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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.

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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<sub>E</sub>) (Chappell et al., 1999), or by exposing them to cold (PMR<sub>C</sub>) (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<sub>E</sub> usually exceeds PMR<sub>C</sub> 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<sub>C</sub> and 39% lower PMR<sub>E</sub> 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<sub>C</sub>) (Burnham and Anderson, 2002). Pagel's model modifies covariances between species by multiplying with a constant,  $\lambda$ , 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  $\alpha$  (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  $\rho$ . 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<sub>C</sub>.

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,

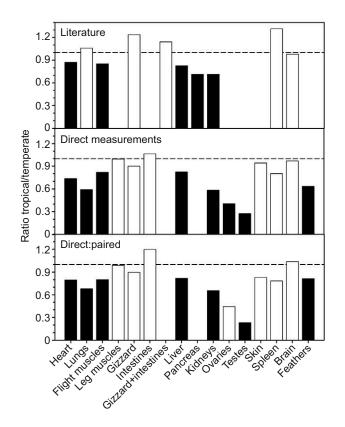


Fig. 1. Ratios of the difference in dry mass between organs of tropical and temperate species. Because models were linear and, except for feather mass, contained no interactions, the results are not affected by body size, sex, migratory strategy or diet. Filled bars represent a significant difference 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, intestines 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+	, 1					
	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 <sub>10</sub> body mass <sup>†</sup>	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	-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
(=tropical)										
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,	403, 408	29, 32	285, 288	9, 12	9, 12	45, 50	5, 8	41, 45	15, 20	134, 139
total)										
AIC <sub>c</sub> 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 <sub>c</sub> Grafen	-536.6 (ρ=0.169)	-6.1 (ρ=0.174)	-479.8 (ρ=0.287)	13.5 (ρ=0.063)	18.7 (ρ=0.000)	–29.0 (ρ=0.000)	32.6 (p=7.676)	-35.8 (ρ=0.108)	59.1 (ρ=0.000)	-189.2 (ρ=0.403)
AIC <sub>c</sub> 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 lo	og <sub>10</sub> tissue or or	gan mass and	were collected	from literature	e 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<sub>c</sub>) values of final model. Significant variables are shaded grey as is the model with the lowest AIC<sub>c</sub>.

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

<sup>†</sup>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  $\lambda$  in Tables 1 and 2), but estimates of model parameters, in particular  $\lambda$  and  $\rho$ , 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

			migratory strateg	gy and dict			
	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 <sub>10</sub> 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 <sub>c</sub> 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 <sub>c</sub> Grafen	–333.5 (ρ=0.141)	–270.7 (ρ=0.127)	-364.8 (ρ=0.373)	–312.0 (ρ=0.336)	–99.8 (ρ=0.330)	-21.7 (ρ=0.096)	–221.8 (ρ=0.138)
AIC <sub>c</sub> 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 <sub>10</sub> 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 <sub>c</sub> 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 <sub>c</sub> Grafen	-302.1 (ρ=0.184)	106.0 (ρ=0.155)	205.7 (ρ=0.162)	–131.6 (ρ=0.233)	152.6 (ρ=0.031)	-401.5 (ρ=0.253)	–201.9 (ρ=0.134)
AIC <sub>c</sub> 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 log<sub>10</sub> 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<sub>C</sub> values of final model. Significant variables are shaded grey as is the model with lowest AIC<sub>C</sub>. When a model did not converge AIC<sub>C</sub>=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 occuring 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

	body	size using log	ury carcass mass	, sex, migratory s	lialegy and uler		
	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 <sub>10</sub> 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)	$-0.0997 \pm 0.0221^{***}$	-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 <sub>10</sub> 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
N (temperate, tropical)	51, 49	18, 17	27, 31	52, 48	49, 29	51, 49	52, 49

Data are log<sub>10</sub> 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 (Ksiazek et al., 2004) or as indexed by maximum metabolic performance in birds, measured by PMR<sub>C</sub> and PMR<sub>E</sub>. Recent insight into genes that

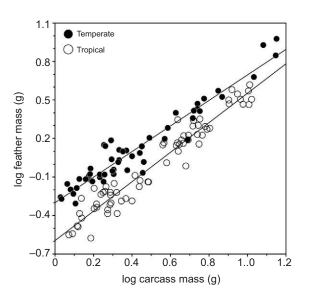


Fig. 2. Dry feather mass in relation to dry carcass mass of 123 specimens of 14 tropical and 13 temperate bird species. The interaction between feather mass and carcass mass was significant: phylogenetic generalized least squares (PGLS) with sex, diet and migratory behaviour as covariates, interaction log feather mass  $\times$  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  $\lambda$ =0.680.

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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#### REFERENCES

 Aiello, L. C. and Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Curr. Anthropol.* 36, 199-221.
Austad, S. N. (2010). Cats, 'rats,' and bats: the comparative biology of aging in the

- 21st century. Integr. Comp. Biol. 50, 783-792. Boyd, J. H., III (2011). Aves-A taxonomy in flux, v2.5, accessed 15-2-2011. Available
- at: http://jboyd.net/Taxo/taxo1.html.
- Brzek, P., Bielawska, K., Ksiazek, A. and Konarzewski, M. (2007). Anatomic and molecular correlates of divergent selection for basal metabolic rate in laboratory mice. *Physiol. Biochem. Zool.* 80, 491-499.
- Burnham, K. P. and Anderson, D. R. (2002). Model Selection and Multimodel Inference. New York: Springer Verlag.
- Burns, J. G. and Ydenberg, R. C. (2002). The effects of wing loading and gender on the escape flights of least sandpipers (*Calidris minutilla*) and western sandpipers (*Calidris mauri*). Behav. Ecol. Sociobiol. 52, 128-136.
- Cardillo, M. (2002). The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? J. Anim. Ecol. 71, 79-87.

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Chappell, M. A., Bech, C. and Buttemer, W. A. (1999). The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. J. Exp. Biol. 202, 2269-2279.

Charnov, E. L. (1993). Life History Invariants. Oxford: Oxford University Press.

Christians, J. K. (1999). Controlling for body mass effects: is part-whole correlation important? Phys. Biochem. Zool. 72, 250-253.

Crile, G. and Quiring, D. P. (1940). A record of the body weight and certain organ and gland weights of 3690 animals. Ohio J. Sci. 40, 219-259.

- Daan, S., Masman, D. and Groenewold, A. (1990). Avian basal metabolic rates: their association with body composition and energy expenditure in nature. Am. J. Physiol. Regul. Integr. Comp. Physiol. 259, R333-R340.
- Elia, M. (1992). Organ and tissue contribution to metabolic rate. In Energy Metabolism: Tissue Determinants and Cellular Corollaries (ed. J. M. Kinney and H. N. Tucker), pp. 61-79. New York: Raven Press
- Else, P. L. and Hulbert, A. J. (1985). An allometric comparison of the mitochondria of mammalian and reptilian tissues-the implications for the evolution of endothermy. J. Comp. Physiol. B 156, 3-11.
- Else, P. L., Brand, M. D., Turner, N. and Hulbert, A. J. (2004). Respiration rate of hepatocytes varies with body mass in birds. J. Exp. Biol. 207, 2305-2311.
- Even, P. C., Rolland, V., Roseau, S., Bouthegourd, J. C. and Tome, D. (2001). Prediction of basal metabolism from organ size in the rat: relationship to strain, feeding, age, and obesity. Am. J. Physiol. Regul. Integr. Comp. Physiol. 280, R1887-R1896
- Felsenstein, J. (1985). Phylogenies and the comparative method. Am. Nat. 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. and Fitzpatrick, J. W. (1999). Survival rates of understorey forest birds in Peru. Int. Ornithol. Congr. 22, 326-335.
- Gallagher, D., Belmonte, D., Deurenberg, P., Wang, Z., Krasnow, N., Pi-Sunyer, F. X. and Heymsfield, S. B. (1998). Organ-tissue mass measurement allows modeling of REE and metabolically active tissue mass. Am. J. Physiol. Endocrinol. Metab. 275, E249-E258
- Garamszegi, L. Z., Møller, A. P. and Erritzøe, J. (2002). Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc. R. Soc. B 269, 961-967
- Garrido, G., Guzman, M. and Odriozola, J. (1996). Effects of physical training on fatty acid metabolism in liver and skeletal muscle of rats fed four different high carbohydrate diets. J. Nutr. Biochem. 7, 348-355.
- Geluso, K. and Hayes, J. P. (1999). Effects of dietary quality on basal metabolic rate and internal morphology of European starlings (Sturnus vulgaris). Phys. Biochem. Zool. 72. 189-197.
- Ghalambor, C. K. and Martin, T. E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. Science 292, 494-497
- Graber, R. R. and Graber, J. W. (1965). Variation in avian brain weights with special reference to age. Condor 67, 300-318.
- Grafen, A. (1989). The phylogenetic regression. Philos. Trans. R. Soc. Lond. Ser. B 326, 199-257.
- Hartman, F. A. (1955). Heart weight in birds. Condor 57, 221-238.
- Hartman. F. A. (1961). Locomotor mechanisms of birds. Smithson. Misc. Coll. 143. 1-
- Hinds, D. S., Baudinette, R. V., MacMillen, R. E. and Halpern, E. A. (1993)
- Maximum metabolism and the aerobic factorial scope of endotherms. J. Exp. Biol. 182, 41-56
- Hulbert, A. J. and Else, P. L. (2005). Membranes and the setting of energy demand. J. Exp. Biol. 208, 1593-1599.
- Husak, J. F., Fox, S. F., Lovern, M. B. and Van Den Bussche, R. A. (2006). Faster lizards sire more offspring: sexual selection on whole-animal performance. Evolution 60. 2122-2130.
- Isler, K. and van Schaik, C. (2006). Costs of encephalization: the energy trade-off hypothesis tested on birds. J. Hum. Evol. 51, 228-243.
- Jayne, B. C. and Bennett, A. F. (1990). Selection on locomotor performance capacity in a natural population of garter snakes. Evolution 44, 1204-1229.
- Johnston, J. P., Peach, W. J., Gregory, R. D. and White, S. A. (1997). Survival rates of tropical and temperate passerines: a Trinidadian perspective. Am. Nat. 150, 771-789
- Kersten, M., Bruinzeel, L. W., Wiersma, P. and Piersma, T. (1998). Reduced basal metabolic rate of migratory waders wintering in coastal Africa. Ardea 86, 71-80.
- Kirkwood, T. B. L. (1977). Evolution of ageing. Nature 270, 301-304.
- Konarzewski, M. and Diamond, J. (1995). Evolution of basal metabolic rate and organ masses in laboratory mice. Evolution 49, 1239-1248.
- Krebs, H. A. (1950). Body size and tissue respiration. Biochem. Biophys. Acta 4, 249-269.
- Ksiazek, A., Konarzewski, M. and Lapo, I. B. (2004). Anatomic and energetic correlates of divergent selection for basal metabolic rate in laboratory mice. Phys. Biochem. Zool. 77, 890-899
- Kulesza, G. (1990). An analysis of clutch-size in New World passerine birds. Ibis 132, 407-422
- Maddison, W. P. and Maddison, D. R. (2010), Mesquite: a modular system for evolutionary analysis. http://mesquiteproject.org.
- Marsh, R. and Dawson, W. (1982). Substrate metabolism in seasonally acclimatized American goldfinches. Am. J. Physiol. Regul. Integr. Comp. Physiol. 242, R563-**B569**
- Martins, E. P. and Hansen, T. F. (1997). Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149, 646-667.
- Mazerolle, M. J. (2011). AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). http://CRAN.R-project.org/package=AICcmodavg.
- McNab, B. K. (1997). On the utility of uniformity in the definition of basal rate of metabolism. Physiol. Zool. 70, 718-720.

