

Passerines *versus* nonpasserines: so far, no statistical differences in the scaling of avian energetics

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Summary

We analyzed and compared the scaling of both basal and maximal thermogenic metabolic rates in passerine and nonpasserine birds using conventional and phylogenetic methods. In spite of the presumed adaptive importance of both metabolic traits, few studies concerning both their relationships and their ecological and evolutionary constraints have been conducted. We found no statistical differences in the scaling of maximal metabolic rate between passerines and nonpasserines; hence, we suggest the use of a single allometric regression

for this trait in birds. In addition, basal and maximal metabolic rates were indeed correlated after removing the effects of body mass and phylogeny. The apparent generality of this correlation within both birds and mammals reinforces the need for general ecological and physiological explanations for the evolution of endothermy.

Key words: basal metabolic rate, maximal metabolic rate, bird, body size, endothermy, phylogeny.

Introduction

Allometric studies have demonstrated that passerines have higher values of basal metabolic rate (BMR) than other avian groups (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970; Bennett and Harvey, 1987). However, using phylogenetically corrected methods, Reynolds and Lee (1996) concluded that these differences were artifacts of phylogeny. Similarly, Garland and Ives (2000), using confidence intervals for regression equations in phylogenetic comparative methods for the same database, arrived at the same conclusion. However, in spite of the presumed adaptive importance of the maximal metabolic rate of thermoregulation (MMR), few studies concerning the ecological and evolutionary constraints and trade-offs of MMR are available in the literature, and all focus mainly on small mammals (Lechner, 1978; Taylor et al., 1980; Bozinovic and Rosenmann, 1989; Bozinovic, 1992). The absence of a standard method of determining MMR and the controversial results arising from different methodologies of analysis are the likely reasons for this shortcoming (Rosenmann and Morrison, 1974; Hayes and Chappell, 1986; Hinds et al., 1993). To our knowledge, only Dutenhoffer and Swanson (1996) and Hinds et al. (1993) have attempted to scale MMR in birds, although these authors worked exclusively with passerines and nonpasserines, respectively.

A high level of energy expenditure is one of the principal characteristics of birds. The basal metabolic rate is the lower limit of a euthermic individual's energy expenditure (McNab, 1986, 1988a,b), being the most common comparative measure

of the metabolic rate of endotherms. In contrast, MMR in endothermic vertebrates is the upper limit for thermogenesis of an individual (Rosenmann and Morrison, 1974), and it has often been considered as an index of thermoregulatory effectiveness and cold-tolerance (Karasov, 1986; Koteja, 1986).

Comparisons between BMR and MMR have shown that, when the effect of body mass (M_b) was removed, residual analysis of BMR *versus* MMR showed a significant correlation between the two variables in small mammals and passerines (Bozinovic, 1992; Dutenhoffer and Swanson, 1996). The close relationship between minimal and maximal metabolic rates is one of the basic assumptions of the aerobic capacity model for the evolution of endothermy (Bennett and Ruben, 1979; Dutenhoffer and Swanson, 1996), although other models have been postulated that incorporate this assumption as well (Koteja, 2000; Farmer, 2000). If avian MMR is a relatively constant multiple of BMR, as documented in small mammals (Bozinovic, 1992), we hypothesize that the MMR of passerines and nonpasserines will not differ after accounting for phylogenetic non-independence of the data. To our knowledge, this is the first study reporting comparisons in MMR allometry between these groups. Because differences in MMR (if they exist) between passerines and nonpasserines may reflect fundamental ecological and evolutionary differences in energetics (see Carey, 1996), the purposes of this study were

