

# The Allometry of Avian Basal Metabolic Rate: Good Predictions Need Good Data

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## ABSTRACT

Basal metabolic rate (BMR) is often predicted by allometric interpolation, but such predictions are critically dependent on the quality of the data used to derive allometric equations relating BMR to body mass ( $M_b$ ). An examination of the metabolic rates used to produce conventional and phylogenetically independent allometries for avian BMR in a recent analysis revealed that only 67 of 248 data unambiguously met the criteria for BMR and had sample sizes with  $n \geq 3$ . The metabolic rates that represented BMR were significantly lower than those that did not meet the criteria for BMR or were measured under unspecified conditions. Moreover, our conventional allometric estimates of BMR ( $W$ ;  $\log \text{BMR} = -1.461 + 0.669 \log M_b$ ) using a more constrained data set that met the conditions that define BMR and had  $n \geq 3$  were 10%–12% lower than those obtained in the earlier analysis. The inclusion of data that do not represent BMR results in the overestimation of predicted BMR and can potentially lead to incorrect conclusions concerning metabolic adaptation. Our analyses using a data set that included only BMR with  $n \geq 3$  were consistent with the conclusion that BMR does not differ between passerine and nonpasserine birds after taking phylogeny into account. With an increased focus on data mining and synthetic analyses, our study suggests that a thorough knowledge of how data sets are generated and the underlying constraints on their interpretation is a necessary prerequisite for such exercises.

## Introduction

Understanding how animals partition energy into maintenance requirements, activity, growth, and reproduction and the evolution of patterns of energy allocation is a central goal of ecological and evolutionary physiology. Attempts to identify the sources of selection responsible for variation in the maintenance energy requirements of endotherms have typically focused on the minimum maintenance metabolic rate during normothermy, or basal metabolic rate (BMR; e.g., Elgar and Harvey 1987; Lovegrove 2000; Tieleman and Williams 2000; Lovegrove 2003). BMR represents a well-defined baseline metabolic parameter measured under experimental conditions that do not elicit an increase in metabolic heat production above minimum maintenance levels, namely resting, postabsorptive, nongrowing, nonreproductive individuals at thermoneutral environmental temperatures during the rest phase of their circadian cycle (McNab 1997; Swanson 2003).

One common approach to identifying metabolic adaptation involves the comparison of observed BMR with that expected on the basis of allometry (Reynolds and Lee 1996; Garland and Ives 2000; Lovegrove 2000; Tieleman and Williams 2000). Typically, hypotheses concerning adaptation in BMR are tested by generating conventional and/or phylogenetically independent prediction intervals (Garland and Ives 2000), with data falling outside these prediction intervals considered to differ significantly from the expected values. In the last 2 decades, considerable effort has been invested in developing the statistical procedures necessary to correct for the potentially confounding effects of phylogenetic relatedness when inferring adaptation (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992, 1993; Garland and Ives 2000). Although phylogenetically independent analyses have become widespread in comparative studies of energetic traits, several authors have questioned their validity (Westoby et al. 1995a, 1995b). Concerns have been raised as to whether such methods should be universally applied, and calls have been made for their selective application based on the degree of phylogenetic dependence exhibited by the trait(s) of interest (Ricklefs and Starck 1996; Björklund 1997). The latter issue has recently been addressed by the development of an index of phylogenetic correlation, which provides a quantitative measure of the phylogenetic dependence of a data set (Pagel 1999). Several avian and mammalian metabolic parameters have been found to exhibit strong phylogenetic dependence (Freckleton et al. 2002).

In a recent analysis, Reynolds and Lee (1996) analyzed data

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for 254 bird species and demonstrated that the BMR of passerines and nonpasserines was not significantly different once the data were corrected for phylogenetic nonindependence. The allometric equations presented in the latter article have been widely used to predict avian BMR (Bosque et al. 1999; Williams 1999; Anava et al. 2001; McKechnie and Lovegrove 2001a; Rezende et al. 2001; Hambly et al. 2002). However, Reynolds and Lee (1996) did not specify the criteria they used for data inclusion, and several authors have questioned the reliability of their allometric equations for BMR (Tieleman and Williams 2000; McNab 2001). The concerns raised by these authors prompted us to examine more closely the data analyzed by Reynolds and Lee (1996). An inspection of the appendix in Reynolds and Lee (1996) reveals that a significant proportion of the data they included in their analyses did not meet the criteria that define BMR. For instance, data for *Hydranassa* spp. and *Egretta thula* were measured during the active phase of the circadian cycle (Ellis 1980). In other cases, data that potentially represent values several times greater than BMR were included. For example, the datum for the wood stork *Mycteria americana* was originally obtained from Kahl (1962). In this study, the metabolic rate of captive nestlings was estimated from food intake and growth rates, assuming an assimilation efficiency of 0.9. The value included by Reynolds and Lee (1996) as BMR for this species was the existence metabolism for 9-wk-old nestlings, calculated as total energy assimilation minus production estimated from growth rates (Kahl 1962).

We show that data inclusion criteria have a significant effect on allometric predictions of avian BMR and on the conclusions reached regarding deviations of observed BMR from expected values. We present conventional and phylogenetically independent allometries calculated using only data that meet the criteria for BMR and  $n \geq 3$ . In addition, we verify Reynolds and Lee's (1996) finding that the BMR of passerines and nonpasserines does not differ once phylogeny is accounted for.

## Material and Methods

We consulted the original references for 248 of the 254 species for which BMR data were analyzed by Reynolds and Lee (1996; App. A). These authors obtained most of their data from Appendix 1 of Bennett and Harvey (1987), and we obtained the original sources for these data from Bennett (1986). No reference was provided in the latter for *Columba unicincta*, and the data for *Sula dactylatra*, *Pygoscelis papua*, *Megadyptes antipodes*, and *Aptenodytes patagonica* were cited as unpublished data in Drent and Stonehouse (1971), Brown (1984), and Ellis (1984). The datum for *Crax alberti* was cited by Lasiewski and Dawson (1967) as obtained from Benedict and Fox (1927), but we could find no datum for this species in the latter article. We were unable to obtain an English translation of Gavrilov (1974; cited in Kendeigh et al. 1977), but were able to obtain information on these data from Gavrilov (1997).

## Data Inclusion Criteria

For each species, we accepted the observed metabolic rate as BMR if it met the following criteria: (1) Measurements were made in normothermic individuals within the thermoneutral zone (TNZ), that is, the range of ambient temperatures ( $T_a$ ) at which metabolic rate was at a minimum. In several studies, measurements were made at only a single temperature, which the author(s) assumed to be within the TNZ (Yarborough 1971; Vleck and Vleck 1979). We assumed that in small species (<50 g),  $30^\circ\text{C} < T_a < 35^\circ\text{C}$  was within the TNZ. (2) Measurements were made in postabsorptive individuals, or it could be reasonably assumed that birds were postabsorptive on the basis of the time elapsed between feeding and the commencement of measurements. (3) Measurements were made during the rest phase of the circadian cycle in darkened chambers. Some high-latitude pelagic species appear not to exhibit a circadian rhythm of metabolic rate (Ricklefs and Matthew 1983), and in such cases we accepted the minimum values observed during a 24-h period as BMR. (4) Estimates of BMR were from a sample of three or more individuals. We consider a minimum sample size of three to represent an appropriate compromise between the need to account for variation among individuals and the practical difficulties involved in measuring BMR in species that are difficult to obtain and/or to maintain in captivity. It can be argued that our criterion of a minimum sample size of three unnecessarily excludes additional BMR data that would increase the predictive power of our allometries (McNab 1997). Since the BMR of an individual is equally likely to be greater than or less than the species mean, the inclusion of BMR data from one or two individuals should have little effect on the slopes or intercepts of BMR versus  $M_b$  regressions. However, in this study, we attempted to reduce intraspecific variation between individuals by including only data measured in three or more individuals.