- McNab, B. K. (2008). An analysis of the factors that influence the level and scaling of mammalian BMR. Comp. Biochem. Physiol. 151A, 5-28.
- McNab, B. K. (2009). Ecological factors affect the level and scaling of avian BMR. Comp. Biochem. Physiol. 152A, 22-45.
- Moyes, C. D. (2003). Controlling muscle mitochondrial content. J. Exp. Biol. 206, 4385-4391
- Nealen, P. and Ricklefs, R. (2001). Early diversification of the avian brain: body relationship. J. Zool. 253, 391-404.
- Oakeson, B. B. (1956). Liver and spleen weight cycles in non-migratory white-crowned sparrows. Condor 58, 45-50.
- Paradis, E. (2006). Analysis of Phylogenetics and Evolution with R. New York: Springer
- Paradis, E., Claude, J. and Strimer, K. (2004). APE: analyses of phylogenetics and evolution in R. Bioinformatics 20, 289-290
- Pearl, R. (1928). The Rate of Living: Being an Account of Some Experimental Studies on the Biology of Life Duration. New York: Knopf.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., van der Meer, J. and Wiersma, P. (1996). Variability in basal metabolic rate of a long-distance migrant shorebird (red knot, Calidris canutus) reflects shifts in organ sizes. Physiol. Zool. 69, 191-217.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R. Development Core, Team (2011). nlme: linear and nonlinear mixed effects models. R package version 3.1-103. Available at: http://cran.r-project.org/web/packages/nlme/index.html.
- Porter, R. K. (2001). Allometry of mammalian cellular oxygen consumption. Cell Mol. Life Sci. 58, 815-822.
- Portsmann, T., Santos. C. R., Lewis, C., Griffiths, B. and Schulze, A. (2009). A new player in the orchestra of cell growth: SREBP activity is regulated by mTORC1 and contributes to the regulation of cell and organ size. Biochem. Soc. Trans. 37. 278-283
- Promislow, D. E. L. and Harvey, P. H. (1990). Living fast and dying young: a comparative analysis of life-history variation among mammals. J. Zool. 220, 417-437.
- R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: http://www.R-project.org.
- Raichlen, D. A., Gordon, A. D., Muchlinski, M. N. and Snodgrass, J. J. (2010). Causes and significance of variation in mammalian basal metabolism. J. Comp. Physiol. B 180, 301-311.
- Rensch, I. and Rensch, B. (1956). Relative Organmaße bei tropischen Warmblütern. Zool. Anz. 156, 106-124.
- Ricklefs, R. E. (1997). Comparative demography of New World populations of thrushes (Turdus spp.). Ecol. Monogr. 67, 23-43.
- Ricklefs, R. E. and Wikelski, M. (2002). The physiology/life-history nexus. Trends Ecol. Evol. 17, 462-468.
- Roff, D. A. (1992). The Evolution of Life Histories; Theory and Analysis. London: Chapman & Hall
- Rohlf, F. J. (2001). Comparative methods for the analysis of continuous variables: geometric interpretations. Evolution 55, 2143-2160.
- Rottenberg, H. (2007). Exceptional longevity in songbirds is associated with high rates of evolution of cytochrome b, suggesting selection for reduced generation of free radicals. J. Exp. Biol. 210, 2170-2180.
- Russell, E. M., Yom-Tov, Y. and Geffen, E. (2004). Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behav. Ecol. 15, 831-838.
- Russell, G. A. and Chappell, M. A. (2007). Is BMR repeatable in deer mice? Organ mass correlates and the effects of cold acclimation and natal altitude. J. Comp. Physiol. B 177, 75-87.
- Savage, V. M., Allen, A. P., Brown, J. H., Gillooly, J. F., Herman, A. B., Woodruff, W. H. and West, G. B. (2007). Scaling of number, size, and metabolic rate of cells with body size in mammals. *Proc. Natl. Acad. Sci. USA* **104**, 4718-4723.
- Schaefer, H. C., Eshiamwata, G. W., Munyekenye, F. B. and Böhning-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., Walters, V., Hock, R. and Irving, L. (1950). Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99, 225-236
- Sheldon, B. C. and Verhulst, S. (1996). Ecological immunology: costly parasite defence and trade-offs in evolutionary ecology. Trends Ecol. Evol. 11, 317-321
- Sibley, C. G. and Ahlquist, J. E. (1990). Phylogeny and Classification of Birds. New Haven, CT: Yale University Press
- Snow, D. W. and Lill, A. (1974). Longevity records for some neotropical land birds. Condor 76, 262-267
- Speakman, J. R. (2005). Body size, energy metabolism and lifespan. J. Exp. Biol. 208, 1717-1730
- Speakman, J. R. (2008). The physiological costs of reproduction in small mammals. Philos. Trans. R. Soc. Lond. B 363. 375-398.
- Speakman, J. R. and Król, E. (2010). The heat dissipation limit theory and evolution of life histories in endotherms - time to dispose of the disposable soma theory? Integr. Comp. Biol. 50, 793-807
- Speakman, J. R. and Selman, C. (2011). The free-radical damage theory: accumulating evidence against a simple link of oxidative stress to ageing and lifespan. BioEssays 33, 255-259.
- Stearns, S. C. (1992). The Evolution of Life Histories. Oxford: Oxford University Press. Stöver, B. and Müller, K. (2010). TreeGraph 2, combining and visualizing evidence
- from different phylogenetic analyses. BMC Bioinformatics 11, 7. Suarez, R. K. (1996). Upper limits to mass specific metabolic rates. Annu. Rev.
- Physiol. 58, 583-605 Swanson, D. L. and Liknes, E. T. (2006). A comparative analysis of thermogenic
- capacity and cold tolerance in small birds. J. Exp. Biol. 209, 466-474
- Tarwater, C. E. and Brawn, J. D. (2010). The post-fledging period in a tropical bird: patterns of parental care and survival. J. Avian Biol. 41, 479-487. Taylor, C. R., Maloiy, G. M. O., Weibel, E. R., Langman, V. A., Kamau, J. M. Z.,
- Seeherman, H. J. and Heglund, N. C. (1981). Design of the mammalian respiratory

system. III. Scaling maximum aerobic capacity to body mass: Wild and domestic mammals. *Resp. Physiol.* 44, 25-37.

- Tieleman, B. I., Williams, J. B., Buschur, M. E. and Brown, C. R. (2003). Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* 84, 1800-1815.
- Vézina, F. and Williams, T. D. (2005). Interaction between organ mass and citrate synthase activity as an indicator of tissue maximal oxidative capacity in breeding European starlings: implications for metabolic rate and organ mass relationships. *Funct. Ecol.* **19**, 119-128.
- Vézina, F., Jalvingh, K. M., Dekinga, A. and Piersma, T. (2006). Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. J. Exp. Biol. 209, 3141-3154.
- Weber, T. P. and Piersma, T. (1996). Basal metabolic rate and the mass of tissues differing in metabolic scope: migration-related covariation between individual knots *Calidris canutus. J. Avian Biol.* 27, 215-224.

Wiersma, P., Selman, C., Speakman, J. R. and Verhulst, S. (2004). Birds sacrifice oxidative protection for reproduction. *Proc. R. Soc. Lond. B* 271, S360-S363.

- Wiersma, P., Muñoz-García, A., Walker, A. and Williams, J. B. (2007a). Tropical birds have a slow pace of life. *Proc. Natl. Acad. Sci. USA* 104, 9340-9345.
  Wiersma, P., Chappell, M. A. and Williams, J. B. (2007b). Cold- and exercise-
- induced peak metabolic rates in tropical birds. *Proc. Natl. Acad. Sci. USA* 104, 20866-20871.
- Williams, G. C. (1957). Pleiotropy, natural selection and evolution of senescence. Evolution 11, 398-411.
- Williams, J. B., Miller, R. A., Harper, J. M. and Wiersma, P. (2010). Functional linkages for the pace of life, life-history, and environment in birds. *Integr. Comp. Biol.* 50, 855-868.
- Wu, B. J., Else, P. L., Storlien, L. H. and Hulbert, A. J. (2001). Molecular activity of Na<sup>+</sup>/K<sup>+</sup>-ATPase from different sources is related to the packing of membrane lipids. *J. Exp. Biol.* 204, 4271-4280.

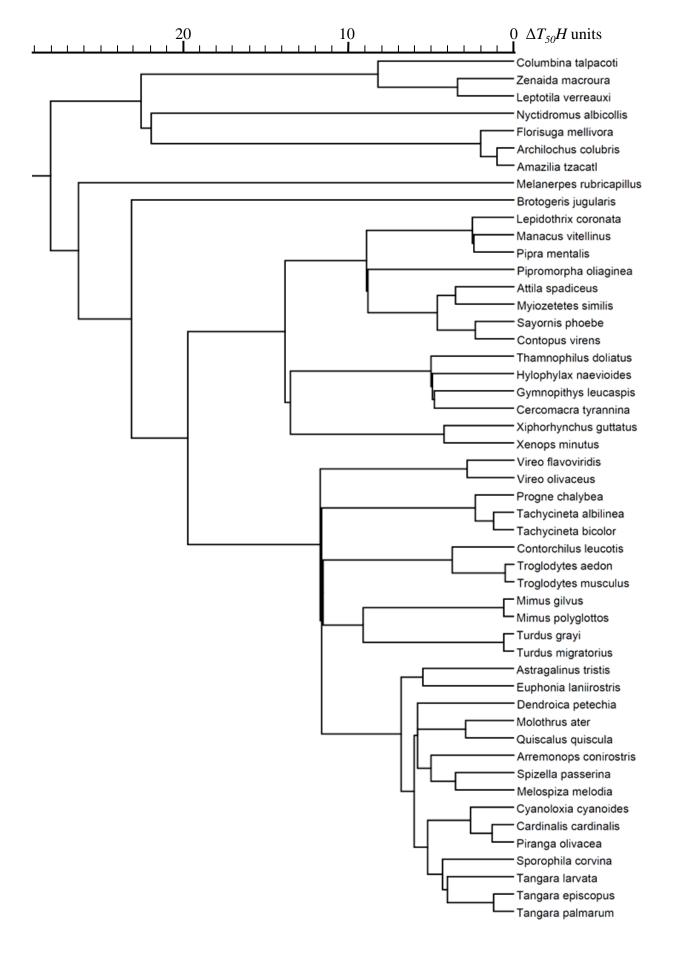


Table S1. Species for which data on organ masses were collected from literature sources

				Litera	ature	source	for da	ata on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan \$	Spl	Bra
Accipitridae	Accipiter bicolor	Bicoloured hawk	tropical	H2		H2							
	Accipiter cooperii	Cooper's Hawk	temperate	H2		H2							
	Accipiter gentilis	Northern Goshawk	temperate										G
	Accipiter nisus	Eurasian Sparrowhawk	temperate										G
	Accipiter striatus	Sharp-Shinned Hawk	temperate	С	С								С
	Aquila rapax	Tawny Eagle	tropical	С	С				С	С			С
	Asturina nitida	Grey-Lined Hawk	tropical	H2		H2							
	Busarellus nigricollis	Black-Collared Hawk	tropical	H2		H2							
	Buteo lagopus	Rough-legged Hawk	temperate										G
	Buteo magnirostris	Roadside Hawk	tropical	H2		H2							
	Buteogallus anthracinus	Common Black-Hawk	tropical	H2		H2							
	Buteogallus meridionalis	Savanna Hawk	tropical	H2		H2							
	Buteogallus urubitinga	Great Black-Hawk	tropical	H1,2		H1,2							
	Chondrohierax uncinatus	Hook-Billed Kite	tropical	H2		H2							
	Circus aeruginosus	Western Marsh-Harrier	temperate										G
	Geranospiza caerulescens	Crane Hawk	tropical	H2		H2							
	Gyps africanus	White-Backed Vulture	tropical	C					С	С			с
	Haliaeetus vocifer	African Fish-Eagle	tropical	C	С			С	C	С			С
	Harpagus bidentatus	Double-Toothed Kite	tropical	H2	0	H2		Ũ	U	Ũ			Ŭ
	Leptodon cayanensis	Grey-Headed Kite	tropical	H2		H2							
	Spizaetus ornatus	Ornate Hawk-Eagle	tropical	H2		H2							
	Spizaetus ornatus Spizastur melanoleucus	Black-And-White Hawk-Eagle	tropical	H2		H2							
Alaudidae	Alauda arvensis	Eurasian Skylark	temperate	R		112			R	R		F	G
laudidae	Eremophila bilopha	Temminck's Lark	tropical	n								1	G
	Galerida cristata	Crested Lark											G
	Lullula arborea	Wood Lark	temperate	R					R	R		R	G
Maadinidaa			temperate	п					п	п		ר	~
Alcedinidae	Alcedo atthis	Common Kingfisher	temperate										G
	Alcedo cristata	Malachite Kingfisher	tropical	0	~				~	~			G
Anatidae	Alopochen aegyptiaca	Egyptian Goose	tropical	С	С			~	С	С		_	C
	Anas acuta	Northern Pintail	temperate	С	С			С	С	С		2	С
	Anas carolinensis	Green-Winged Teal	temperate	С	С			С	С	С	(	С	С
	Anas penelope	Eurasian Wigeon	temperate	H2		H2							_
	Anas platyrhynchos	Mallard	temperate	_	_				_	_			G
	Aythya affinis	Lesser Scaup	temperate	С	С				С	С			
	Aythya marila	Greater Scaup	temperate	С	С			С	С	С			С
	Clangula hyemalis	Long-tailed Duck	temperate										G
	Mergus merganser	Common Merganser	temperate										G
	Mergus serrator	Red-Breasted Merganser	temperate	С	С			С	С	С	(	С	G
	Nomonyx dominicus	Masked Duck	tropical	H2		H2							
	Somateria mollissima	Common Eider	temperate										G
Ardeidae	Agamia agami	Agami Heron	tropical	H2		H2							
	Ardea alba	Great Egret	tropical	H1									
	Ardea cinerea	Grey Heron	temperate										G
	Ardea herodias	Great Blue Heron	temperate	H1									
	Butorides virescens	Green Heron	tropical	H2		H2							
	Cochlearius cochlearius	Boat-Billed Heron	tropical	H2		H2							
	Egretta caerulea	Little Blue Heron	tropical	H2		H2							
	Egretta intermedia	Yellow-Billed Egret	tropical	С	С				С	С			С
	Ixobrychus exilis	Least Bittern	temperate	H1									
	Tigrisoma fasciatum	Fasciated Tiger-Heron	tropical	H1									
	Tigrisoma lineatum	Rufescent Tiger-Heron	tropical	H2		H2							
	Tigrisoma mexicanum	Bare-Throated Tiger-Heron	tropical	H2		H2							
Bombycillidae	Bombycilla cedrorum	Cedar Waxwing	temperate	H1									
	•	-	-										G
		-	-										G
-	Bombycilla garrulus Bombycilla japonica	Bohemian Waxwing Japanese Waxwing	temperate temperate										