Table 1. Maximal and basal metabolic rates and body mass of birds

Species	M_b (g)	MMR (ml O ₂ g ⁻¹ h ⁻¹)	BMR (ml O ₂ g ⁻¹ h ⁻¹)	Refs	Species	M_b (g)	MMR (ml O ₂ g ⁻¹ h ⁻¹)	BMR (ml O ₂ g ⁻¹ h ⁻¹)	Refs
Order Anseriformes					Order Passeriformes (<i>Continued</i>)				
<i>Anas castanea</i>	969	3.81	0.78	1	<i>Icterus galbula</i>	32	13.58	2.81	3
Order Apodiformes					<i>Junco hyemalis</i>	17	20.75	3.32	7
<i>Patagona gigas</i>	20	19.47	2.70	12, 13	<i>Passer domesticus</i>	26	15.74	2.09	8, 9
<i>Sephanoides sephanioides</i>	6	26.51	3.17	2	<i>Pheucticus ludovicianus</i>	41	13.15	2.42	6
Order Ciconiiformes					<i>Phrygilus gayi</i>	27	13.80	–	3
<i>Eudiptula minor</i>	983	3.51	0.74	1	<i>Phytotoma rara</i>	42	11.69	2.13	10
Order Columbiformes					<i>Poecile atricapillus</i>	13	26.29	3.80	18
<i>Columba livia</i>	362	4.69	0.86	1	<i>Poecile gambeli</i>	11	25.47	4.06	19
<i>Zenaida auriculata</i>	124	9.00	–	3	<i>Poephila guttata</i>	12	20.49	3.61	1
Order Galliformes					<i>Regulus calendula</i>	5.9	23.63	–	16
<i>Colinus virginianus</i>	218	5.87	0.98	5	<i>Regulus satrapa</i>	5.8	25.97	–	3
<i>Coturnix chinensis</i>	43	9.13	1.71	1	<i>Sicalis auriventris</i>	31	15.03	–	3
<i>Coturnix japonica</i>	148	8.30	1.64	1	<i>Sitta carolinensis</i>	20	20.15	3.31	17
<i>Coturnix japonica</i>	102	10.73	–	3	<i>Spizella arborea</i>	19	24.12	4.14	6
Order Gruiformes					<i>Spizella passerina</i>	11	19.55	3.48	
<i>Gallinula porphyrio</i>	857	3.65	0.65	1	<i>Spizella pusilla</i>	13	21.28	3.64	6
Order Passeriformes					<i>Troglodytes aedon</i>	10	23.33	3.40	6
<i>Baeolophus griseus</i>	17	19.68	3.24	19	<i>Tyrannus tyrannus</i>	37	13.07	2.22	3
<i>Cardinalis cardinalis</i>	46	12.68	–	3	<i>Vireo gilvus</i>	13	18.96	3.16	14
<i>Carduelis barbatus</i>	15	15.81	–	3	<i>Zonotrichia capensis</i>	20	16.30	3.31	11
<i>Carduelis flammea</i>	14	21.80	3.70	4	<i>Zosterops lateralis</i>	11	15.64	2.30	15
<i>Carduelis tristis</i>	13	19.91	4.00	20	Order Piciformes				
<i>Carpodacus mexicanus</i>	22	17.65	3.19	21	<i>Picoides pubescens</i>	25	19.05	3.06	17
<i>Contopus virens</i>	14	16.57	2.75	6	Order Psittaciformes				
<i>Dendroica coronata</i>	12	19.69	3.73	16	<i>Melospittacus undulatus</i>	38	12.52	2.13	1
<i>Dendroica petechia</i>	9	19.47	3.72	6	<i>Platycercus eximius</i>	89	8.58	–	1
<i>Diuca diuca</i>	34	16.06	–	3	Order Strigiformes				
<i>Dumetella carolinensis</i>	34	14.38	2.74	6	<i>Glauclidium nanum</i>	98	6.67	1.47	3

BMR, basal metabolic rate; MMR, maximal metabolic rate; M_b , body mass.

1, Hinds et al. (1993); 2, López-Calleja and F. Bozinovic (1995); 3, F. Bozinovic, D. L. Swanson and F. F. Novoa (unpublished data); 4, Rosenmann and Morrison (1974); 5, Swanson and Weinacht (1997); 6, Dutenhoffer and Swanson (1996); 7, Swanson (1990); 8, Koteja (1986); 9, Daan et al. (1990); 10, Rezende et al. (2001); 11, Novoa et al. (1990); 12, R. F. Nespolo and M. J. Fernández (unpublished data); 13, Lasiewski et al. (1967); 14, Swanson (1995); 15, Maddocks and Geiser (1999); 16, Swanson and Dean (1999); 17, Liknes and Swanson (1996); 18, Cooper and Swanson (1994); 19, Cooper (1998); 20, Dawson and Smith (1986); 21, O'Connor (1995).

