of dry tissue masses of 10 pairs of closely related temperate–tropical species, controlling for body size using log dry carcass mass, sex, migratory strategy and diet

	Heart	Lungs	Flight muscles	Leg muscles	Gizzard	Intestines	Liver
Intercept	-1.359±0.090***	-1.517±0.089***	-0.343±0.076***	-1.018±0.139***	-2.179±0.142***	-1.345±0.161***	-0.903±0.058***
log ₁₀ dry carcass mass	0.718±0.076***	0.813±0.087***	1.147±0.068***	1.166±0.080***	1.197±0.139***	1.024±0.161***	0.957±0.054***
Climate (=tropical)	-0.0997±0.0221***	-0.167±0.029***	-0.0970±0.0206***	-0.0044±0.0212	-0.0483±0.0469	0.0793±0.0607	-0.0876±0.0295*
Sex (=male)	0.0371±0.0146*	0.0343±0.0198	-0.0007±0.0135	-0.0361±0.0137*	-0.0336±0.0318	-0.136±0.042**	-0.0560±0.0211
Migrant (=yes)	-0.0287±0.0314	0.0633±0.0420	-0.0080±0.0290	-0.0126±0.0296	-0.115±0.068	-0.0577±0.0890	-0.0517±0.0414
Diet (=granivorous)	0.0133±0.0432	0.125±0.061*	-0.0155±0.0408	-0.110±0.0412**	0.711±0.098***	-0.324±0.126*	-0.301±0.064***
Diet (=insectivorous)	-0.112±0.0970	0.0031±0.0904	-0.141±0.081	0.0091±0.1619	0.974±0.145***	-0.167±0.160	-0.179±0.054**
Diet (=nectivorous)	-0.159±0.153	-0.0923±0.1506	0.183±0.129	-0.0545±0.2397	0.779±0.241**	-0.306±0.272	-0.137±0.097
Diet (=omnivorous)	0.0994±0.0981	-0.0366±0.0915	0.232±0.081*	-0.106±0.168	-0.710±0.146**	0.0958±0.1624	0.208±0.061**
Diet (=frugivorous)	0	0	0	0	0	0	0
N (temperate, tropical)	51, 48	50, 49	51, 49	51, 49	51, 46	51, 48	52, 48
	Kidneys	Ovaries	Testes	Skin	Spleen	Brain	Feathers
Intercept	-1.462±0.058***	-0.424±0.358*	-1.369±0.467*	-1.061±0.104***	-2.725±0.245***	-1.015±0.042***	-0.237±0.117
log ₁₀ dry carcass mass	0.833±0.058***	0.317±0.610	1.362±0.735	1.231±0.137***	1.190±0.267***	0.365±0.040***	0.675±0.104***
Climate (=tropical)	-0.185±0.024***	-0.352±0.209	-0.634±0.247*	-0.0810±0.0537	-0.106±0.116	0.0158±0.0179	-0.0907±0.0285**
Sex (=male)	-0.0417±0.0165*			-0.0399±0.0252	-0.145±0.084	0.0250±0.0127	-0.000±0.014
Migrant (=yes)	-0.0497±0.0344	-0.406±0.261	0.221±0.331	0.101±0.066	0.147±0.160	-0.0240±0.0260	0.172±0.037***
Diet (=granivorous)	-0.144±0.051**	-1.897±0.338***	-0.662±0.492	-0.0356±0.0759	-0.229±0.246	-0.0505±0.0402	0.189±0.042***
Diet (=insectivorous)	0.0547±0.0564	-1.480±0.352*	-0.874±0.460	0.0205±0.1001	-0.179±0.208	-0.0323±0.0410	-0.104±0.131
Diet (=nectivorous)	-0.102±0.097		-1.303±0.749			-0.369±0.069***	0.148±0.132
Diet (=omnivorous)	0.0106±0.0588	1.163±0.520*	-0.787±0.664	0.239±0.108*	-0.365±0.262	-0.147±0.043**	-0.148±0.132
Diet (=frugivorous)	0	0	0	0	0	0	0
N (temperate, tropical)	51, 49	18, 17	27, 31	52, 48	49, 29	51, 49	52, 49

Data are log₁₀ dry tissue or organ mass.

Migratory strategy: long-distance migrants that breed in North America and migrate at least as far as Central America vs sedentary birds and short-distance migrants.

Parameter estimates for alternative variable values are used as reference and equal 0 and are not shown. For diet, frugivory is used as reference category.

Data were collected in Panama and Ohio. Shown are parameter estimates with standard errors and *P*-value categories, as well as sample sizes.

Significant variables are shaded grey.

P*<0.05; *P*<0.01; ****P*<0.001.

argue that there is strong selection on organ systems that support levels of activity measured as sustained metabolic rates (Książek et al., 2004) or as indexed by maximum metabolic performance in birds, measured by PMR_C and PMR_E. Recent insight into genes that

regulate cell and organ growth through transcriptional regulation of protein and lipid synthesis may point to the specific targets for natural selection (Portsmann et al., 2009).

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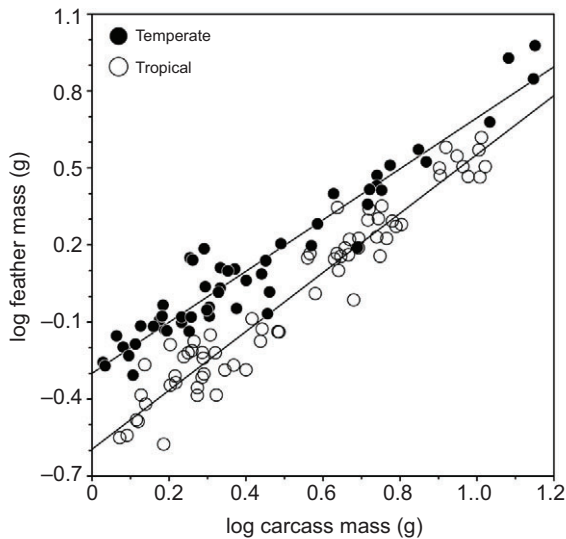


Fig. 2. Dry feather mass in relation to dry carcass mass of 123 specimens of 14 tropical and 13 temperate bird species. The interaction between feather mass and carcass mass was significant: phylogenetic generalized least squares (PGLS) with sex, diet and migratory behaviour as covariates, interaction log feather mass × log carcass mass: 0.150±0.054 (mean ± s.e.m.) for tropical species and 0 for temperate species, *t*=2.80, *P*<0.01; Pagel's λ =0.680.

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