Wherever possible, we confirmed that metabolic measurements were made in adult, nonreproductive birds. In cases in which the age of the birds used was not specified, we assumed that adults were used. To increase the predictive power of our allometries, we obtained an additional 59 BMR data that met the above criteria (App. B), although our survey of the literature was not exhaustive. In a few cases, we replaced BMR data used in Reynolds and Lee (1996) with more recent data based on larger sample sizes (e.g., *Colinus striatus*). When studies demonstrated seasonal variation in BMR (Liknes and Swanson 1996), we calculated a mean value.

## Data Analyses

For phylogenetic analyses, we constructed a phylogeny (Fig. 1) based primarily on Sibley and Ahlquist (1990), using the phylogenies in Reynolds and Lee (1996), Tieleman and Williams (2000), McKechnie (2001), Schleichner and Withers (2002), and

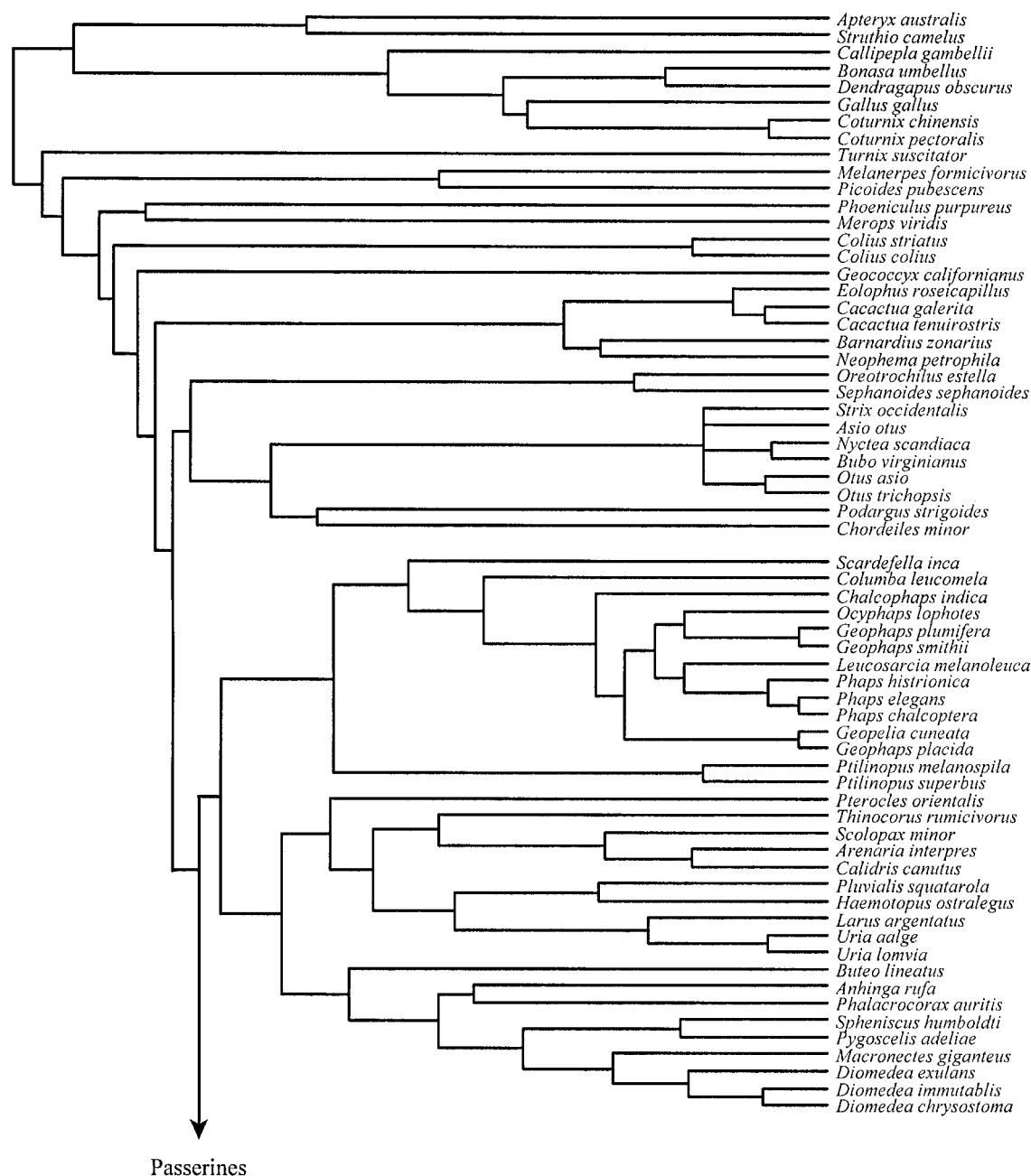


Figure 1. Phylogeny for 126 avian species used in the analyses of basal metabolic rate, constructed using phylogenetic data from sources listed in the text. The total height of the phylogeny is 28.0  $\Delta T_{30}H$  units (Sibley and Ahlquist 1990).

Tieleman et al. (2002). We  $\log_{10}$  transformed all body mass ( $M_b$ ; g) and BMR (W) data before analyses.

We used independent contrasts (Felsenstein 1985; Garland et al. 1992) to compare the BMR of passerines and nonpasserines and to calculate phylogenetically independent allometries and prediction intervals (Garland and Ives 2000) for our updated BMR data set (126 species). All analyses were carried

out using the PDTREE module of PDAP (Garland et al. 1993). Reynolds and Lee (1996) standardized independent contrasts using a modified Box-Cox algorithm to determine the optimum branch length transformation. However, a recent reanalysis of their data found that passerines exhibit a relatively low rate of phenotypic evolution compared with nonpasserines and that differential branch length transformations were required to ad-