(i) to assess the relationship between mass-independent MMR in passerines and nonpasserines and (ii) to evaluate whether MMR and BMR are correlated, after removing the effects of M_b and phylogeny, within a broader phylogenetic context than previously studied.

Materials and methods

Values of BMR and MMR of 32 avian species were collected from the literature, and 10 species for which no data are available in the literature were also included (F. Bozinovic, D. L. Swanson and F. F. Novoa, unpublished data) (Table 1). Because our main goal was to analyze MMR, we chose species for which MMR has already been measured, even when no value of BMR was available. To avoid problems arising from the use of different experimental procedures to

determine MMR, we selected values obtained with the He-O₂ method (Rosenmann and Morrison, 1974). Data published as resting metabolic rates (RMRs) were taken as BMR whenever the authors specified that they were determined as the minimum metabolic rate observed in animals within their range of thermoneutrality. Whenever more than one value of BMR, MMR or M_b was given (e.g. values for summer and winter), we used the average value. Data for BMR, MMR and M_b were log₁₀-transformed, and least-square regressions were performed to determine the relationship between the metabolic variables and M_b . For simplicity, we will refer to log₁₀-transformed data as MMR and BMR.

Conventional and phylogenetically independent analyses of covariance (ANCOVA) were performed to determine differences in allometric relationships between passerines and nonpasserines. The latter analysis requires that both the