				Litera	ature s	source	for da	ata on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan	Spl	Bra
-	Ptilogonys caudatus	Long-Tailed Silky-Flycatcher	tropical	H2		H2							
Bucconidae	Malacoptila panamensis	White-Whiskered Puffbird	tropical	H2		H2							
	Nonnula frontalis	Grey-Cheeked Nunlet	tropical	H2		H2							
	Notharchus macrorhynchos	White-Necked Puffbird	tropical	H2		H2							
Bucorvidae	, Bucorvus leadbeateri	Southern Ground-Hornbill	tropical	С	С			С	С	С			С
Caprimulgidae	Chordeiles acutipennis	Lesser Nighthawk	tropical	H2		H2							
(Caprimulgidae)	Nyctidromus albicollis	Pauraque	tropical	H2		H2							
Cathartidae	Cathartes aura	Turkey Vulture	tropical	H2		H2							
Sumanual	Coragyps atratus	Black Vulture	tropical	H2		H2							
Centropidae	Centropus sinensis	Greater Coucal	tropical	R		112	R		R				
Certhiidae	Certhia americana		-	H2		H2							
Jentinidae		Brown Treecreeper	temperate			пΖ							~
	Certhia familiaris	Eurasian Treecreeper	temperate	H1									G
	Cistothorus palustris	Marsh Wren	temperate	H1									
	Cyphorhinus phaeocephalus	Song Wren	tropical	H2		H2							
	Henicorhina leucophrys	Grey-Breasted Wood-Wren	tropical	H2		H2							
	Henicorhina leucosticta	White-Breasted Wood-Wren	tropical	H2		H2							
	Polioptila caerulea	Blue-Grey Gnatcatcher	temperate	H1									
	Polioptila plumbea	Tropical Gnatcatcher	tropical	H2		H2							
	Ramphocaenus melanurus	Long-Billed Gnatwren	tropical	H2		H2							
	Thryothorus fasciatoventris	Black-Bellied Wren	tropical	H2		H2							
	Thryothorus modestus	Plain Wren	tropical	H2		H2							
	Thryothorus rutilus	Rufous-Breasted Wren	tropical	H2		H2							
	Troglodytes aedon aedon	Northern House-Wren	temperate	H1									G
	Troglodytes ochraceus	Ochraceous Wren	tropical	H2		H2							
	Troglodytes troglodytes	House Wren	temperate										G
Cerylidae	Chloroceryle aenea	American Pygmy Kingfisher	tropical	H2		H2							ŭ
Jorynauc	Chloroceryle amazona	Amazon Kingfisher	tropical	H2		H2							
	-	Green Kingfisher	-			H2							
	Chloroceryle americana		tropical	H2		пΖ							
	Megaceryle alcyon	Belted Kingfisher	temperate	H1									
	Megaceryle torquata	Ringed Kingfisher	tropical	H2		H2							
Charadriidae	Charadrius vociferus	Killdeer	temperate	H1									_
	Pluvialis apricaria	Eurasian/European Golden-Plover	temperate										G
	Vanellus vanellus	Northern Lapwing	temperate										G
Ciconiidae	Ciconia abdimii	Abdim's Stork	tropical	С	С				С	С			С
	Leptoptilos crumeniferus	Marabou Stork	tropical	С	С			С	С	С			С
	Sarcoramphus papa	King Vulture	tropical	H1									
Cinclidae	Cinclus cinclus	White-throated Dipper	temperate										G
Coccyzidae	Coccycua minuta	Little Cuckoo	tropical	H2		H2							
	Piaya cayana	Squirrel Cuckoo	tropical	H2		H2							
Columbidae	Chalcophaps indica	Emerald Dove	tropical										G
	Claravis mondetoura	Maroon-Chested Ground-Dove	tropical	H2		H2							
	Claravis pretiosa	Blue Ground-Dove	tropical	H2		H2							
	Columba albinucha	White-Naped Pigeon	tropical	H1									
	Columba palumbus	Common Wood-Pigeon	temperate										G
		Plain-Breasted Ground-Dove	-	ЦQ		ЦQ							u
	Columbina minuta		tropical	H2		H2							
	Geotrygon chiriquensis	Rufous-Breasted Quail-Dove	tropical	H2		H2							
	Geotrygon costaricensis	Buff-Fronted Quail-Dove	tropical	H2		H2							
	Geotrygon montana	Ruddy Quail-Dove	tropical	H2		H2							
	Leptotila cassini	Grey-Chested Dove	tropical	H2		H2							
1	Leptotila verreauxi	White-Tipped Dove	tropical	H2		H2							
	Patagioenas fasciata	Band-Tailed Pigeon	tropical	H2		H2							
	Patagioenas nigrirostris	Short-Billed Pigeon	tropical	H2		H2							
	Patagioenas subvinacea	Ruddy Pigeon	tropical	H2		H2							
	Streptopelia decaocto	Eurasian Collared-Dove	temperate										G
	Zenaida macroura	Mourning Dove	temperate	H1									
Corvidae	Corvus brachyrhynchos	American Crow	temperate	H1									

				Litera	ature	source	for da	ita on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan	Spl	Bra
	Corvus corax	Common Raven	temperate										G
	Corvus cornix	Hooded Crow	temperate										G
	Corvus corone	Carrion Crow	temperate										G
	Corvus frugilegus	Rook	temperate										G
	Corvus monedula	Eurasian Jackdaw	temperate										G
	Cyanocitta cristata	Blue Jay	temperate	H2		H2							
	Cyanocorax affinis	Black-Chested Jay	tropical	H2		H2							
	Cyanolyca argentigula	Silvery-Throated Jay	tropical	H2		H2							
	Garrulus glandarius	Eurasian Jay	temperate										G
	Nucifraga caryocatactes	Spotted Nutcracker	temperate										G
	Pica pica	Black-billed Magpie	temperate										G
	Platysteira cyanea	Brown-throated Wattle-eye	tropical										G
	Tephrodornis pondicerianus	Common Woodshrike	tropical	R			R		R	R	R	R	
Cracidae	Chamaepetes unicolor	Black Guan	tropical	H2		H2							
	Ortalis garrula	Chestnut-Winged Chachalaca	tropical	H2		H2							
Crotophagidae	Crotophaga ani	Smooth-Billed Ani	tropical	H2		H2							
(Crotophagidae)	Crotophaga major	Greater Ani	tropical	H2		H2							
(,	Crotophaga sulcirostris	Groove-Billed Ani	tropical	H2		H2							
Falconidae	Caracara cheriway	Crested Caracara	tropical	H1									
	Falco rufigularis	Bat Falcon	tropical	H2		H2							
	Falco sparverius	American Kestrel	temperate	C	С	112		С	С	С			С
	Falco tinnunculus	Common Kestrel	temperate	0	U			U	U	Ŭ			G
	Herpetotheres cachinnans	Laughing Falcon	tropical	H2		H2							u
	Micrastur ruficollis	Barred Forest-Falcon	-	H2		H2							
			tropical										
	Micrastur semitorquatus	Collared Forest-Falcon	tropical	H2		H2							
	Milvago chimachima	Yellow-Headed Caracara	tropical	H2		H2							
Formicariidae	Formicarius analis	Black-Faced Antthrush	tropical	H2		H2			~				~
Fregatidae	Fregata aquila	Ascension Frigatebird	temperate	С					С				С
Fringillidae	Agelaius phoeniceus	Red-Winged Blackbird	temperate	H1									
	Amblycercus holosericeus	Yellow-Billed Cacique	tropical	H2		H2							
	Ammodramus henslowii	Henslow's Sparrow	temperate	H1									
	Ammodramus savannarum	Grasshopper Sparrow	temperate	H1									
	Atlapetes gutturalis	Yellow-Throated Brush-Finch	tropical	H2		H2							
	Basileuterus culicivorus	Golden-Crowned Warbler	tropical	H2		H2							
	Basileuterus fulvicauda	Buff-Rumped Warbler	tropical	H2		H2							
	Basileuterus melanogenys	Black-Cheeked Warbler	tropical	H2		H2							
	Buarremon brunneinucha	Chestnut-Capped Brush-Finch	tropical	H2		H2							
	Buarremon torquatus	Stripe-Headed Brush-Finch	tropical	H2		H2							
	Cacicus cela	Yellow-Rumped Cacique	tropical	H2		H2							
	Cacicus uropygialis	Scarlet-Rumped Cacique	tropical	H2		H2							
	Cardinalis cardinalis	Northern Cardinal	temperate	H1									
	Carduelis cannabina	Eurasian Linnet	temperate										G
	Carduelis carduelis	European Goldfinch	temperate										G
	Carduelis chloris	European Greenfinch	temperate										G
	Carduelis flammea	Common Redpoll	temperate										G
	Carduelis spinus	Eurasian Siskin	temperate										G
	Carduelis tristis	American Goldfinch	temperate	H2		H2							
	Carduelis xanthogastra	Yellow-Bellied Siskin	tropical	H2		H2							
	Carpodacus roseus	Pallas's Rosefinch	temperate	112		. 12							G
Eringillidae)	-		-	ЦО		LUN							u
Fringillidae)	Chlorophanes spiza	Green Honeycreeper	tropical	H2		H2							
	Chlorophonia callophrys	Golden-Browed Chlorophonia	tropical	H2		H2							
	Chlorospingus ophthalmicus	Common Bush-Tanager	tropical	H2		H2							
	Chlorospingus pileatus	Sooty-Capped Bush-Tanager	tropical	H2		H2							
	Cyanerpes cyaneus	Red-Legged Honeycreeper	tropical	H2		H2							
	Cyanerpes lucidus	Shining Honeycreeper	tropical	H2		H2							
	Dacnis cayana	Blue Dacnis	tropical	H1									