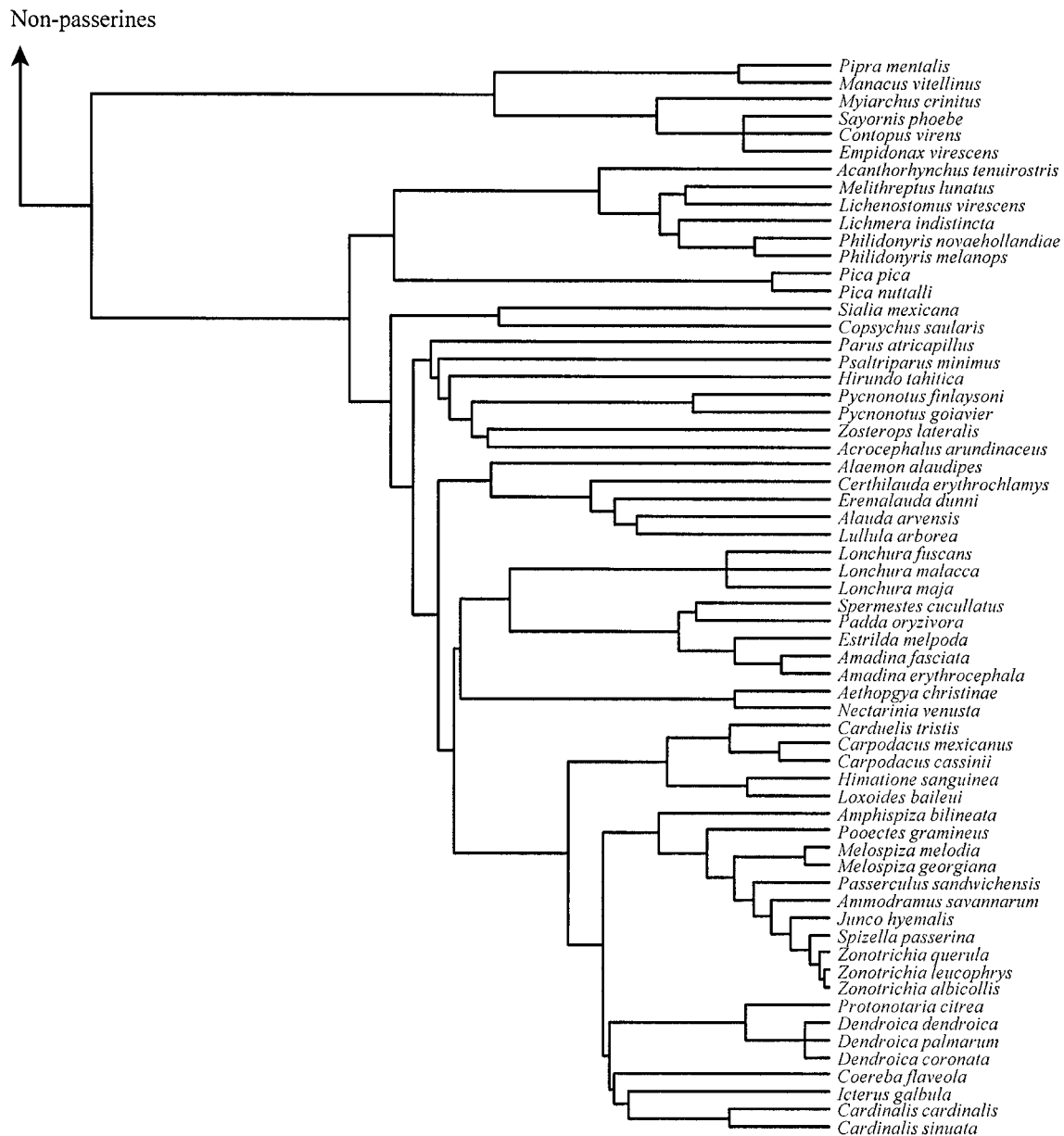


Figure 1 (Continued)

equately standardize contrasts (Garland and Ives 2000). Similar differences in the rate of phenotypic evolution to those observed by Garland and Ives (2000) were evident in our data set. After we raised all branch lengths to the power of  $-0.2$  (the optimal branch length transformation determined using a modified Box-Cox procedure [Reynolds and Lee 1996]), the absolute values of standardized contrasts for passerines were significantly smaller than those for nonpasserines (Mann-Whitney  $U = 2,926.5$ ;  $P < 0.001$ ). Hence, we followed the differential branch

length transformation approach suggested by Garland and Ives (2000) and rescaled the passerine subclade to a total height of 4.0, which resulted in adequate standardization of the contrasts (Mann-Whitney  $U = 3,808.5$ ;  $P = 0.986$ ). For calculating the phylogenetically independent regression (Garland and Ives 2000), we subtracted one degree of freedom for each of five soft polytomies in the phylogeny.

We also compared the BMR of passerines and nonpasserines using phylogenetically independent ANCOVAs (PI-ANCOVA)

Table 1: Conventional and phylogenetically independent ANCOVA comparing the log basal metabolic rate (BMR; W) of nonpasserines (NP) and passerines (P), with log body mass ( $M_b$ ; g) as the covariate

Source of Variation	<i>n</i>	SS	df	MS	<i>F</i>	Conventional		Gradual (Correlation)		Gradual		Speciational (Correlation)		Speciational	
						Critical Value	<i>P</i>	Critical Value	<i>P</i>	Critical Value	<i>P</i>	Critical Value	<i>P</i>	Critical Value	<i>P</i>
BMR data in Reynolds and Lee															
	67														
Slopes		.003	1	.002	.180	3.992	.673	8.335	.799	9.322	.786	14.322	.836	12.825	.800
NP vs. P		.154	1	.154	10.451	3.992	.002*	43.949	.339	41.118	.329	61.143	.393	51.653	.390
Updated BMR data set															
	126														
Slopes		.000	1	.000	.002	3.920	.964	11.001	.976	13.407	.976	22.726	.982	19.856	.989
NP vs. P		.340	1	.340	20.267	3.920	.000*	77.696	.310	75.555	.280	106.570	.360	93.752	.334

Note. Critical values for *F* were calculated as the ninety-fifth percentile of null distributions of *F* generated using the PDSIMUL module of PDAP (Garland et al. 1993). Conventional critical values for *F* were obtained from Zar (1999).

\* Significance at  $\alpha = 0.95$ .

after verifying homogenous slopes of the BMR versus  $M_b$  regressions (Zar 1999; Table 1). PI-ANCOVAs were performed using the program PDANOVA on 1,000 tip values simulated by PDSIMUL (Garland et al. 1993). The significance of conventional *F* statistics was tested against the critical *F* values for  $\alpha = 0.05$  (95% percentile) of the PI null *F* distributions. We generated PI null *F* distributions using four evolutionary models, following Reynolds and Lee (1996): (1) gradual brownian with bounds, correlation set to that obtained from the regression of independent contrasts of the variables; (2) gradual brownian with bounds, correlation set to 0; (3) speciational brownian with bounds, correlation set to that obtained from the regression of independent contrasts of the variables; (4) speciational brownian with bounds, correlation set to 0. For bounds, we used a minimum  $M_b$  of 1 g (the  $M_b$  of the smallest extant bird species, *Calypte helenae*, is 1.6 g [Calder 1985]) and a maximum  $M_b$  of 450,000 g (estimated  $M_b$  for the extinct *Aepyornis maximus* [Calder 1985]). To obtain BMR bounds, we predicted BMRs for *C. helenae* and *A. maximus* of 0.035 W and 209.411 W, respectively, using a conventional regression of BMR and  $M_b$  for the 126 species in our updated data set (discussed subsequently). The bounds algorithm was set to “replace.” No trends were set.

## Results

Of the 248 data we examined, only 67 met all four of our criteria for inclusion in this analysis of avian BMR (App. A). An additional 80 data met the criteria for experimental conditions but represented  $n < 3$  or unspecified sample sizes (App. A). Of the remaining 101 data, 42 were not obtained under suitable conditions for the measurement of BMR. The remaining 59 data were obtained under conditions not adequately described to determine whether or not these data represent BMR (App. A).