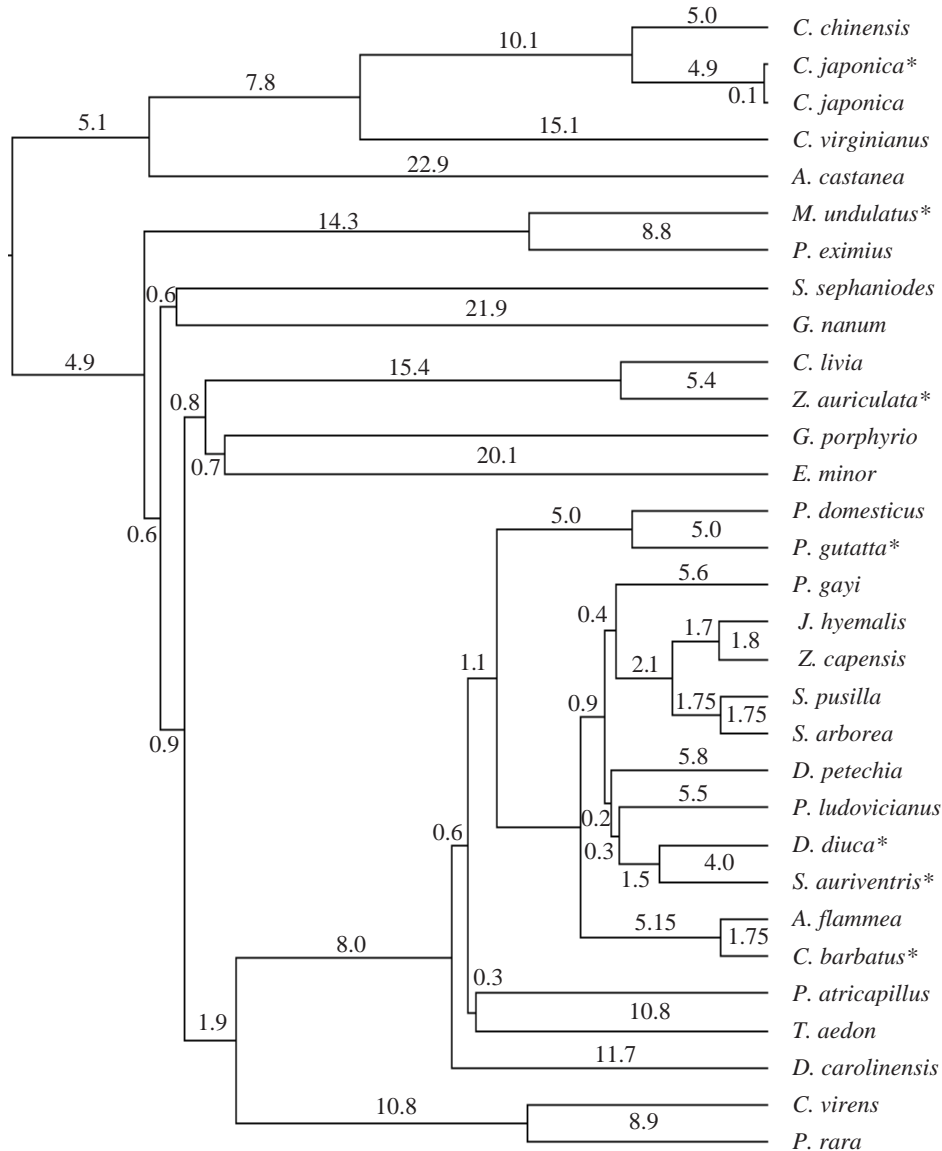


Fig. 1. Phylogenetic tree of birds based on Sibley and Ahlquist (1990) for maximal metabolic rate (MMR). Numbers represent the genetic distance between adjacent taxa according to DNA/DNA hybridization. In some cases, branch lengths were chosen arbitrarily (see Materials and methods). Asterisks indicate species that were not incorporated into the basal metabolic rate phylogenetic tree (see Table 1, where full genus names are given).

contrasts to any great extent (Garland et al., 1999). A phylogenetic distance of 5.0 was arbitrarily set between *Poephila guttata* and *Passer domesticus* and a phylogenetic distance of 0.1 between the two *Coturnix japonica*. Two separate values for the latter species were considered because these were measured in geographically distant locations (Australia and central Chile) and M_b differed considerably (see Table 1). Unfortunately, BMRs were not available for all species, and two different phylogenetic trees had to be constructed (see Fig. 1).

Evolution rates (*sensu* Garland, 1992) of M_b differed significantly between passerines and nonpasserines (Mann-Whitney $U=90.0$, $Z=-3.11$, $P<0.01$), as did evolution rates of BMR and MMR ($U=74.0$, $Z=-2.06$, $P<0.04$ for BMR; $U=111.0$, $Z=-2.60$, $P<0.01$ for MMR). Passerines showed

order of speciation and the divergence time of species be known (Felstenstein, 1985; Garland et al., 1992). All phylogenetically independent analyses were performed using the Phenotypic Diversity Analysis Program (Garland et al., 1993).

We constructed the phylogenetic tree on the basis of Sibley and Ahlquist (1990). Although some species were not listed, we used another species within the same genus as equivalent to determine branch lengths in our phylogeny. The phylogenetic distance between *Patagona gigas* and *Sephanoides sephaniodes* was taken as 8.1, the maximum distance observed within the Trochilidae. In addition, the phylogenetic distance between *Zonotrichia capensis* and *Junco hyemalis* was estimated from Patten and Fugate (1998), while the phylogeny of genera *Carduelis* and *Spizella* were based on Arnaiz-Villena et al. (1998) and Dodge et al. (1995), respectively. Arbitrary branch lengths were chosen for the genus *Spizella* because variation in branch length does not seem to affect the results of phylogenetically independent

higher evolution rates for all variables, and branch lengths were therefore raised to the power 0.8, and the passerine subclade was rescaled to a total height of 4.0, as in Garland and Ives (2000). Such transformation suppressed previous differences, allowing comparisons between groups ($P>0.39$ for all variables). The adequacy of branch lengths for standardizing contrasts was then tested through correlation analyses between standardized contrasts and the square root of the sum of branch lengths for all variables (see Garland et al., 1992). The correlations were non-significant in all cases ($P>0.05$).