				Literature source for data on										
amily	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan	Spl	Br	
	Dacnis venusta	Scarlet-Thighed Dacnis	tropical	H2		H2								
	Dendroica virens	Black-Throated Green Warbler	temperate	H1										
	Emberiza citrinella	Yellowhammer	temperate										G	
	Emberiza schoeniclus	Reed Bunting	temperate										G	
	Eucometis penicillata	Grey-Headed Tanager	tropical	H2		H2								
	Euphagus carolinus	Rusty Blackbird	temperate	H1										
	Euphonia elegantissima	Elegant(/Blue-Hooded) Euphonia	tropical	H2		H2								
	Euphonia fulvicrissa	Fulvous-Vented Euphonia	tropical	H2		H2								
	Euphonia hirundinacea	Yellow-Throated Euphonia	-	H2		H2								
	Euphonia imitans	Spot-Crowned Euphonia	tropical tropical	H2		H2								
	-		-	H2		H2								
	Euphonia luteicapilla	Yellow-Crowned Euphonia	tropical											
	Euphonia minuta	White-Vented Euphonia	tropical	H2		H2								
	Fringilla coelebs	Chaffinch	temperate										(	
	Fringilla montifringilla	Brambling	temperate										(	
	Geothlypis chiriquensis	Chiriqui Yellowthroat	tropical	H2		H2								
	Geothlypis trichas	Common Yellowthroat	temperate	H1										
	Habia fuscicauda	Red-Throated Ant-Tanager	tropical	H2		H2								
	Habia rubica	Red-Crowned Ant-Tanager	tropical	H2		H2								
	lcterus mesomelas	Yellow-Tailed Oriole	tropical	H2		H2								
	Melospiza georgiana	Swamp Sparrow	temperate	H1										
	Melospiza melodia	Song Sparrow	temperate	H1										
	Mniotilta varia	Black-And-White Warbler	temperate	H1										
	Molothrus ater	Brown-Headed Cowbird	temperate	H1										
	Oryzoborus angolensis	Lesser Seed-Finch	tropical	H2		H2								
	Parula gutturalis	Flame-Throated Warbler	tropical	H2		H2								
	Parula pitiayumi	Tropical Parula	tropical	H2		H2								
ringillidae)	Passerculus sandwichensis	Savannah Sparrow	temperate	H1										
5	Pezopetes capitalis	Large-Footed Finch	tropical	H2		H2								
	Pheucticus Iudovicianus	Rose-Breasted Grosbeak	temperate	H1									(	
	Pheucticus tibialis	Black-Thighed Grosbeak	tropical	H2		H2							`	
	Pipilo erythrophthalmus	Eastern Towhee	temperate	H1		112								
	Piranga bidentata	Flame-Colored Tanager	tropical	H2		H2								
	-	6	-			H2								
	Piranga leucoptera	White-Winged Tanager	tropical	H2										
	Psarocolius decumanus	Crested Oropendola	tropical	H2		H2								
	Psarocolius wagleri	Chestnut-Headed Oropendola	tropical	H2		H2								
	Pselliophorus tibialis	Yellow-Thighed Finch	tropical	H2		H2								
	Quiscalus mexicanus	Great-Tailed Grackle	tropical	H2		H2								
	Quiscalus quiscula	Common Grackle	temperate	С	С			С	С	С		С	(	
	Ramphocelus dimidiatus	Crimson-Backed Tanager	tropical	H2		H2								
	Ramphocelus flammigerus	Flame-Rumped Tanager	tropical	H2		H2								
	Ramphocelus passerinii	Passerini's/Scarlet-Rumped Tanager	tropical	H2		H2								
	Rhodinocichla rosea	Rosy Thrush-Tanager	tropical	H2		H2								
	Saltator albicollis	Lesser Antillean(/Streaked) Saltator	tropical	H2		H2								
	Saltator atriceps	Black-Headed Saltator	tropical	H2		H2								
	Saltator maximus	Buff-Throated Saltator	tropical	H2		H2								
	Saltator striatipectus	Streaked Saltator	tropical	H1										
	Scaphidura oryzivora	Giant Cowbird	tropical	H2		H2								
	Seiurus aurocapilla	Ovenbird	temperate	H1									(	
	Seiurus noveboracensis	Northern Waterthrush	temperate	H2		H2								
	Serinus burtoni	Thick-billed Seedeater	tropical	112		112							(	
			-	c	С			с	С	С		с	0	
	Serinus canaria	Island Canary	temperate	С	U			U	U	U		U	C	
	Spizella passerina	Chipping Sparrow	temperate	H1										
	Spizella pusilla	Field Sparrow	temperate	H1										
	Sturnella magna	Eastern Meadowlark	tropical	H2		H2								
	Sturnella militaris	Red-Breasted Blackbird	tropical	H2		H2								
	Tachyphonus luctuosus	White-Shouldered Tanager	tropical	H2		H2								

				Literature source for data on										
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan S	ol Br		
	Tachyphonus rufus	White-Lined Tanager	tropical	H2		H2								
	Tangara guttata	Speckled Tanager	tropical	H2		H2								
	Tangara gyrola	Bay-Headed Tanager	tropical	H2		H2								
-ringillidae)	Tangara icterocephala	Silver-Throated Tanager	tropical	H2		H2								
g,	Tangara inornata	Plain-Colored Tanager	tropical	H2		H2								
	Tangara larvata	Golden-Hooded Tanager	tropical	H2		H2								
	Thraupis palmarum	Palm Tanager	tropical	H2		H2						G		
	Tiaris olivaceus	Yellow-Faced Grassquit	tropical	H2		H2						u		
			-	H2		H2								
	Volatinia jacarina Zonatriabia albiaallia	Blue-Black Grassquit	tropical			ПΖ								
	Zonotrichia albicollis	White-Throated Sparrow	temperate	H1		110						~		
	Zonotrichia capensis	Rufous-Collared Sparrow	tropical	H2		H2			~		0	G		
	Zonotrichia leucophrys	White-Crowned Sparrow	temperate	0					0		0			
urnariidae	Anabacerthia striaticollis	Montane Foliage-Gleaner	tropical	H2		H2								
	Anabacerthia variegaticeps	Scaly-Throated Foliage-Gleaner	tropical	H1										
	Automolus ochrolaemus	Buff-Throated Foliage-Gleaner	tropical	H2		H2								
	Campylorhamphus pusillus	Brown-Billed Scythebill	tropical	H2		H2								
	Cranioleuca erythrops	Red-Faced Spinetail	tropical	H2		H2								
	Dendrocincla fuliginosa	Plain-Brown Woodcreeper	tropical	H2		H2								
	Dendrocincla homochroa	Ruddy Woodcreeper	tropical	H2		H2								
	Dendrocolaptes certhia	Amazonian Barred-Woodcreeper	tropical	H2		H2								
	Glyphorynchus spirurus	Wedge-Billed Woodcreeper	tropical	H2		H2								
	Lepidocolaptes affinis	Spot-Crowned Woodcreeper	tropical	H2		H2								
	Margarornis rubiginosus	Ruddy Treerunner	tropical	H2		H2								
	Premnoplex brunnescens	Spotted Barbtail	tropical	H2		H2								
	Pseudocolaptes lawrencii	Buffy Tuftedcheek	tropical	H2		H2								
	Sclerurus guatemalensis	Scaly-Throated Leaftosser	tropical	H2		H2								
	Sittasomus griseicapillus	Olivaceous Woodcreeper	tropical	H2		H2								
	Synallaxis albescens	Pale-Breasted Spinetail	tropical	H2		H2								
	Synallaxis brachyura	Slaty Spinetail	tropical	H2		H2								
	Syndactyla subalaris	Lineated Foliage-Gleaner	tropical	H2		H2								
		-	-											
	Thripadectes rufobrunneus	Streak-Breasted Treehunter	tropical	H2		H2								
	Xenops rutilans	Streaked Xenops	tropical	H2		H2								
	Xiphorhynchus erythropygius	•	tropical	H2		H2								
	Xiphorhynchus guttatus	Buff-Throated Woodcreeper	tropical	H2		H2								
	Xiphorhynchus susurrans	Cocoa Woodcreeper	tropical	H1										
iaviidae	Gavia immer	Common Loon	temperate	H1										
Gaviidae)	Gavia stellata	Red-Throated Loon	temperate	С	С			С	С	С		С		
iruidae	Balearica pavonina	Black Crowned-Crane	tropical	С	С				С	С		С		
	Grus canadensis	Sandhill Crane	temperate	С	С			С	С	С	С	С		
leliornithidae	Heliornis fulica	Sungrebe	tropical	H2		H2								
lirundinidae	Notiochelidon cyanoleuca	Blue-And-White Swallow	tropical	H2		H2								
	Tachycineta bicolor	Tree Swallow	temperate	H1										
enidae	Irena puella	Asian Fairy-bluebird	tropical									G		
acanidae	Jacana spinosa	Northern Jacana	tropical	H2		H2								
aniidae	Lanius excubitor	Northern Shrike	temperate									G		
aridae	Alle alle	Dovekie	temperate	С	С			С	С	С		G		
	Fratercula arctica	Atlantic Puffin	temperate									G		
	Larus argentatus	Herring Gull	temperate	С					С			C		
	Larus atricilla	Laughing Gull	temperate	H1					-			0		
	Larus canus	Mew Gull	temperate									G		
			-	C	С			C	С	с		C		
	Larus delawarensis	Ring-Billed Gull	temperate	C C				C						
	Larus philadelphia	Boneparte's Gull	temperate	С	С			С	С	С		c		
	Larus ridibundus	Black-headed Gull	temperate									G		
	Uria aalge	Common Murre	temperate									G		
legalaimidae	Megalaima asiatica	Blue-throated Barbet	tropical									G		
/lomotidae	Momotus momota	Blue-Crowned Motmot	tropical	H2		H2								

				Liter	ature	source	for da	ita on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan	Spl	Bra
<i>Auscicapidae</i>	Catharus aurantiirostris	Orange-Billed Nightingale-Thrush	tropical	H2		H2							
	Catharus frantzii	Ruddy-Capped Nightingale-Thrush	tropical	H2		H2							
	Catharus guttatus	Hermit Thrush	temperate	H1									
	Erithacus rubecula	European Robin	temperate										G
	Myadestes melanops	Black-Faced Solitaire	tropical	H2		H2							
	Oenanthe oenanthe	Northern Wheatear	temperate										G
	Sialia sialis	Eastern Bluebird	temperate	H1									
	Turdus assimilis	White-Throated Thrush	tropical	H2		H2							
	Turdus merula	Eurasian Blackbird	temperate										G
	Turdus migratorius	American Robin	temperate	H1									
	Turdus philomelos	Song Thrush	temperate										G
	Turdus pilaris	Fieldfare	temperate										G
	Turdus plebejus	American Mountain Thrush	tropical	H2		H2							
lectariniidae	Nectarinia minima	Crimson-Backed Sunbird	tropical	R			R		R	R			
	Nectarinia venusta	Variable Sunbird	tropical										G
leomorphidae	Dromococcyx phasianellus	Pheasant Cuckoo	tropical	H2		H2							
	Tapera naevia	Striped Cuckoo	tropical	H2		H2							
lumididae	Numida meleagris	Helmeted Guineafowl	tropical	С	С				С	С			С
lyctibiidae	Nyctibius griseus	Common( /Grey) Potoo	tropical	H2		H2							
Ddontophoridae	Callipepla gambelii	Gambel's Quail	temperate										G
Dtididae	Ardeotis kori	Kori Bustard	tropical	С	С			С	С	С			С
	Lissotis melanogaster	Black-Bellied Bustard	tropical	С	С			С	С	С			С
Paridae	Baeolophus bicolor	Tufted Titmouse	temperate	H1	-			-	-	-			-
	Cyanistes caeruleus	Blue Tit	temperate										G
	Cyanistes cyanus	Azure Tit	temperate										G
	Parus major	Great Tit	temperate	R			R		R	R	R	R	G
	Parus xanthogenys	Black-Lored Tit	tropical	R			R		R	R		R	u
	Periparus ater	Coal Tit	temperate										G
	•	Yellow-bellied Tit	-										G
	Periparus venustulus		temperate	LI 4									G
	Poecile atricapillus	Black-Capped Chickadee	temperate	H1									
a multata a	Poecile carolinensis	Carolina Chickadee	temperate	H1									
arulidae	Myioborus miniatus	Slate-Throated Redstart	tropical	H2		H2							
	Myioborus torquatus	Collared Redstart	tropical	H2		H2							
asseridae	Anthus lutescens	Yellowish Pipit	tropical	H2		H2	_		_	_	_	_	
	Anthus rufulus	Paddyfield Pipit	tropical	R			R		R	R	R	R	
	Anthus spinoletta	Water Pipit	temperate	H1									
	Lonchura molucca	Black-faced Munia	tropical										G
	Motacilla alba	White Wagtail	temperate	R			R		R	R	R	R	G
	Passer domesticus	House Sparrow	temperate										G
	Passer montanus	Eurasian Tree Sparrow	temperate										G
	Passer rutilans	Russet Sparrow	temperate										G
	Prunella modularis	Hedge Accentor	temperate										G
	Pyrenestes sanguineus	Crimson Seedcracker	tropical										G
elecanidae	Pelecanus occidentalis	Brown Pelican	temperate	С	С			С	С				С
halacrocoracidae	Phalacrocorax brasilianus	Neotropic/Olivaceous Cormorant	tropical	H2		H2							
	Phalacrocorax carbo	Great Cormorant	temperate										G
hasianidae	Dendroperdix sephaena	Crested Francolin	tropical	С					С	С			С
	Gallus sonneratii	Grey Junglefowl	tropical	R			R		R	R	R	R	G
	Lagopus lagopus	Willow Ptarmigan	temperate	С	С		-		С	С			С
	Lagopus muta	Rock Ptarmigan	temperate	C	2				2	2			G
	Odontophorus guttatus	Spotted Wood-Quail	tropical	H2		H2							u
		•	-	112		112							~
	Perdix perdix	Grey Partridge	temperate	C	C			C	c	c			G
	Phasianus colchicus	Common Pheasant	temperate	С	С			С	С	С			G
	Tetrao urogallus	Western Capercaillie	temperate	~	6				~	~			G
Phoenicopteridae	Phoeniconaias minor	Lesser Flamingo	tropical	С	С				С	С			С
Picidae	Campephilus guatemalensis	Pale-Billed Woodpecker	tropical	H2		H2							