The 67 metabolic rates that represented BMR with  $n \geq 3$  were significantly lower than the 101 metabolic rates that did not meet the criteria for BMR or that were measured under conditions that were not adequately specified (ANCOVA,  $F_{1,167} = 8.833$ ;  $P = 0.003$ ; Fig. 2). The conventional least squares regression for the 67 good BMR data in Reynolds and Lee’s (1996) data set was  $\log \text{BMR} = -1.462 + 0.675 \log M_b$ . The conventional least squares regression for our updated data set (126 species) was  $\log \text{BMR} = -1.461 + 0.669 \log M_b$  (Fig. 2). The corresponding phylogenetically independent regression for our updated data set was  $\log \text{BMR} = -1.581 + 0.677 \log M_b$ .

The independent contrast between the passerines and the nearest nonpasserine taxon fell within the 95% prediction intervals of a linear regression of standardized contrasts (Fig. 3). Conventional ANCOVA of both the 67 good BMR data from Reynolds and Lee (1996) and the updated data set of 126 species suggested that the BMR of passerines was significantly higher than nonpasserines (Table 1). However, PI-ANCOVA of these data sets revealed no significant differences once phylogenetic relatedness was taken into account (Table 1).

## Discussion

Our analysis shows that allometric equations based on the data set used by Reynolds and Lee (1996) overestimate expected BMR and can potentially lead to incorrect conclusions regarding physiological adaptation. There was significant variation within the data set used by Reynolds and Lee (1996), corresponding with the conditions under which metabolic rate was measured. Since many of the data used by these authors to calculate regressions of BMR versus  $M_b$  were not measured under the conditions required for BMR, their allometries are not appropriate for predicting avian BMR.

Our analyses are consistent with the dichotomy between the results of conventional and phylogenetically independent anal-

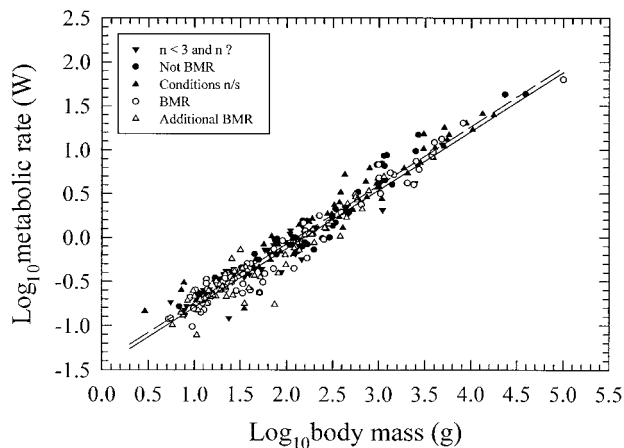


Figure 2. Metabolic rates for 248 avian species used by Reynolds and Lee (1996; App. A) and basal metabolic rate (BMR) for an additional 59 species (App. B) as a function of body mass ( $M_b$ ). Open symbols indicate data that meet the criteria for BMR, and filled symbols indicate data that do not meet the criteria for BMR or were measured in less than three individuals. The classification of data follows that used in Appendix A. The solid line is the conventional least squares regression through the 126 BMR data ( $\log \text{BMR} = -1.461 + 0.669 \log M_b$ ), and the dashed line is the conventional least squares regression calculated by Reynolds and Lee (1996).

yses of avian BMR (Reynolds and Lee 1996; Rezende et al. 2002). Whereas conventional analyses show the BMR of passerines to be significantly higher than that of nonpasserines (Lasiewski and Dawson 1967; Zar 1968; Reynolds and Lee 1996; Rezende et al. 2002; but see also Prinzing and Hänsler 1980), phylogenetically independent analyses suggest that the higher metabolic rate of passerines reflects phylogenetic relatedness rather than adaptive variation (Reynolds and Lee 1996; Garland and Ives 2000; Rezende et al. 2002).

#### Implications for Comparative Studies and Synthetic Analyses

Allometric equations calculated using only data that met the criteria for BMR and a minimum sample size of three predicted lower BMR than the equations presented by Reynolds and Lee (1996). Over the  $M_b$  range of 2 g–10 kg, BMRs predicted by our conventional linear regression were 10.9%–11.9% lower than predicted by the corresponding equation in Reynolds and Lee (1996), with the difference greatest at the upper end of this  $M_b$  range. Our conventional equation also predicted lower values than other recent allometries. For instance, compared with Rezende et al.'s (2002) conventional equation for mass-specific BMR, our equation predicted values ranging from 25.4% lower at  $M_b = 2$  g to 0.4% lower at  $M_b = 10$  kg. Our PI equation predicted values 18.3%–23.7% lower than our conventional regression, with the greatest difference at smaller  $M_b$ 's. These differences between the BMRs predicted by conventional and

PI equations are similar to those obtained by Tieleman and Williams (2000) and Rezende et al. (2002). Because our PI equation had a steeper slope (0.677) than Reynolds and Lee's (0.635), it predicted lower BMRs at  $M_b < \text{ca. } 500$  g but higher BMRs at  $M_b > \text{ca. } 500$  g. However, predicted values and prediction intervals from such PI equations need to be used with caution because they effectively assume that the species of interest diverged at the base of the phylogeny (Garland and Ives 2000). A more biologically realistic approach to comparing observed BMR with expected values involves the calculation of prediction intervals based on the position of the species of interest within a phylogeny (Garland and Ives 2000). Our phylogeny and  $M_b$  and BMR data (in PDI format) are available for this purpose from the corresponding author.

The differences in predicted BMR between our equations based on 126 species and those predicted by Reynolds and Lee (1996) have important implications for hypothesis testing, using both conventional and phylogenetically independent methods. In a conventional analysis, data for six species (*Otus asio*, *Podargus strigoides*, *Geophaps plumifera*, *Thinocorus rumicivorous*, *Scardefella inca*, *Lonchura fuscans*) fall outside the lower 95% prediction interval for Reynolds and Lee's (1996) conventional regression but within the corresponding prediction interval for our equation. Hence, these species would be erroneously considered to exhibit BMR significantly lower than expected. Conversely, the data for *Uria lomvia*, *Uria aalge*, and *Lullula arborea* fall within the 95% prediction intervals for Reynolds and Lee's (1996) conventional regression but are outside the upper 95% prediction interval for our equation.

Phylogenetically independent prediction intervals, calculated for a particular species within a phylogeny (Garland and Ives 2000), are likely to be similarly affected by the criteria used for data inclusion, particularly if the metabolic rates of closely related species were measured under different experimental conditions. For instance, the metabolic rate for *Pterocles orientalis* included by Reynolds and Lee (1996) represented BMR (Hinsley et al. 1993; App. A). However, the metabolic rates for two congeners, *Pterocles bicinctus* and *Pterocles alchata*, were not measured under the correct conditions for BMR (Hinsley 1992; Hinsley et al. 1993; App. A). Hence, phylogenetically independent prediction intervals for the BMR of *P. orientalis*, calculated using Reynolds and Lee's (1996) phylogeny, could easily lead to the erroneous conclusion that a low BMR has evolved in this species.