The results obtained from the ANCOVA for BMR and MMR were tested against the F -null distributions obtained from 1000 Monte-Carlo simulations carried out with PDSIMUL and PDANOVA (Garland et al., 1993). We used bounded gradual and speciation Brownian motion models for the simulations, employing the 'Flip' algorithm, and no trends (*sensu* Garland et al., 1993). The correlation coefficient r was equal to zero, or -0.950 and -0.964 , from BMR and MMR,

Table 2. Results of conventional and phylogenetically independent analyses of covariance (ANCOVA) testing the hypothesis of no difference in maximal and basal metabolic rate between passerines and nonpasserines

	Source of variation	d.f.	F	Conventional ANCOVA	Critical value			
					Monte Carlo (no correlation)		Monte Carlo (correlation)	
					Gradual	Speciational	Gradual	Speciational
MMR	Slope	1	1.02	4.07	1.96	2.83	2.56	3.07
	Error	43						
	Body mass	1	298.46	4.06*	3.81*	3.28*	554.46	592.75
	Groups	1	2.13	4.06	12.90	12.33	11.02	12.59
	Explained	2	308.73	3.21*	9.66*	9.47*	358.93	379.78
	Error	44						
BMR	Slope	1	0.06	4.14	1.67	2.66	2.16	2.64
	Error	33						
	Body mass	1	164.20	4.13*	3.23*	3.24*	285.15	324.33
	Groups	1	6.10	4.13 *	8.76	10.77	7.41	11.65
	Explained	2	188.81	3.28 *	6.58*	8.26*	181.74*	219.12
	Error							

BMR, basal metabolic rate; MMR, maximal metabolic rate.

All phylogenetically independent analyses were performed using the Phenotypic Diversity Analysis Program (Garland et al., 1993) (see Materials and methods).

Asterisks represent significant effects ($P < 0.05$).

respectively (obtained from the correlation between BMR and MMR with M_b) (for methods, see Garland et al., 1993). Limits for M_b were 2 and 4.5×10^4 g, and limits for BMR were 10^{-2} and $12 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$, as in Reynolds and Lee (1996). MMR limits were set arbitrarily as 3×10^{-2} and $40 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$. We assumed an aerobic expansivity of 3 to obtain the lower limit, while the higher limit was set to exceed the highest value of MMR we observed ($26.51 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ for *S. sephaniodes*). Initial values for M_b (88.1 and 86.3 g for BMR and MMR analysis, respectively), BMR ($1.65 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) and MMR ($9.44 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$) were computed because these values were the root node estimates from independent contrast analysis (see Garland and Ives, 2000; Garland et al., 1999).

Finally, to analyze the relationship between BMR and MMR after removing the effects of M_b and phylogeny, we plotted the residuals of the mass-independent contrasts of MMR and BMR against each other. Because residuals of independent contrasts need to derive from the same phylogenetic tree, in this analysis we used the phylogeny previously described for BMR, which contains fewer species (Fig. 1), to obtain MMR residuals. The correlation between these variables was tested with a regression through the origin, as described by Garland et al. (1992).

Results

There were no significant differences in MMR between passerines and nonpasserines using either conventional or phylogenetically corrected ANCOVA, although we observed significant differences in BMR between passerines and nonpasserines by conventional analysis (Table 2).

Phylogenetically corrected allometric curves for both MMR

Table 3. Slopes and intercepts of regressions of maximal and basal metabolic rate with body mass (\log_{10} -transformed data), with their 95% confidence intervals in parentheses, obtained using least-square regressions and independent contrasts analysis

		Least-square regression	Independent contrasts
MMR	Slope	-0.400 (-0.433, -0.368)	-0.349 (-0.437, -0.262)
	Intercept	1.749 (1.696, 1.802)	1.647 (1.390, 1.904)
BMR	Slope	-0.365 (-0.407, -0.322)	-0.279 (-0.366, -0.192)
	Intercept	0.930 (0.862, 0.998)	0.756 (0.516, 0.997)

BMR, basal metabolic rate; MMR, maximal metabolic rate.

and BMR showed higher intercepts and lower slopes than those obtained with least-square regressions (Table 3). Nevertheless, the 95% confidence intervals of the curves obtained with conventional and phylogenetically corrected analyses overlap, indicating that these are not statistically different. Also, no significant differences between slopes of MMR and BMR could be detected when we considered the 95% confidence intervals of the slopes of both variables, although the intercepts did differ, as expected (Fig. 2).