				Liter	ature	source	for da	ata on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Pan	Spl	Bra
	Campephilus melanoleucos	Crimson-Crested Woodpecker	tropical	H2		H2							
	Dendrocopos major	Great Spotted Woodpecker	temperate										G
	Dryocopus lineatus	Lineated Woodpecker	tropical	H2		H2							
	Dryocopus pileatus	Pileated Woodpecker	temperate	H1									
	Melanerpes carolinus	Red-Bellied Woodpecker	temperate	H1									
	Melanerpes chrysauchen	Golden-Naped Woodpecker	tropical	H2		H2							
	Melanerpes formicivorus	Acorn Woodpecker	tropical	H2		H2							
	Melanerpes pucherani	Black-Cheeked Woodpecker	tropical	H2		H2							
	Melanerpes rubricapillus	Red-Crowned Woodpecker	tropical	H2		H2							
	Picoides pubescens	Downy Woodpecker	temperate	H1									
	Picoides villosus	Hairy Woodpecker	temperate	H1									
	Piculus rubiginosus	Golden-Olive Woodpecker	tropical	H2		H2							
	Picumnus olivaceus	Olivaceous Piculet	tropical	H2		H2							
	Picus canus	Grey-Faced Woodpecker	temperate	R			R		R	R	R	R	
	Picus viridis	Eurasian Green Woodpecker	temperate										G
	Sphyrapicus varius	Yellow-Bellied Sapsucker	temperate	H1									
	Veniliornis fumigatus	Smoky-Brown Woodpecker	tropical	H2		H2							
Pittidae	Pitta brachyura	Indian Pitta	tropical	R			R		R	R	R	R	
	Pitta sordida	Hooded Pitta	tropical										G
Podicipedidae	Podiceps cristatus	Great Crested Grebe	temperate										G
	Tachybaptus dominicus	Least Grebe	tropical	H2		H2							
Procellariidae	Puffinus griseus	Sooty Shearwater	temperate	С	С			С	С	С			С
Psittacidae	Amazona aestiva	Blue-fronted Parrot	tropical										G
(Psittacidae)	Amazona amazonica	Orange-winged Parrot	tropical										G
(	Amazona autumnalis	Red-Lored Parrot	tropical	H2		H2							
	Ara ararauna	Blue-and-yellow Macaw	tropical										G
	Bolborhynchus lineola	Barred Parakeet	tropical	H2		H2							
	Brotogeris jugularis	Orange-Chinned Parakeet	tropical	H2		H2							
	Orthopsittaca manilata	Red-bellied Macaw	tropical										G
	Pionopsitta haematotis	Brown-Hooded Parrot	tropical	H2		H2							
	Pionus senilis	White-Crowned Parrot	tropical	H2		H2							
	Platycercus caledonicus	Green Rosella	temperate										G
	Poicephalus meyeri	Meyer's Parrot	tropical										G
	Pyrrhura hoffmanni	Sulphur-Winged Parakeet	tropical	H2		H2							-
Rallidae	Aramides cajanea	Grey-Necked Wood-Rail	tropical	H2		H2							
	Fulica americana	American Coot	temperate	H1									
	Fulica atra	Common Coot	temperate										G
	Gallinula chloropus	Common Moorhen	temperate										G
	Laterallus albigularis	White-Throated Crake	tropical	H2		H2							G
Ramphastidae	Aulacorhynchus prasinus	Guatemalan Emerald-Toucanet	tropical	H2		H2							
namphasiidae	Eubucco bourcierii	Red-Headed Barbet	tropical	H2		H2							
	Pteroglossus frantzii	Fiery-Billed Aracari	tropical	H2		H2							
	Pteroglossus torquatus	Collared Aracari	tropical	H2		H2							
	Ramphastos swainsonii	Chestnut-Mandibled Toucan	•	H2		H2							
Regulidae		Ruby-Crowned Kinglet	tropical	H1		ΠZ							
neguliuae	Regulus calendula Bogulus rogulus	Goldcrest	temperate	пт									G
	Regulus regulus		temperate	Ш4									G
Saalanaaidaa	Regulus satrapa	Golden-Crowned Kinglet	temperate	H1									0
Scolopacidae	Calidris maritima	Purple Sandpiper	temperate										G
Que a si de a	Scolopax rusticola	Eurasian Woodcock	temperate	~	~								G
Scopidae	Scopus umbretta	Hamerkop	tropical	С	С								С
Sittidae	Sitta canadensis	Red-Breasted Nuthatch	temperate	H1		110							
	Sitta carolinensis	White-Breasted Nuthatch	temperate	H2		H2			_	-		-	~
	Sitta europaea	Wood Nuthatch	temperate	R			_		R	R		R	G
	Sitta frontalis	Velvet-Fronted Nuthatch	tropical	R			R		R	R		R	~
Strigidae	Asio flammeus	Short-eared Owl	temperate										G
	Asio otus	Long-eared Owl	temperate										G

				Litera	ature s	source	for da	ita on					
Family	Species	Name	Climate	Hea	Lun	FIMu	Giz	Giln	Liv	Kid	Par	n Spl	Bra
(Strigidae)	Bubo virginianus	Great Horned Owl	temperate	H1									
	Megascops choliba	Tropical Screech-Owl	tropical	H2		H2							
	Pseudoscops clamator	Striped Owl	tropical	H2		H2							
	Pulsatrix perspicillata	Spectacled Owl	tropical	H2		H2							
	Strix aluco	Tawny Owl	temperate										G
	Strix nigrolineata	Black-And-White Owl	tropical	H2		H2							
	Strix varia	Barred Owl	temperate	H1									
	Strix virgata	Mottled Owl	tropical	H2		H2							
Sturnidae	Dumetella carolinensis	Grey Catbird	temperate	H1									
	Sturnus vulgaris	Common Starling	temperate	H1									G
	Toxostoma rufum	Brown Thrasher	temperate	H1									
Sylviidae	Panurus biarmicus	Bearded Parrotbill	temperate										G
Famaliidae	Sylvia atricapilla	Blackcap	temperate										G
Thamnophilidae	Cercomacra nigricans	Jet Antbird	tropical	H2		H2							
	Cymbilaimus lineatus	Fasciated Antshrike	tropical	H2		H2							
	Dysithamnus mentalis	Plain Antvireo	tropical	H2		H2							
	Gymnopithys leucaspis	Bicolored Antbird	tropical	H2		H2							
	Hylophylax naevioides	Spotted Antbird	tropical	H2		H2							
	Myrmeciza exsul	Chestnut-Backed Antbird	tropical	H2		H2							
	Myrmeciza longipes	White-Bellied Antbird	tropical	H2		H2							
	Myrmotherula schisticolor	Slaty Antwren	tropical	H2		H2							
	Myrmotherula surinamensis	Guianan Streaked-Antwren	tropical	H2		H2							
	Taraba major	Great Antshrike	tropical	H2		H2							
	Thamnistes anabatinus	Russet Antshrike	tropical	H2		H2							
	Thamnophilus doliatus	Barred Antshrike	tropical	H2		H2							
	Thamnophilus punctatus	Eastern Slaty-Antshrike	tropical	H2		H2							
Finamidae	Crypturellus soui	Little Tinamou	tropical	H2		H2							
Indinidae	Nothocercus bonapartei	Highland Tinamou	tropical	H2		H2							
		Great Tinamou	-	H2		H2							
Trochilidae	Tinamus major Amazilia tzacatl	Rufous-Tailed Hummingbird	tropical	C	С	ΠZ			С	С			с
TIOCIIIIUae	Campylopterus hemileucurus	C C	tropical	H1	C				U	U			U
		Ŭ	tropical	H2		H2							
	Glaucis hirsutus	Rufous-Breasted Hermit	tropical			ПΖ							
Fragonidaa	Selasphorus scintilla	Scintillant Hummingbird	tropical	H1 D			п		П	п	Б	п	
Trogonidae	Harpactes fasciatus	Malabar Trogon	tropical	R			R		R	R	R	R	
	Pharomachrus mocinno	Resplendent Quetzal	tropical	H2		H2							
	Trogon collaris	Collared Trogon	tropical	H2		H2							
	Trogon curucui T	Blue-Crowned Trogon	tropical	H2		H2							
	Trogon massena	Slaty-Tailed Trogon	tropical	H2		H2							
	Trogon melanurus	Black-Tailed Trogon	tropical	H2		H2							
	Trogon violaceus	Violaceous Trogon	tropical	H2		H2							
	Trogon viridis	White-Tailed Trogon	tropical	H2		H2							
Tyrannidae	Attila spadiceus	Bright-Rumped Attila	tropical	H2		H2							
	Camptostoma obsoletum	Southern Beardless-Tyrannulet	tropical	H2		H2							
	Capsiempis flaveola	Yellow Tyrannulet	tropical	H2		H2							
	Chiroxiphia lanceolata	Lance-Tailed Manakin	tropical	H2		H2							
	Cnipodectes subbrunneus	Twistwing	tropical	H2		H2							
	Contopus lugubris	Dark Pewee	tropical	H2		H2							
	Corapipo leucorrhoa	White-Bibbed Manakin	tropical	H2		H2							
	Cotinga ridgwayi	Turquoise Cotinga	tropical	H2		H2							
	Elaenia chiriquensis	Lesser Elaenia	tropical	H2		H2							
	Elaenia flavogaster	Yellow-Bellied Elaenia	tropical	H2		H2							
	Elaenia frantzii	Mountain Elaenia	tropical	H2		H2							
	Empidonax flavescens	Yellowish Flycatcher	tropical	H2		H2							
	Empidonax minimus	Least Flycatcher	temperate	H1									
	Empidonax traillii	Willow Flycatcher	temperate	H1									
	Fluvicola pica	Pied Water-Tyrant	tropical	H2		H2							