We have emphasized the importance of data inclusion criteria for generating allometries to predict avian BMR. However, the use of a single equation potentially obscures patterns of broad-scale variation in BMR that should be taken into account when testing hypotheses concerning adaptation in BMR. For instance, Tieleman and Williams (2000) demonstrated that birds inhabiting desert habitats exhibit lower BMR than their mesic counterparts and presented equations that predict BMR for desert and mesic species, respectively. These authors used criteria for

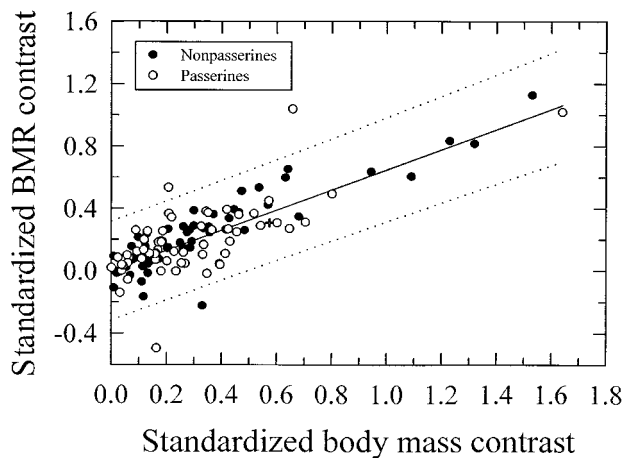


Figure 3. Standardized independent contrasts for basal metabolic rate (BMR) and body mass ( $M_b$ ) for 126 avian species, with a least squares regression through the origin (solid line). The dotted lines are the 95% prediction intervals. The contrast between the passerines and the nearest nonpasserine taxon is indicated by a cross.

BMR similar to those in the present study. In mammals, the slopes of regressions of BMR versus  $M_b$  vary among zoogeographic zones and among size classes (Lovegrove 2000). Moreover, the BMR of small mammals exhibits a slow-fast continuum, with the high and low extremes of the continuum associated with colder, highly seasonal environments at higher latitudes and warmer, less predictable habitats at lower latitudes, respectively (Lovegrove 2003). Zoogeographical variation in avian BMR has received considerably less attention, although a conventional analysis demonstrated a correlation between avian BMR and ambient temperature (Weathers 1979).

The need for careful selection of data also has implications for the current interest in the allometric scaling of metabolic rate (Darveau et al. 2002; West et al. 2002). Darveau et al. (2002) have criticized single-cause models seeking to explain metabolic rate allometry (e.g. West et al. 1999; Banavar et al. 2002). Instead, Darveau et al. (2002) have proposed a multiple-causes model based on the concept of multiple metabolic control sites, where the overall scaling exponent is determined by the scaling exponent and control contribution of each major step in energy demand and supply pathways. This allometric cascade approach predicts that variation should exist in the scaling exponents of endotherm BMR (Darveau et al. 2002), as has been demonstrated in mammals by Lovegrove (2000). Our examination of the importance of data inclusion criteria suggests that careful selection of data from the literature will be a critical aspect of future studies that seek to demonstrate similar variation in the scaling of avian BMR or to elucidate the mechanisms underlying such variation.

#### Avian BMR: Additional Considerations

One major potential shortcoming of current allometries for avian BMR, including those we have presented in this article, is the implicit assumption that BMR is a static metabolic parameter. There is increasing evidence that the BMR of many species is temporally variable (for a review, see Swanson 2003). Temporal variation in BMR has been correlated with thermal acclimatization/acclimation (Dawson and O'Conner 1996), habitat aridity (Ambrose and Bradshaw 1988), and migratory disposition (Piersma et al. 1995; Lindström 1997; Swanson and Dean 1999). However, patterns of temporal variation in avian BMR differ within and among species, and at present, few generalized patterns are evident (Swanson 2003).

An additional potential source of variation in measures of avian BMR concerns the fact that in some studies, the reported BMR represented the mean metabolic rate over the entire rest-phase, whereas in other studies, the minimum value observed during the rest phase was considered to represent BMR (Bennett and Harvey 1987). Of the 126 BMR data in our updated data set, 36 represented mean metabolic rate, 76 represented minimum metabolic rate, and the remaining 14 data were unspecified. The 36 data based on mean metabolic rates did not differ significantly from the 76 data representing minimum levels (ANCOVA,  $F_{1,111} = 1.540$ ;  $P = 0.217$ ).

Finally, few studies have investigated the effects of time since capture and stress associated with experimental conditions on measurements of avian BMR. Weathers et al. (1983) investigated the effects of time in captivity on the BMR of apapane (*Himatione sanguinea*) and found that the BMR of freshly caught birds was similar to that of long-term (1 yr) captives. However, the observed BMR was approximately 30% higher than the value previously measured in birds from the same population, raising questions about the influence of experimental protocol on BMR (Weathers et al. 1983). A more dramatic example of variation in BMR measurements concerns the green woodhoopoe (*Phoeniculus purpureus*). Williams et al. (1991a) reported a BMR of 0.666 W for this species, but Boix-Hinzen and Lovegrove (1998) subsequently observed a BMR of 0.173 W, equivalent to 26% of the earlier value, and the lowest avian BMR relative to allometrically predicted values of which we are aware. In the former study, metabolic rates of woodhoopoes were measured during trials lasting 1 h, conducted between 2000 and 2400 hours. Rest phase body temperature ( $T_b$ ), measured at the end of each trial using a thermocouple inserted into the proventriculus, averaged 39.7°C (Williams et al. 1991a). In Boix-Hinzen and Lovegrove's (1998) study, however,  $T_b$  was measured using surgically implanted telemeters, and metabolic rate was measured over 24 h at a constant  $T_a$ , during which time the birds were undisturbed. The minimum rest phase  $T_b$  observed in this study was 37.7°C. The differences in BMR and  $T_b$  between these two studies may well reflect differing levels of stress associated with the respective

experimental protocols. More compelling evidence that measurements of BMR may be affected by stress associated with laboratory conditions is provided by Weimerskirch et al. (2002). These authors used heart rate monitors to estimate energy expenditure in free-ranging wandering albatrosses (*Diomedea exulans*) during the incubation period. The relationship between heart rate and metabolic rate was determined by capturing albatrosses and measuring both parameters simultaneously in a metabolic chamber (Weimerskirch et al. 2002). The BMR during these laboratory measurements was equivalent to 163% of the BMR estimated for incubating (i.e., free-ranging) birds (Weimerskirch et al. 2002). Collectively, these observations suggest that avian metabolic rates are sensitive to the experimental conditions under which they are measured, and considerable care needs to be taken to measure BMR in individuals that are not stressed.

### Conclusions

Analyses of BMR remain widespread in the comparative physiology literature and have proven fundamental to understanding selection acting on endotherm metabolic parameters (Love-

grove 2000, 2003). The ability of such analyses to identify metabolic adaptation has been greatly enhanced by the development of comparative methods that take into account the statistical nonindependence of data (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1992, 1993; Garland and Ives 2000). The validity of the conclusions reached in these analyses, however, remains strongly dependent on data quality. Our critical examination of Reynolds and Lee's (1996) analysis of avian BMR highlights some of the problems that can arise from indiscriminate data inclusion and emphasizes the need to carefully select data for synthetic analyses.