MMR and BMR were positively and significantly correlated after removing the effects of phylogeny and M_b ($r^2 = 0.75$, $F_{1,36} = 108.67$, $P < 0.001$) (Fig. 3).

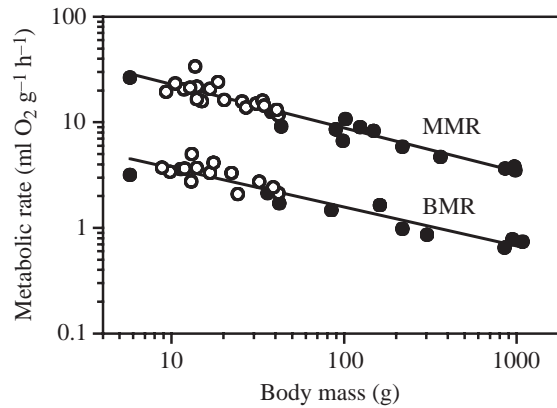


Fig. 2. Scaling of basal (BMR) and maximal (MMR) metabolic rate in passerines (open circles) and nonpasserines (filled circles). Lines represent least-square regression for all data (equations are listed in Table 3).

Discussion

Two issues regarding the data used in our analyses merit some discussion before considering the results. First, captivity may induce changes in metabolic rate in birds (Warkentin and West, 1990), and both wild and captive birds were included in the analyses. However, some studies have demonstrated no effect of captivity on BMR (Weathers et al., 1983) or MMR (Hill et al., 1993) in birds. Consequently, in the absence of any clear trend of the effect of captivity on metabolic rates in birds, the use of data from both groups is justified.

Second, season may have a pronounced influence on both BMR and MMR in birds, although seasonal effects on metabolic rate are absent in some species (Dawson and O'Connor, 1996; Liknes and Swanson, 1996). We used data from birds measured at all seasons in this study, and in some cases in the literature the season of measurement of metabolic rates was not mentioned. When data from different seasons were available for a species, we used the average value. This practice should moderate the effect of seasonal differences in metabolic rates in the analyses. In addition, analyses were carried out on mass-specific metabolic rates, which typically show less seasonal variation than whole-animal metabolic rates. This is because birds are often fatter during winter or migration than during summer, and fat contributes to mass but is relatively inert metabolically (Dawson and Smith, 1986). Thus, seasonal differences in metabolic rates should introduce only a small amount of variation into our analyses. Given the absence of any differences that even remotely approach significance between passerine and nonpasserine regression equations after the removal of mass and phylogeny (Table 2), it is very unlikely that such variation influenced our results.

Our results show that BMR allometric curves have similar slopes for passerines and nonpasserines (Table 2), in agreement with Reynolds and Lee (1996) and Garland and Ives (2000). This result would suggest the use of a single allometric curve for both passerines and nonpasserines. Nevertheless, because passerines showed lower evolution

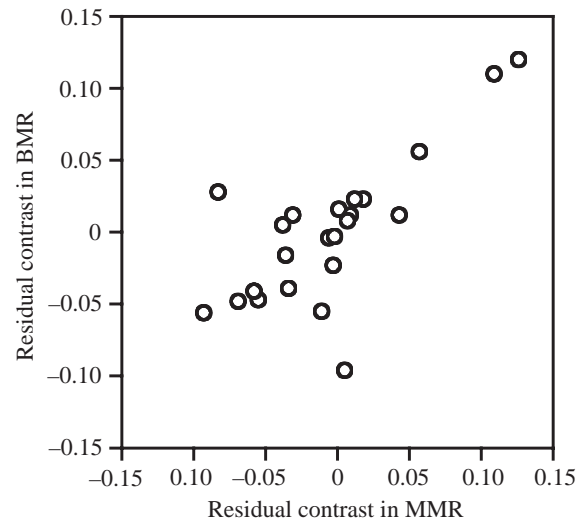


Fig. 3. Correlation between mass-independent basal (BMR) and maximal (MMR) metabolic rate after removing the effects of phylogeny. Contrasts were calculated according to Felsenstein (1985) and using residuals obtained after plotting BMR and MMR against body mass.

rates in both M_b and mass-independent BMR, Garland and Ives (2000) recommended the use of two separate allometric equations for passerines and nonpasserines.