				Literature source for data on				
Family	Species	Name	Climate	Hea Lun	FIMu Giz	Giln Liv	Kid Pan Sp	ol Bra
	Laniocera rufescens	Speckled Mourner	tropical	H1				
	Legatus leucophaius	Piratic Flycatcher	tropical	H2	H2			
	Leptopogon superciliaris	Slaty-Capped Flycatcher	tropical	H2	H2			
	Lipaugus unirufus	Rufous Piha	tropical	H2	H2			
	Lophotriccus pileatus	Scale-Crested Pygmy-Tyrant	tropical	H2	H2			
	Manacus vitellinus	Golden-Collared Manakin	tropical	H2	H2			
	Megarynchus pitangua	Boat-Billed Flycatcher	tropical	H2	H2			
	Mionectes olivaceus	Olive-Striped Flycatcher	tropical	H2	H2			
	Mitrephanes phaeocercus	Tufted Flycatcher	tropical	H2	H2			
	Myiarchus ferox	Short-Crested Flycatcher	tropical	H2	H2			
Tyrannidae)	Myiarchus tuberculifer	Dusky-Capped Flycatcher	tropical	H2	H2			
,,	Myiobius atricaudus	Black-Tailed Flycatcher	tropical	H2	H2			
	Myiobius barbatus	Sulphur-Rumped Flycatcher	tropical	H2	H2			
	Myiodynastes hemichrysus	Golden-Bellied Flycatcher	tropical	H2	H2			
	Myiodynastes maculatus	Streaked Flycatcher	tropical	H2	H2			
		Greenish Elaenia	-	H2	H2			
	Myiopagis viridicata		tropical					
	Myiophobus fasciatus	Bran-Colored Flycatcher	tropical	H2	H2			
	Myiozetetes cayanensis	Rusty-Margined Flycatcher	tropical	H2	H2			
	Myiozetetes granadensis	Grey-Capped Flycatcher	tropical	H2	H2			
	Myiozetetes similis	Social Flycatcher	tropical	H2	H2			
	Oncostoma olivaceum	Southern Bentbill	tropical	H2	H2			
	Onychorhynchus coronatus	Royal Flycatcher	tropical	H2	H2			
	Pachyramphus cinnamomeus		tropical	H2	H2			
	Pachyramphus polychopterus	White-Winged Becard	tropical	H2	H2			
	Pachyramphus versicolor	Barred Becard	tropical	H2	H2			
	Pipra mentalis	Red-Capped Manakin	tropical	H2	H2			
	Platyrinchus mystaceus	White-Throated Spadebill	tropical	H2	H2			
	Poecilotriccus sylvia	Slate-Headed Tody-Tyrant	tropical	H2	H2			
	Querula purpurata	Purple-Throated Fruitcrow	tropical	H2	H2			
	Rhynchocyclus brevirostris	Eye-Ringed Flatbill	tropical	H2	H2			
	Rhynchocyclus olivaceus	Olivaceous Flatbill	tropical	H2	H2			
	Rhytipterna holerythra	Rufous Mourner	tropical	H2	H2			
	Sayornis phoebe	Eastern Phoebe	temperate	H1				
	Schiffornis turdina	Thrush-Like Schiffornis	tropical	H2	H2			
	Serpophaga cinerea	Torrent Tyrannulet	tropical	H2	H2			
	Terenotriccus erythurus	Ruddy-Tailed Flycatcher	tropical	H2	H2			
	Tityra inquisitor	Black-Crowned Tityra	tropical	H2	H2			
	Tityra semifasciata	Masked Tityra	tropical	H2	H2			
	Todirostrum cinereum	-	-	H2	H2			
		Common Tody-Flycatcher	tropical					
	Tolmomyias sulphurescens	Yellow-Olive Flycatcher	tropical	H2	H2			
	Tyranniscus zeledoni	White-Fronted Tyrannulet	tropical	H2	H2			
	Tyrannulus elatus	Yellow-Crowned Tyrannulet	tropical	H2	H2			
	Tyrannus melancholicus	Tropical Kingbird	tropical	H2	H2			
Fyrannidae)	Tyrannus savana	Fork-Tailed Flycatcher	tropical	H2	H2			
	Zimmerius vilissimus	Paltry Tyrannulet	tropical	H2	H2			
ytonidae	Tyto alba	Barn Owl	temperate					G
'ireonidae	Cyclarhis gujanensis	Rufous-Browed Peppershrike	tropical	H2	H2			
	Hylophilus aurantiifrons	Golden-Fronted Greenlet	tropical	H2	H2			
	Hylophilus decurtatus	Lesser Greenlet	tropical	H2	H2			
	Hylophilus flavipes	Scrub Greenlet	tropical	H2	H2			
	Hylophilus ochraceiceps	Tawny-Crowned Greenlet	tropical	H2	H2			
	Vireo carmioli	Yellow-Winged Vireo	tropical	H2	H2			
	Vireo leucophrys	Brown-Capped Vireo	tropical	H2	H2			
	Vireo solitarius	Blue-Headed Vireo	temperate	H1				

Species are ordered alphabetically on family and species name. Literature sources are abbreviated as follows: C: (Crile and Quiring, 1940), G: (Garamszegi et al., 2002), GG: (Graber and Graber, 1965), H1: (Hartman, 1955), H2: (Hartman, 1961), O: (Oakeson, 1956), R: (Rensch and Rensch,

1956). References are presented below. Organs names are indicated by Hea: heart, Lun: lungs, FIMu: flight muscles, Giz: gizzard, Giln: gizzard+intestines, Liv: liver, Kid: kidneys, Pan: pancreas, Spl: spleen, Bra: brain.

REFERENCES

Crile, G. and Quiring, D. P. (1940) A record of the body weight and certain organ and gland weights of 3690 animals. *Ohio J. Sci.* 40, 219-259. Garamszegi, L. Z., Møller, A. P. and Erritzøe, J. (2002) Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. R. Soc. B* 269, 961-967.

Graber, R. R. and Graber, J. W. (1965) Variation in avian brain weights with special reference to age. Condor 67, 300-318.

Hartman, F. A. (1955) Heart weight in birds. Condor 57, 221-238.

Hartman, F. A. (1961) Locomotor mechanisms of birds. Smithson. Misc. Coll. 143, 1-91.

Oakeson, B. B. (1956) Liver and spleen weight cycles in non-migratory White-crowned Sparrows. Condor 58, 45-50.

Rensch, I. and Rensch, B. (1956) Relative Organmaße bei tropischen Warmblütern. Zool. Anz. 156, 106-124.

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					sizes in parent	, ,	_
	Amazilia	Archilochus	Arremonops	Astragalinus	Attila	Brotogeris	Cardinalis
	tzacatl	colubris	conirostris	tristis	spadiceus	jugularis	cardinalis
Climate	Tropical	Temperate	Tropical	Temperate	Tropical	Tropical	Temperate
Diet	Nectivorous	Nectivorous	Omnivorous	Granivorous	Insectivorous	Granivorous	Granivorous
Migratory	No	Yes	No	No	No	No	No
Body mass (n)	6.5 (1)	2.7 (1)	39.9 (5)	11.4 (7)	36.2 (1)	57.2 (1)	38.8 (6)
Brain	0.070 (1)	0.016 (1)	0.295±0.004 (5)	0.114±0.004 (7)	0.191 (1)	0.479 (1)	0.301±0.007 (6)
Carcass	0.865 (1)	0.298 (1)	5.731±0.245 (5)	1.708±0.086 (7)	4.931 (1)	7.942 (1)	4.920±0.323 (6)
Fat	0.001 (1)	0.001 (1)	0.014±0.007 (5)	0.028±0.010 (7)	0.001 (1)	0.001 (1)	0.060±0.032 (6)
Gallbladder	0.000 (1)	(0)	0.005 (1)	(0)	0.000 (1)	0.000 (1)	0.005±0.003 (3)
Gizzard	0.057 (1)	0.003 (1)	0.332±0.008 (5)	0.051±0.004 (6)	0.265 (1)	0.130 (1)	0.354±0.032 (6)
Heart	0.017 (1)	0.018 (1)	0.093±0.006 (4)	0.051±0.001 (7)	0.097 (1)	0.239 (1)	0.121±0.011 (6)
Intestines	0.006 (1)	0.013 (1)	0.191±0.015 (5)	0.032±0.004 (7)	0.122 (1)	0.168 (1)	0.163±0.021 (6)
Kidneys	0.016 (1)	0.007 (1)	0.079±0.006 (5)	0.037±0.002 (6)	0.107 (1)	0.085 (1)	0.127±0.013 (5)
Leg muscles	0.086 (.1)	0.014 (1)	1.177±0.054 (5)	0.144±0.008 (7)	0.585 (1)	0.811 (1)	0.600±0.033 (6)
Liver	0.034 (1)	0.037 (1)	0.350±0.042 (5)	0.092±0.011 (7)	0.29 (1)	0.381 (1)	0.291±0.022 (6)
Lungs	0.010 (1)	0.018 (1)	0.076±0.007 (5)	0.057±0.003 (6)	0.111 (1)	0.193 (1)	0.116±0.007 (5)
Ovaries	(0)	(0)	(0)	0.006±0.002 (3)	0.581 (1)	(0)	0.018±0.006 (2)
Oviduct	(0)	(0)	(0)	0.002±0 (0)	(0)	(0)	0.018±0.018 (2)
Flight muscles	0.358 (1)	0.221 (1)	1.450±0.08 (5)	0.682±0.022 (7)	1.524 (1)	3.349 (1)	1.891±0.123 (6)
Skin	(0)	(0)	0.352±0.027 (5)	0.141±0.017 (6)	(0)	(0)	0.328±0.038 (5)
Spleen	0.001 (1)	(0)	0.014±0.005 (4)	0.002±0.001 (7)	0.001 (1)	0.001 (1)	0.008±0.001 (6)
Testes	0.001 (1)	0.000 (1)	0.037±0.009 (4)	0.023±0.006 (4)	(0)	0.009 (1)	0.051±0.006 (4)

Table S2. Climate of breeding area, diet, migratory behaviour (long-distance or not), mean (±s.e.m. where available) body mass (g) and dry mass of organs (mg) of birds collected for this study (sample

	Columbina talpacoti	Contopus virens	Contorchilus leucotis	Cyanoloxia cyanoides	Dendroica petechia	Euphonia Ianiirostris	Florisuga mellivora
Climate	Tropical	Temperate	Tropical	Tropical	Temperate	Tropical	Tropical
Diet	Granivorous	Insectivorous	Insectivorous	Omnivorous	Insectivorous	Frugivorous	Nectivorous
Migratory	No	Yes	No	No	Yes	No	No
Body mass (n)	37.9 (8)	11.6 (1)	20.3 (5)	26.8 (5)	7.2 (1)	12.8 (5)	7.0 (1)
Brain	0.119±0.004 (7)	0.090 (1)	0.192±0.006 (5)	0.250±0.011 (5)	0.088 (1)	0.133±0.007 (4)	0.034 (1)
Carcass	4.577±0.196 (8)	1.530 (1)	2.801±0.072 (5)	4.175±0.239 (5)	1.154 (1)	1.859±0.054 (5)	0.923 (1)
Fat	0.001±0.000 (8)	0.001 (1)	0.028±0.014 (5)	0.001±0.000 (5)	0.001 (1)	0.015±0.007 (5)	0.001 (1)
Gallbladder	0.004±0.002 (4)	(0)	0.002±0.001 (3)	0.004 (1)	(0)	0.002±0.000 (3)	0.000 (1)
Gizzard	0.407±0.013 (8)	0.079 (1)	0.177±0.009 (5)	0.210±0.027 (5)	0.045 (1)	0.010±0.000 (5)	0.017 (1)
Heart	0.095±0.006 (8)	0.039 (1)	0.053±0.008 (5)	0.067±0.006 (5)	0.028 (1)	0.043±0.002 (5)	0.049 (1)
Intestines	0.101±0.012 (8)	0.011 (1)	0.099±0.005 (5)	0.082±0.010 (5)	0.017 (1)	0.086±0.007 (5)	0.026 (1)
Kidneys	0.044±0.002 (8)	0.038 (1)	0.058±0.006 (5)	0.044±0.003 (5)	0.028 (1)	0.036±0.002 (5)	0.019 (1)
Leg muscles	0.506±0.021 (8)	0.101 (1)	0.621±0.018 (5)	0.448±0.032 (5)	0.151 (1)	0.202±0.011 (5)	0.027 (1)
Liver	0.210±0.024 (8)	0.073 (1)	0.188±0.018 (5)	0.174±0.035 (5)	0.057 (1)	0.171±0.019 (5)	0.048 (1)
Lungs	0.077±0.005 (8)	0.036 (1)	0.042±0.004 (5)	0.059±0.009 (5)	0.034 (1)	0.032±0.003 (5)	0.017 (1)
Ovaries	0.005±0.002 (5)	(0)	0.014 (1)	0.006±0.003 (3)	(0)	0.205±0.010 (2)	0.005 (1)
Oviduct	0.000±0.000 (3)	(0)	0.000 (1)	0.000±0.000 (3)	(0)	0.000±0.000 (2)	(0)
Flight muscles	2.605±0.146 (8)	0.643 (1)	0.580±0.044 (5)	1.282±0.087 (5)	0.346 (1)	0.636±0.030 (5)	0.470 (1)
Skin	0.497±0.074 (5)	0.092 (1)	0.237±0.013 (4)	0.187±0.016 (5)	(0)	0.145±0.013 (5)	(0)
Spleen	0.001±0.000 (4)	(0)	0.003±0.001 (5)	0.013±0.005 (5)	0.001 (1)	0.004±0.001 (4)	0.001 (1)
Testes	0.013±0.003 (2)	0.008 (1)	0.007±0.002 (4)	0.019±0.013 (2)	0.020 (1)	0.024±0.006 (3)	(0)