### Acknowledgments

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### Appendix A

Table A1: Metabolic rate and body mass for 254 avian species analyzed by Reynolds and Lee (1996)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Nothoprocta perdicaria</i>	458	1.868	Withers et al. 1987	Not BMR
<i>Apteryx australis</i>	2,380	4.029	Calder and Dawson 1978	BMR
<i>Apteryx haasti</i>	2,450	4.179	Calder and Dawson 1978	$n < 3$
<i>Apteryx owenii</i>	1,096	2.068	Calder and Dawson 1978	$n < 3$
<i>Casurarius bennetti</i>	17,600	24.988	Benedict and Fox 1927	Conditions ns
<i>Dromaius novaehollandiae</i>	38,925	43.399	Calder and Dawson 1978	Not BMR
<i>Struthio camelus</i>	100,000	63.051	Withers 1983	BMR
<i>Penelope purpurescens</i>	2,040	5.424	Benedict and Fox 1927	Conditions ns
<i>Crax alberti</i>	2,800	6.586	No reference found	
<i>Crax daubentoni</i>	2,800	7.186	Benedict and Fox 1927	Conditions ns
<i>Leipoa ocellata</i>	1,390	4.036	Booth 1989	Not BMR
<i>Colinus virginianus</i>	194	1.114	Lasiewski and Dawson 1967	Conditions ns
<i>Callipepla californica</i>	138	.760	Brush 1965	Not BMR
<i>Callipepla gambelii</i>	126.1	.755	Weathers 1981	BMR
<i>Meleagris gallopavo</i>	3,700	8.910	Gaja 1931	Not BMR
<i>Bonasa umbellus</i>	644	2.383	Rasmussen and Brander 1973	BMR
<i>Lagopus lagopus</i>	567	2.872	Kendeigh et al. 1977	$n < 3$
<i>Lagopus leucurus</i>	326	2.363	Johnson 1968	Conditions ns
<i>Tetrao urogallus</i>	4,010	11.816	Kendeigh et al. 1977	$n < 3$
<i>Tetrao tetrix</i>	1,079	6.998	Rintamaki et al. 1983	Not BMR
<i>Gallus gallus</i>	2,710	6.005	Winchester 1940	BMR
<i>Coturnix coturnix</i>	97	.891	Kendeigh et al. 1977	$n < 3$
<i>Coturnix japonica</i>	115	.978	Prinzinger and Hänsler 1980	Conditions ns



Table A1 (Continued)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Alectoris graeca</i>	633	2.533	Kendeigh et al. 1977	$n < 3$
<i>Alectoris chukar</i>	475	1.961	Marder and Bernstein 1983	Not BMR
<i>Chauna chavaria</i>	2,620	6.876	Benedict and Fox 1927	Conditions ns
<i>Cygnus buccinator</i>	8,800	20.242	Benedict and Fox 1927	Conditions ns
<i>Branta bernicla</i>	1,168	4.523	Irving et al. 1955	Not BMR
<i>Aix sponsa</i>	448	2.247	Kendeigh et al. 1977	$n < 3$
<i>Anas strepera</i>	791	6.203	Prinzinger and Hänssler 1980	Conditions ns
<i>Anas acuta</i>	721	4.363	Prinzinger and Hänssler 1980	Conditions ns
<i>Anas platyrhynchos</i>	1,020	4.068	Kendeigh et al. 1977	$n?$
<i>Turnix suscitator</i>	58.1	.387	Prinzinger et al. 1993	BMR
<i>Melanerpes formicivorus</i>	73	.737	Weathers et al. 1990	BMR
<i>Picoides major</i>	117	1.041	Kendeigh et al. 1977	$n < 3$
<i>Upupa epops</i>	67	.552	Prinzinger and Hänssler 1980	Conditions ns
<i>Trogon rufus</i>	53	.431	Yarbrough 1971	$n < 3$
<i>Merops viridis</i>	33.8	.295	Bryant et al. 1984	BMR
<i>Alcedo atthis</i>	34.3	.378	Kendeigh et al. 1977	$n?$
<i>Colius striatus</i>	52.5	.322	Bartholomew and Trost 1970	BMR
<i>Colius castanotus</i>	69	1.036	Prinzinger et al. 1981	Conditions ns
<i>Geococcyx californianus</i>	284.7	1.462	Calder and Schmidt-Nielsen 1967	BMR
<i>Centropus senegalensis</i>	175	1.506	Prinzinger and Hänssler 1980	Conditions ns
<i>Eudynamis scolopacea</i>	188	1.646	Prinzinger and Hänssler 1980	Conditions ns
<i>Cacomantis variolosus</i>	23.8	.121	Hails 1983	$n < 3$
<i>Cuculus canorus</i>	111.6	.838	Kendeigh et al. 1977	$n?$
<i>Nymphicus hollandicus</i>	85.6	.688	Kendeigh et al. 1977	Conditions ns
<i>Amazona viridigenalis</i>	337.8	2.126	Bucher 1985	Not BMR
<i>Apus apus</i>	44.9	.436	Kendeigh et al. 1977	$n < 3$
<i>Anthracothonax nigricollis</i>	7.7	.305	Krüger et al. 1982	Conditions ns
<i>Agleactis cupripennis</i>	7.2	.252	Prinzinger et al. 1981	Conditions ns
<i>Patagona gigas</i>	19.1	.286	Lasiewski et al. 1967	Conditions ns
<i>Chlorostilbon mellisugus</i>	2.9	.145	Krüger et al. 1982	Conditions ns
<i>Strix aluco</i>	520	2.082	Herzog 1930	Conditions ns
<i>Nyctea scandiaca</i>	2,026	4.213	Gessaman 1972	BMR
<i>Bubo virginianus</i>	1,450	5.230	Ganey et al. 1993	BMR
<i>Asio flammeus</i>	406	1.288	Graber 1962	Conditions ns
<i>Asio otus</i>	252	.954	Wijnandts 1984	BMR
<i>Otus asio</i>	166	.586	Ligon 1969	BMR
<i>Otus trichopsis</i>	120	.446	Ligon 1969	BMR
<i>Aegolius acadicus</i>	124	.654	Ligon 1969	$n < 3$
<i>Glaucidium cuculoides</i>	163	.867	Johnson and Collins 1975	Conditions ns
<i>Glaucidium gnoma</i>	54	.441	Ligon 1969	$n < 3$
<i>Podargus ocellatus</i>	145	.567	Lasiewski et al. 1970	$n < 3$
<i>Eurostopodus argus</i> (= <i>Eurostopodus</i> <i>guttatus</i> )	88	.407	Dawson and Fisher 1969	$n < 3$
<i>Chordeiles minor</i>	72	.441	Lasiewski and Dawson 1964	BMR
<i>Caprimulgus europaeus</i>	77.4	.644	Kendeigh et al. 1977	Not BMR
<i>Phalaenoptilus nuttalli</i>	35	.155	Withers 1977	Conditions ns
<i>Zenaidura macroura</i>	123	.736	Riddle et al. 1932	$n?$
<i>Leptotila verreauxi</i>	131	.886	Vleck and Vleck 1979	$n < 3$
<i>Columba livia</i>	372	1.719	Herzog 1930	Conditions ns