Despite the differences in evolution rates in M_b , MMR and BMR between passerines and nonpasserines in our analyses, these do not justify the use of different allometric equations for MMR in passerines and nonpasserines, as is the case for BMR (Garland and Ives, 2000). Previous studies (and our own) of BMR scaling in birds have obtained significant differences in BMR between passerines and nonpasserines when phylogenetic effects were not removed. Garland and Ives (2000) reported differences between conventional and phylogenetically corrected regressions for BMR, which we did not obtain for MMR regressions (Table 3). Different phenotypic evolution rates justify the use of two allometric curves for BMR, and passerines do have higher BMR values after conventional statistical analyses (Reynolds and Lee, 1996; Garland and Ives, 2000). However, there are no differences in avian MMR after either conventional or phylogenetic analyses, and we may exclude a phylogenetic effect on MMR scaling. Certainly, the small number of data points available may affect our comparisons because the 95% confidence intervals of the regression, after removing the effects of phylogeny, are considerably wider than the values obtained with a conventional least-square regression (Table 3). Nevertheless, until more data are available, we suggest that a single allometric equation may be used for MMR in birds (see Fig. 2).

The linkage between BMR and MMR has been a central theme in the evolution of endothermy (e.g. Bennett and Ruben, 1979), although no causality has been demonstrated. Whether activity level or thermoregulatory performance has been selected remains unclear, and more than one theory on

the evolution of endothermy may explain the phenotypic linkage between these traits. Our results indicate that BMR and MMR are indeed correlated, even after removing the effects of body mass and phylogeny, confirming the generality and importance of this phenomenon within birds.

The latter is particularly important because it arose independently in birds and mammals (Bennett, 1991; Ruben, 1991). Thus, the relationship between BMR and MMR demonstrated for birds in this study, and previously described for mammals (Bozinovic, 1992), suggests convergent mechanisms explaining the evolution of endothermy (but see Koteja, 1987; Sparti, 1992; Chappell and Bachman, 1994). Although correlated BMR and MMR values may support the aerobic capacity model proposed by Bennett and Ruben (1979), these results should be interpreted with care. Maximum metabolic rates elicited by cold exposure are considerably lower than MMRs elicited by intense exercise: aerobic scopes (MMR/BMR) calculated from metabolic flight measurements are approximately 15 (see Bishop, 1999), higher than the aerobic scopes observed in our study (4.5–8.4). In addition, one might expect that the mass of the central organs involved in oxygen delivery should be correlated with exercise MMR, while the mass of the food-processing organs might be more likely to be correlated with thermoregulatory MMR. Since a number of studies have shown tight linkages between BMR and the mass of the visceral organs in birds (Daan et al., 1990; Piersma et al., 1996), the choice of exercise or cold-exposure to elicit MMR could have a considerable influence on the degree of correlation between BMR and MMR.

Nevertheless, even though activity metabolic rate rather than heat production was postulated to be the trait experiencing direct selection in the aerobic capacity model, it is not clear whether selection has acted mainly on activity or thermogenesis. Also, the relative importance of activity and thermogenesis on the fitness of an animal must be considered to be mass-dependent because thermoregulation becomes increasingly restrictive as M_b decreases (McNab, 1983; Pough, 1980). The energetics of flight is also mass-dependent (both hummingbirds and albatrosses hover, but differences in their exercise intensity are extremely marked). Thus, we may postulate that both variables may be important in the evolution of endothermy in both birds and mammals, and the apparent generality of the correlation between BMR and thermoregulatory MMR reinforces the need for general ecological and physiological explanations for the evolution of endothermy (e.g. Bennett and Ruben, 1979; Koteja, 2000; Farmer, 2000).

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