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	Gymnopithys leucaspis	Hylophylax naevioides	Lepidothrix coronata	Leptotila verreauxi	Manacus vitellinus	Melanerpes rubricapillus	Melospiza melodia
Climate	Tropical	Tropical	Tropical	Tropical	Tropical	Tropical	Temperate
Diet	Insectivorous	Insectivorous	Frugivorous	Granivorous	Frugivorous	Insectivorous	Omnivorous
Migratory Body mass	No	No	No	No	No	No	No
(n)	30.2 (1)	16.1 (2)	8.6 (2)	132.1 (1)	15.0 (2) 0.111±0.002	43.5 (1)	19.3 (5)
Brain	0.160 (1)	0.124±0.020 (2)	0.079±0.013 (2)	0.247 (1)	(2) 1.993±0.118	0.300 (1)	0.187±0.009 (5)
Carcass	4.386 (1)	2.037±0.046 (2)	1.149±0.041 (2)	19.964 (1)	(2) 0.122±0.121	6.314 (1)	2.619±0.145 (5)
Fat	0.001 (1)	0.001±0.000 (2)	0.001±0.000 (2)	5.193 (1)	(2) 0.001±0.001	0.001 (1)	0.042±0.018 (5)
Gallbladder	0.000 (1)	0.000±0.000 (2)	0.000±0.000 (2)	0.000 (1)	(2) 0.200±0.029	0.002 (1)	(0)
Gizzard	0.200 (1)	0.151±0.001 (2)	0.102±0.018 (2)	2.042 (1)	(2) 0.046±0.001	0.324 (1)	0.145±0.023 (5)
Heart	0.102 (1)	0.044±0.000 (2)	0.028±0.004 (2)	0.477 (1)	(2) 0.068±0.011	0.110 (1)	0.055±0.003 (5)
Intestines	0.064 (1)	0.055±0.009 (2)	0.023±0.000 (2)	0.354 (1)	(2) 0.048±0.002	0.119 (1)	0.084±0.031 (5)
Kidneys	0.114 (1)	0.049±0.003 (2)	0.033±0.000 (2)	0.149 (1)	(2) 0.212±0.028	0.091 (1)	0.063±0.008 (5)
Leg muscles	1.059 (1)	0.375±0.026 (2)	0.102±0.010 (2)	2.003 (1)	(2) 0.138±0.012	0.598 (1)	0.454±0.029 (5)
Liver	0.298 (1)	0.167±0.007 (2)	0.064±0.012 (2)	0.960 (1)	(2) 0.040±0.008	0.330 (1)	0.165±0.015 (5)
Lungs	0.108 (1)	0.033±0.000 (2)	0.023±0.001 (2)	0.320 (1)	(2) 0.003±0.001	0.108 (1)	0.059±0.005 (5)
Ovaries	(0)	0.003 (1)	0.003 (1)	(0)	(2)	0.012 (1)	0.059±0.059 (5)
Oviduct Flight	(0)	(0)	(0)	(0)	(0) 0.681±0.113	(0)	0.066±0.066 (5)
muscles	0.961 (1)	0.436±0.045 (2)	0.386±0.011 (2)	11.395 (1)	(2)	1.654 (1)	0.728±0.091 (5)
Skin	(0)	(0)	(0)	(0)	(0) 0.001±0.000	(0)	(0)
Spleen	0.001 (1)	0.001±0.000 (2)	0.001±0.000 (2)	0.001 (1)	(2)	0.001 (1)	0.003±0.001 (4)
Testes	0.004 (1)	0 (1)	0.002 (1)	(0)	(0)	(0)	0.037±0.003 (3)

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	Mimus gilvus	Mimus polyglottos	Molothrus ater	Myiozetetes similis	Nyctidromus albicollis	Pipra mentalis	Pipromorpha oliaginea
limate	Tropical	Temperate	Temperate	Tropical	Tropical	Tropical	Tropical
liet	Omnivorous	Omnivorous	Omnivorous	Insectivorous	Insectivorous	Frugivorous	Omnivorous
ligratory	No	No	No	No	No	No	No
ody mass	59.8 (5)	46.6 (5)	39.0 (2)	22.8 (2)	49.5 (3)	12.2 (3)	9.5 (6)
rain	0.338±0.012 (5)	0.269±0.011 (5)	0.251±0.001 (2)	0.127±0.004 (2)	0.146±0.014 (3)	0.091±0.004 (3)	0.089±0.006 (6)
arcass	8.781±0.271 (5)	6.636±0.382 (5)	4.644±0.202 (2)	3.144±0.084 (2)	7.755±0.794 (3)	1.576±0.053 (3)	1.278±0.029 (6)
at	0.038±0.020 (5)	0.082±0.061 (5)	0.079±0.040 (2)	0.001±0.000 (2)	0.162±0.161 (3)	0.001±0.000 (3)	0.010±0.009 (6)
allbladder	(0)	0.008±0.001 (5)	0.003 (1)	0.001±0.001 (2)	0.001±0.001 (3)	0.003±0.001 (3)	0.001 (1)
aizzard	0.397±0.022 (5)	0.365±0.022 (5)	0.256±0.013 (2)	0.193±0.025 (2)	0.727±0.028 (3)	0.134±0.034 (3)	0.083±0.008 (6)
leart	0.128±0.005 (5)	0.166±0.008 (5)	0.114±0.011 (2)	0.073±0.013 (2)	0.114±0.013 (3)	0.036±0.003 (3)	0.033±0.001 (6)
ntestines	0.368±0.044 (5)	0.235±0.039 (5)	0.222±0.111 (2)	0.083±0.046 (2)	0.100±0.016 (3)	0.035±0.009 (3)	0.035±0.007 (6)
idneys	0.151±0.008 (5)	0.162±0.014 (5)	0.111±0.003 (2)	0.051±0.009 (2)	0.080±0.004 (3)	0.042±0.002 (3)	0.027±0.002 (6)
eg muscles	1.624±0.051 (5)	1.051±0.055 (5)	0.638±0.066 (2)	0.263±0.050 (2)	0.635±0.076 (3)	0.171±0.012 (3)	0.122±0.007 (6)
iver	0.462±0.026 (5)	0.450±0.033 (5)	0.329±0.008 (2)	0.155±0.037 (2)	0.246±0.045 (3)	0.081±0.006 (3)	0.067±0.008 (6)
ungs	0.150±0.023 (5)	0.182±0.016 (5)	0.162±0.011 (2)	0.059±0.001 (2)	0.103±0.013 (3)	0.040±0.002 (3)	0.024±0.002 (6)
Varies	0.020±0.008 (2)	0.027 (1)	0.088±0.066 (2)	0.008 (1)	0.007±0.002 (2)	(0)	0.000 (1)
Viduct	0.000±0.000 (2)	0.085 (1)	0.545±0.123 (2)	(0)	(0)	(0)	0.035 (1)
light uscles	2.289±0.110 (5)	2.142±0.141 (5)	2.062±0.157 (2)	1.197±0.026 (2)	2.306±0.121 (3)	0.643±0.060 (3)	0.556±0.042 (6)
kin	0.644±0.027 (5)	0.464±0.013 (2)	(0)	(0)	(0)	(0)	0.098±0.006 (5)
pleen	0.005±0.000 (5)	0.008±0.002 (5)	0.01±0.004 (2)	0.001±0.000 (2)	0.001±0.000 (3)	0.001±0.000 (3)	0.003±0.002 (6)
estes	0.013±0.010 (3)	0.034±0.003 (4)	(0)	0.003 (1)	0.009 (1)	0.002±0.000 (3)	0.005±0.001 (5)

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	Piranga olivacea	Progne chalybea	Quiscalus quiscula	Sayornis phoebe	Spizella passerina	Sporophila corvina	Tachycineta albilinea
Climate	Temperate	Tropical	Temperate	Temperate	Temperate	Tropical	Tropical
Diet	Insectivorous	Insectivorous	Omnivorous	Insectivorous	Granivorous	Granivorous	Insectivorous
Migratory	Yes	No	No	Yes	No	No	No
Body mass (n)	27.3 (4)	35.7 (5)	108.2 (1)	16.6 (5)	11.0 (5)	10.1 (1)0)	13.4 (5)
Brain	0.196±0.005 (4)	0.206±0.005 (5)	0.596 (1)	0.121±0.005 (4)	0.102±0.004 (5)	0.121±0.003 (1)0	0.102±0.006 (5)
Carcass	3.891±0.373 (4)	5.393±0.301 (5)	16.205 (1)	2.127±0.059 (4)	1.357±0.066 (5)	1.535±0.042 (1)0	1.811±0.064 (5)
Fat	0.011±0.008 (4)	0.182±0.167 (5)	0.078 (1)	0.010±0.009 (4)	0.003±0.002 (5)	0.003±0.002 (1)0	0.010±0.009 (5)
Gallbladder	(0)	(0)	0.008 (1)	0.003 (1)	(0)	0.000±0.000 (5)	0.000 (1)
Gizzard	0.158±0.005 (4)	0.343±0.033 (5)	0.763 (1)	0.134±0.008 (4)	0.097±0.004 (5)	0.070±0.004 (1)0	0.124±0.006 (5)
Heart	0.088±0.004 (4)	0.155±0.009 (4)	0.325 (1)	0.050±0.005 (4)	0.036±0.002 (5)	0.034±0.002 (1)0	0.046±0.002 (5)
Intestines	0.094±0.010 (4)	0.184±0.034 (5)	0.574 (1)	0.035±0.005 (4)	0.031±0.003 (5)	0.035±0.005 (1)0	0.106±0.018 (5)
Kidneys	0.095±0.006 (4)	0.103±0.010 (5)	0.297 (1)	0.065±0.002 (4)	0.033±0.003 (5)	0.017±0.001 (1)0	0.046±0.003 (5)
Leg muscles	0.353±0.014 (4)	0.407±0.035 (5)	2.553 (1)	0.170±0.013 (4)	0.146±0.007 (5)	0.165±0.008 (1)0	0.108±0.012 (5)
Liver	0.220±0.015 (4)	0.246±0.030 (5)	0.928 (1)	0.149±0.018 (4)	0.089±0.006 (5)	0.095±0.009 (1)0	0.132±0.009 (5)
Lungs	0.104±0.008 (4)	0.123±0.012 (5)	0.610 (1)	0.057±0.005 (4)	0.037±0.004 (5)	0.029±0.002 (1)0	0.041±0.002 (5)
Ovaries	(0)	0.005±0.005 (2)	(0)	0.005±0.002 (3)	0.005 (1)	0.001±0.001 (5)	0.002 (1)
Oviduct	(0)	0.000±0.000 (2)	(0)	0.006±0.002 (3)	0 (1)	0.000±0.000 (3)	0.000 (1)
Flight muscles	1.614±0.084 (4)	1.833±0.164 (5)	5.396 (1)	0.870±0.063 (4)	0.613±0.077 (5)	0.420±0.017 (1)0	0.607±0.057 (5)
Skin	0.224±0.025 (4)	0.600±0.126 (5)	(0)	0.163±0.017 (4)	0.073±0.005 (4)	0.112±0.010 (5)	0.183±0.008 (4)
Spleen	0.006±0.001 (4)	0.004±0.001 (5)	0.015 (1)	0.002±0.000 (3)	0.003±0.001 (5)	0.002±0.001 (8)	0.003±0.001 (5)
Testes	0.103±0.013 (4)	0.117±0.024 (3)	0.245 (1)	0.017 (1)	0.030±0.006 (4)	0.002±0.001 (5)	0.001±0.001 (4)

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	Tachycineta bicolor	Tangara episcopus	Tangara larvata	Tangara palmarum	Thamnophilus doliatus	Troglodytes aedon	Troglodytes musculus
Climate	Temperate	Tropical	Tropical	Tropical	Tropical	Temperate	Tropical
Diet	Insectivorous	Frugivorous	Frugivorous	Frugivorous	Insectivorous	Insectivorous	Insectivorous
Migratory	Yes	No	No	No	No	No	No
Body mass (n)	16.3 (5)	31.2 (8)	32.3 (1)	34.5 (1)	29.9 (1)	9.4 (6)	12.8 (9)
Brain	0.106±0.004 (5)	0.213±0.007 (8)	0.176 (1)	0.235 (1)	0.201 (1)	0.112±0.002 (5)	0.127±0.003 (9)
Carcass	2.017±0.104 (5)	4.701±0.136 (8)	4.715 (1)	4.648 (1)	4.138 (1)	1.176±0.043 (5)	1.780±0.061 (9)
Fat	0.051±0.033 (5)	0.047±0.037 (8)	0.001 (1)	0.001 (1)	0.001 (1)	0.011±0.005 (5)	0.014±0.010 (9)
Gallbladder	0.004 (1)	0.005±0.001 (4)	0.000 (1)	0.004 (1)	0.000 (1)	(0)	0.000±0.000
	0.156±0.010	0.087±0.009 (8)	0.243 (1)	0.119 (1)	0.384 (1)	0.082±0.006 (5)	(4) 0.095±0.003
Gizzard	(5) 0.052±0.002	0.110±0.005 (8)	0.121 (1)	0.108 (1)	0.090 (1)	0.033±0.001 (5)	(8) 0.041±0.002
Heart	(5) 0.090±0.018	0.178±0.015 (8)	0.091 (1)	0.183 (1)	0.140 (1)	0.030±0.007 (5)	(9) 0.054±0.008
Intestines	(5) 0.066±0.002	0.070±0.006 (8)	0.101 (1)	0.070 (1)	0.100 (1)	0.038±0.004 (5)	(9) 0.036±0.003
Kidneys	(5) 0.150±0.012	0.576±0.028 (8)	0.485 (1)	0.590 (1)	0.683 (1)	0.232±0.012 (5)	(9) 0.369±0.014
Leg muscles	(5) 0.148±0.013	0.321±0.022 (8)	0.307 (1)	0.303 (1)	0.408 (1)	0.093±0.010 (5)	(9) 0.109±0.009
Liver	(5) 0.077±0.004	0.088±0.006 (8)	0.079 (1)	0.122 (1)	0.065 (1)	0.033±0.003 (5)	(9) 0.033±0.003
Lungs	(5) 0.006±0.001	0.018±0.007 (4)	(0)	(0)	(0)	0.013±0.003 (2)	(9) 0.005 (1)
Ovaries	(3) 0.009±0.000	0.020±0.020 (2)	(0)	(0)	(0)	0.088±0.057 (2)	0.000 (1)
Oviduct Flight	(3) 0.709±0.060	1.682±0.089 (8)	1.308 (1)	1.853 (1)	0.730 (1)	0.302±0.015 (5)	0.411±0.026
muscles	(5) 0.247±0.045	0.321±0.024 (5)	(0)	(0)	(0)	0.104±0.007 (4)	(9) 0.163±0.010
Skin	(5)						(5)
Spleen	0.002±0.001 (5)	0.004±0.001 (8)	0.001 (1)	0.001 (1)	0.001 (1)	0.001±0.000 (5)	0.003±0.002 (7)
Testes	0.056±0.027 (2)	0.049±0.016 (4)	0.003 (1)	0.012 (1)	0.004 (1)	0.031±0.001 (3)	0.006±0.002 (8)