Table A1 (Continued)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Columba unicincta</i>	318	1.714	No reference found	
<i>Streptopelia senegalensis</i>	108	.847	Kendeigh et al. 1977	<i>n?</i>
<i>Streptopelia turtur</i>	154	1.138	Kendeigh et al. 1977	<i>n?</i>
<i>Streptopelia decaocto</i>	155	.886	Gelineo 1955	Not BMR
<i>Scardefella inca</i>	40.5	.252	MacMillen and Trost 1967	BMR
<i>Fulica atra</i>	412	2.039	Kendeigh et al. 1977	$n < 3$
<i>Grus paradisea</i>	4,030	10.654	Benedict and Fox 1927	Conditions ns
<i>Grus canadensis</i>	3,890	8.136	Benedict and Fox 1927	Conditions ns
<i>Pterocles bicinctus</i>	196.7	.732	Hinsley 1992	Not BMR
<i>Pterocles orientalis</i> <sup>s</sup>	386.4	1.947	Hinsley et al. 1993	BMR
<i>Pterocles alchata</i>	242.9	.981	Hinsley et al. 1993	Not BMR
<i>Thinocorus rumicivorus</i>	55.5	.310	Ehlers and Morton 1982	BMR
<i>Scolopax rusticola</i>	430	2.160	Kendeigh et al. 1977	<i>n?</i>
<i>Tringa totanus</i>	149	1.560	Speakman 1984	Not BMR
<i>Tringa ochropus</i>	90	.920	Prinzinger and Hänssler 1980	Conditions ns
<i>Arenaria interpres</i>	90	.920	Kersten and Piersma 1987	BMR
<i>Calidris alba</i>	50	.560	Castro 1987	Not BMR
<i>Charadrius dubius</i>	36	.416	Kendeigh et al. 1977	<i>n?</i>
<i>Pluvialis squatarola</i>	226	1.780	Kersten and Piersma 1987	BMR
<i>Pluvialis dominica</i>	118	.644	Johnston and MacFarlane 1967	Conditions ns
<i>Haematopus ostralegus</i>	554	2.910	Kersten and Piersma 1987	$n < 3$
<i>Uria aalge</i>	956	6.804	Johnson and West 1975	BMR
<i>Uria lomvia</i>	989	6.804	Johnson and West 1975	BMR
<i>Catharactus skua</i>	970	4.746	Benedict and Fox 1927	Conditions ns
<i>Catharactus maccornmicki</i>	1,130	8.591	Ricklefs and Matthew 1983	Not BMR
<i>Larus argentatus</i>	1,000	4.804	Lustick et al. 1978	BMR
<i>Larus hyperboreus</i>	1,210	8.722	Scholander et al. 1950	Not BMR
<i>Larus canus</i>	431	2.257	Kendeigh et al. 1977	$n < 3$
<i>Larus atricilla</i>	275.6	1.874	Ellis 1980	Conditions ns
<i>Larus ridibundus</i>	306	1.860	Davydov 1972	Conditions ns
<i>Sterna lunata</i>	131.7	.702	Pettit et al. 1985	Not BMR
<i>Sterna fuscata</i>	148	.794	MacMillen et al. 1977	Not BMR
<i>Sterna maxima</i>	373	2.513	Ellis 1980	Conditions ns
<i>Falco sparverius</i>	117	.843	Shapiro and Weathers 1981	Conditions ns
<i>Falco tinnunculus</i>	108	.823	Giaja and Males 1928	Not BMR
<i>Falco subbuteo</i>	208	1.298	Kendeigh et al. 1977	<i>n?</i>
<i>Gypaetus barbatus</i>	5,070	11.041	Benedict and Fox 1927	Conditions ns
<i>Accipiter nisus</i>	135	.949	Kendeigh et al. 1977	<i>n?</i>
<i>Buteo buteo</i>	1,012	3.758	Prinzinger and Hänssler 1980	Conditions ns
<i>Phaethon rubricauda</i>	593.2	3.327	Pettit et al. 1985	Not BMR
<i>Sula dactylatra</i>	1,289	5.506	Unpublished data (see Ellis 1984)	
<i>Sula sula</i>	1,017	4.353	Ellis et al. 1982	Not BMR
<i>Anhinga rufa (anhinga)</i>	1,040	3.191	Henneman 1983	BMR
<i>Phalacrocorax auritus</i>	1,330	5.492	Henneman 1983	BMR
<i>Phalacrocorax atriceps</i>	2,660	14.949	Ricklefs and Matthew 1983	Not BMR
<i>Botaurus lentiginosus</i>	600	2.712	Benedict and Fox 1927	Conditions ns
<i>Ardea herodias</i>	1,870	6.199	Benedict and Fox 1927	Conditions ns
<i>Hydranassa caerulea</i>	290.3	1.002	Ellis 1980	Not BMR
<i>Hydranassa tricolor</i>	309.9	1.719	Ellis 1980	Not BMR