	Turdus grayi	Turdus migratorius	Vireo flavoviridis	Vireo olivaceus	Xenops minutus	Xiphorhynchus guttatus	Zenaida macroura
Climate	Tropical	Temperate	Tropical	Temperate	Tropical	Tropical	Temperate
Diet	Omnivorous	Omnivorous	Insectivorous	Insectivorous	Insectivorous	Insectivorous	Granivorous
Migratory	No	No	No	Yes	No	No	No
Body mass (n)	65 9 (11)	73.7 (5)	17.1 (5)	15.1 (7)	11.0 (1)	43.6 (1)	122.8 (6)
Brain	0.328±0.016 (11	0.332±0.012 (4)	0.136±0.008 (5)	0.125±0.005 (6)	0.084 (1)	0.316 (1)	0.226±0.008 (6)
Carcass	9.546±0.510 (11)	9.383±0.624 (4)	2.443±0.17 (5)	2.134±0.139 (7)	1.536 (1)	7.299 (1)	14.154±0.781 (6)
	0.042±0.016 (11	0.026±0.017	0.342±0.336 (5)	0.016±0.009 (7)	0.001 (1)	0.001 (1)	0.359 (0).1 (6)
Fat	0.006±0.001 (7)	(4) 0.010±0.003	0.009 (1)	(0)	0.000 (1)	0.002 (1)	(0)
Gallbladder Gizzard	0.345±0.052 (10)	(2) 0.300±0.053	0.107±0.004 (4)	0.079±0.005 (7)	0.077 (1)	0.319 (1)	0.863±0.019 (6)
Heart	0.169±0.009 (11)	(4) 0.245±0.018	0.060±0.004 (4)	0.072±0.005 (7)	0.049 (1)	0.108 (1)	0.427±0.010 (6)
Intestines	0.421±0.049 (11)	(4) 0.374±0.041	0.080±0.004 (4)	0.038±0.005 (7)	0.011 (1)	0.049 (1)	0.280±0.043 (6)
Kidneys	0.135±0.007 (11)	(4) 0.230±0.024 (4)	0.055±0.006 (5)	0.061±0.005 (7)	0.020 (1)	0.126 (1)	0.211±0.008 (6)
Leg muscles	1.144±0.082 (11)	(4) 1.242±0.053 (4)	0.271±0.015 (5)	0.205±0.008 (7)	0.205 (1)	0.787 (1)	1.434±0.069 (6)
Liver	0.488±0.036 (10)	(4) 0.661±0.025 (4)	0.148±0.012 (5)	0.119±0.007 (7)	0.065 (1)	0.264 (1)	0.778±0.033 (6)
	0.183±0.013 (11)	0.251±0.012	0.052±0.008 (5)	0.071±0.006 (7)	0.025 (1)	0.073 (1)	0.448±0.020 (6)
Lungs Ovaries	0.030±0.013 (7)	(4) 0.025 (1)	0.018±0.018 (2)	0.009 (1)	(0)	(0)	0.026±0.026 (2)
Oviduct	0.000±0.000 (2)	0.031 (1)	0.092±0.092 (2)	0.018 (1)	(0)	(0)	0.139±0.139 (2)
Flight	3.474±0.268 (11)	4.392±0.136 (4)	0.740±0.078 (5)	0.819±0.061 (7)	0.512 (1)	2.244 (1)	10.897±0.258 (6)
Skin	0.555±0.059 (5)	(0)	0.168±0.007 (4)	0.137±0.021 (6)	(0)	(0)	2.019 (1)
Spleen	0.005±0.002 (1)0	0.031±0.011 (4)	0.003±0.001 (5)	0.004±0.001 (7)	0.001 (1)	0.001 (1)	0.025±0.005 (6)
Testes	0.215±0.082 (4)	0.102±0.037 (3)	0.030±0.015 (3)	0.032±0.004 (6)	0.009 (1)	0.003 (1)	0.107±0.008 (4)

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Table S3. Species pairs used in temperate-tropical pair-wise comparison of tissue masses

Temperate species	Tropical species		
Mourning dove Zenaida macroura	White-tipped dove Leptotila verreauxi		
Ruby-throated hummingbird Archilochus colubris	Rufous-tailed hummingbird Amazilia tzacatl		
Eastern phoebe Sayornis phoebe	Social flycatcher Myiozetetes similis		
Red-eyed vireo Vireo olivaceus	Yellow-green vireo Vireo flavoviridis		
Tree swallow Tachycineta bicolor	Mangrove swallow Tachycineta albilinea		
Northern house wren Troglodytes aedon	Southern house wren Troglodytes musculus		
Northern mockingbird Mimus polyglottos	Tropical mockingbird Mimus gilvus		
American robin Turdus migratorius	Clay-colored thrush Turdus grayi		
American goldfinch Astragalinus tristis	Thick-billed euphonia Euphonia laniirostris		
Song sparrow Melospiza melodia	Black-striped sparrow Arremonops conirostris		

Table S4. Results of phylogenetic generalized least squares models describing dry organ mass as a function of body mass, tropical or temperate climate, sex, 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) and diet

America vs sedentary birds and short-distance migrants) and diet								
	Heart	Lungs	Flight muscles	Leg muscles	Gizzard	Intestines	Liver	
Intercept	-2.284±0.077***	-2.382±0.084***	-1.308±0.087***	-2.133±0.108***	-2.420±0.169***	-2.587±0.160***	-1.903±0.099***	
log <sub>10</sub> (dry carcass mass)	0.897±0.034***	0.984±0.041***	1.050±0.037***	1.159±0.0414***	0.977±0.075***	1.109±0.074***	0.927±0.044***	
Climate(=tropical)	-0.0937±0.0167***	-0.192±0.026***	-0.0477±0.0237*	0.0432±0.0157**	-0.0046±0.0471	0.0748±0.0394	-0.0427±0.0223	
Sex(=male)	0.0281±0.0116*	0.0268±0.0139	0.0088±0.0100	-0.0225±0.0109*	-0.0351±0.0212	-0.110±0.028***	-0.0355±0.0156*	
Migrant(=yes)	-0.0525±0.0287	0.0391±0.0404	0.0674±0.0364	0.0007±0.0281	-0.203±0.073**	-0.0179±0.0670	-0.0135±0.0379	
Diet(=granivorous)	-0.0281±0.0297	0.0447±0.0405	0.0204±0.0395	-0.00465±0.0372	0.356±0.078***	-0.167±0.066*	-0.144±0.039***	
Diet(=insectivorous)	-0.0283±0.0352	-0.0283±0.0448	-0.106±0.046*	0.0101±0.047	0.391±0.090***	-0.160±0.073*	-0.101±0.045*	
Diet(=nectivorous)	0.140±0.106	-0.0290±0.0913	0.0530±0.0811	-0.169±0.174	-0.231±0.164	-0.0208±0.2081	-0.0536±0.1345	
Diet(=omnivorous)	-0.0742±0.0302*	-0.0294.0428	-0.0221±0.0429	0.0864±0.0406*	0.286±0.084***	-0.107±0.065	-0.129±0.039**	
Diet(=frugivorous)	0	0	0	0	0	0	0	
df (residual, total)	175, 184	176, 185	178, 187	178, 187	174, 183	177, 186	177, 186	
AIC <sub>C</sub> Pagel	-339.6 (λ=0.654)	-268.3 (λ=0.527)	-354.9 (λ=0.819)	-335.7 (λ=0.926)	-80.0 (λ=0.828)	-34.1 (λ=0.462)	-239.0 (λ=0.601)	
AIC <sub>C</sub> Grafen	-348.9 (ρ=0.186)	-275.6 (ρ=0.180)	-366.5 (ρ=0.392)	-327.2 (ρ=0.371)	-105.1 (ρ=0.339)	-29.4 (p=0.097)	-236.2 (p=0.137)	
AIC <sub>C</sub> Martins	-325.7 (α=0.393)	-250.6 (α=0.926)	-328.6 (α=0.160)	-327.0 (α=0.070)	-42.6 (α=0.180)	-8.1 (α=0.588)	-221.0 (α=0.495)	

	Kidneys	Ovaries	Testes	Skin	Spleen	Brain	Feathers
Intercept	-2.365±0.080***	-2.602±0.552***	-2.963±0.479***	-1.990±0.094***	-3.541±0.346***	-1.769±0.074***	-1.387±0.089***
log <sub>10</sub> (dry carcass mass)	0.943±0.036***	0.979±0.335**	1.138±0.245***	1.037±0.060***	0.936±0.165***	0.628±0.030***	1.0693±0.0405***
Climate(=tropical)	-0.196±0.018***	-0.310±0.140*	-0.542±0.159**	0.0296±0.0279	-0.0543±0.0977	0.0127±0.0127	-0.150±0.019***
Sex(=male)	-0.0258±0.0125*			-0.0614±0.0186**	-0.101±0.722	0.0134±0.0088	-0.0184±0.0128*
Migrant(=yes)	-0.0765±0.0303*	-0.325±0.286	0.186±0.252	-0.0154±0.0453	-0.061±0.157	-0.0386±0.0222	0.0693±0.0128
Diet(=granivorous)	-0.154±0.032***	-0.828±0.311*	-0.275±0.242	0.0229±0.0580	-0.090±0.181	0.0305±0.0269	0.0794±0.0345*
Diet(=insectivorous)	-0.0147±0.0366	-0.451±0.332	-0.167±0.258	0.0294±0.0662	-0.158±0.189	0.0151±0.0333	0.0107±0.0439
Diet(=nectivorous)	0.0459±0.1090	-0.208±0.682	-0.710±0.558			-0.0531±0.1114	
Diet(=omnivorous)	-0.124±0.032***	-0.402±0.352	-0.001±0.248	-0.079±0.061	-0.068±0.167	0.0703±0.0284*	0.0490±0.0357
Diet(=frugivorous)	0	0	0	0	0	0	0
df (residual, total)	176, 185	50, 58	105, 113	101, 109	112, 120	175, 184	112, 120
AIC <sub>c</sub> Pagel	-316.6 (λ=0.613)	106.5 (λ=0.812)	207.0 (λ=0.171)	-123.0 (λ=0.843)	151.8 (λ=0.304)	-424.3 (λ=0.848)	-228.8 (λ=0.745)
AIC <sub>C</sub> Grafen	-314.0 (ρ=0.186)	105.6 (ρ=0.162)	202.5 (ρ=0.152)	-119.8 (ρ=0.228)	152.2 (ρ=0.049)	-410.8 (ρ=0.295)	-226.8 (p=0.213)
AIC <sub>C</sub> Martins	-282.2 (α=0.860)	101.1 (α=0.160)	210.6 (α=19.5)	-124.9 (α=0.233)	153.3 (α=0.978)	-387.7 (α=0.052)	-205.8 (α=0.371)

Data are log<sub>10</sub> tissue or organ mass.

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<sub>C</sub> values of final model. Significant variables are emphasized with grey as is the model with lowest AIC<sub>C</sub>. When a model did not converge AIC<sub>c</sub>=NA. \**P*<0.05; \*\**P*<0.01; \*\*\* *P*<0.001.

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