Table A1 (Continued)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Egretta thula</i>	314	1.366	Ellis 1980	Not BMR
<i>Phoenicopterus ruber</i> (= <i>Phoenicopterus antiquorum</i> )	3,040	15.254	Benedict and Fox 1927	Conditions ns
<i>Eudocimus albus</i> (= <i>Guara alba</i> )	940	4.116	Benedict and Fox 1927	Conditions ns
<i>Mycteria americana</i>	2,500	9.734	Kahl 1962	Not BMR
<i>Leptoptilos javanicus</i>	5,710	14.867	Benedict and Fox 1927	Conditions ns
<i>Jabiru mycteria</i>	5,470	13.172	Benedict and Fox 1927	Conditions ns
<i>Vultur gryphus</i>	10,320	16.998	Benedict and Fox 1927	Conditions ns
<i>Pelecanus occidentalis</i>	3,038	10.363	Benedict and Fox 1927	Conditions ns
<i>Pelecanus conspicillatus</i>	5,090	18.111	Benedict and Fox 1927	Conditions ns
<i>Fregata magnificens</i>	1,078	2.775	Enger 1957	Conditions ns
<i>Eudypitula minor</i>	960	3.734	Stahel et al. 1984	Conditions ns
<i>Eudypitula albosignata</i>	1,150	6.610	Pinshow et al. 1977	Not BMR
<i>Spheniscus humboldti</i>	3,870	9.491	Drent and Stonehouse 1971	BMR
<i>Megadyptes antipodes</i>	4,800	11.525	Unpublished data (see Drent and Stonehouse 1971)	
<i>Pygoscelis papua</i>	6,290	18.576	Unpublished data (see Brown 1984)	
<i>Pygoscelis adeliae</i>	3,970	12.232	Ricklefs and Matthew 1983	BMR
<i>Aptenodytes patagonica</i>	13,270	25.889	Unpublished data (see Brown 1984)	
<i>Aptenodytes forsteri</i>	23,370	42.871	Pinshow et al. 1976	Not BMR
<i>Oceanodroma furcata</i>	44.6	.450	Iverson and Krog 1972	Conditions ns
<i>Oceanodroma leucorhoa</i>	45	.649	Ricklefs et al. 1986	Not BMR
<i>Pelacanoides georgicus</i>	127	.983	Adams and Brown 1984	Not BMR
<i>Pelacanoides urinatrix</i>	136	1.395	Ricklefs and Roby 1983	Conditions ns
<i>Macronectes giganteus</i>	4,780	13.356	Adams and Brown 1984	BMR
<i>Pterodroma brevirostris</i>	315	1.772	Adams and Brown 1984	Not BMR
<i>Pterodroma hypoleuca</i>	167	.838	Grant and Whittow 1983	Not BMR
<i>Pterodroma phaeopygia</i>	425	5.249	Simons and Whittow 1984	Conditions ns
<i>Pachyptila salvini</i>	165	1.550	Adams and Brown 1984	Not BMR
<i>Puffinus griseus</i>	740	2.886	Krasnow 1979	Conditions ns
<i>Puffinus pacificus</i>	337.8	1.487	Pettit et al. 1985	Not BMR
<i>Puffinus nativitatus</i>	307.6	1.472	Pettit et al. 1985	Not BMR
<i>Diomedea exulans</i>	8,130	20.310	Brown and Adams 1984	BMR
<i>Diomedea immutabilis</i>	2,522	7.462	Adams and Brown 1984	BMR
<i>Diomedea chrysostoma</i>	3,753	8.508	Adams and Brown 1984	BMR
<i>Xiphorhynchus guttatus</i>	45.2	.446	Vleck and Vleck 1979	$n < 3$
<i>Thamnophilus punctatus</i>	21	.344	Vleck and Vleck 1979	$n < 3$
<i>Pipra mentalis</i>	12.3	.194	Bartholomew et al. 1983	BMR
<i>Manacus vitellinus</i>	15.5	.232	Bartholomew et al. 1983	BMR
<i>Sayornis phoebe</i>	21.6	.344	Yarbrough 1971	BMR
<i>Contopus virens</i>	13.9	.257	Yarbrough 1971	BMR
<i>Empidonax virescens</i>	12.3	.179	Yarbrough 1971	BMR
<i>Tyrannus tyrannus</i>	35.7	.436	Yarbrough 1971	$n < 3$
<i>Myiarchus crinitus</i>	33.9	.383	Yarbrough 1971	BMR
<i>Lichenostomus virescens</i>	25	.354	Collins et al. 1980	BMR
<i>Lichmera indistincta</i>	9	.208	Collins et al. 1980	BMR
<i>Chloropsis sonnerati</i>	39.7	.378	Hails 1983	$n < 3$
<i>Lanius excubitor</i>	72.4	.814	Kendeigh et al. 1977	$n?$
<i>Lanius collurio</i>	27	.383	Kendeigh et al. 1977	$n?$

Table A1 (Continued)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Corvus brachyrhynchos</i>	384.8	3.283	Wunder and Trebella 1976	Conditions ns
<i>Nucifraga caryocatactes</i>	147	1.346	Kendeigh et al. 1977	n?
<i>Perisoreus canadensis</i>	71.2	.678	Veghte 1964	Conditions ns
<i>Pica pica</i>	158.9	1.196	Hayworth and Weathers 1984	BMR
<i>Pica nuttalli</i>	151.9	1.467	Hayworth and Weathers 1984	BMR
<i>Aphelocoma coerulescens</i>	78.7	.969	Mann 1983	Not BMR
<i>Cyanocitta cristata</i>	80.8	.833	Misch 1960	Conditions ns
<i>Oriolus oriolus</i>	64.9	.649	Kendeigh et al. 1977	n?
<i>Bombycilla garrulus</i>	72.5	.954	Kendeigh et al. 1977	n?
<i>Cinclus mexicanus</i>	50.2	.460	Murrish 1970	Conditions ns
<i>Sialia mexicana</i>	27.5	.423	Mock 1991	BMR
<i>Turdus iliacus</i>	58	.722	Kendeigh et al. 1977	n < 3
<i>Turdus philomelos</i>	62.8	.726	Gavrilov 1974	n < 3
<i>Turdus viscivorus</i>	108.2	1.104	Kendeigh et al. 1977	n?
<i>Ficedula hypoleuca</i>	11.7	.232	Kendeigh et al. 1977	n?
<i>Muscicapa striata</i>	14.4	.247	Kendeigh et al. 1977	n?
<i>Copsychus saularis</i>	33.5	.232	Hails 1983	BMR
<i>Phoenicurus phoenicurus</i>	13	.232	Kendeigh et al. 1977	n?
<i>Erithacus rubecula</i>	17.6	.281	Kendeigh et al. 1977	n < 3
<i>Sturnus vulgaris</i>	75	.877	Kendeigh et al. 1977	n?
<i>Acridotheres cristatellus</i>	109.4	1.206	Johnson and Cowan 1975	n?
<i>Sitta canadensis</i>	11.2	.232	Mugaas and Templeton 1970	Not BMR
<i>Auriparus flaviceps</i>	6.8	.165	Goldstein 1974	Not BMR
<i>Troglodytes troglodytes</i>	9	.213	Gavrilov 1974	n < 3
<i>Parus atricapillus</i>	10.3	.252	Rising and Hudson 1974	BMR
<i>Parus major</i>	18	.324	Hissa and Palonkangas 1970	Conditions ns
<i>Aegithalos caudatus</i>	8.9	.199	Gavrilov 1974	n < 3
<i>Psaltriparus minimus</i>	5.5	.121	Chaplin 1982	BMR
<i>Hirundo tahitica</i>	14.1	.179	Bryant et al. 1984	BMR
<i>Hirundo rustica</i>	18	.315	Gavrilov 1974	n?
<i>Riparia riparia</i>	13.6	.232	Kendeigh et al. 1977	n?
<i>Regulus regulus</i>	5.5	.184	Kendeigh et al. 1977	n < 3
<i>Alophoixus bres</i>	35	.354	Hails 1983	n < 3
<i>Pycnonotus goiavier</i>	28.6	.247	Hails 1983	BMR
<i>Acrocephalus palustris</i>	10.8	.203	Kendeigh et al. 1977	n?
<i>Acrocephalus schoenobaenus</i>	11.5	.218	Kendeigh et al. 1977	n?
<i>Acrocephalus arundinaceus</i>	21.9	.257	Hails 1983	BMR
<i>Acrocephalus bistrigiceps</i>	7.9	.131	Hails 1983	n < 3
<i>Hippolais icterina</i>	12.5	.252	Kendeigh et al. 1977	n?
<i>Phylloscopus collybita</i>	8.2	.165	Kendeigh et al. 1977	n?
<i>Phylloscopus trochilus</i>	10.7	.208	Kendeigh et al. 1977	n?
<i>Malacopteron cinereum</i>	15.8	.213	Hails 1983	n < 3
<i>Sylvia borin</i>	24.8	.416	Kendeigh et al. 1977	n?
<i>Sylvia atricapilla</i>	21.9	.416	Kendeigh et al. 1977	n?
<i>Sylvia curruca</i>	10.6	.199	Kendeigh et al. 1977	n?
<i>Alauda arvensis</i>	46.1	.562	Shilov 1973	Conditions ns
<i>Eremophila alpestris</i>	26	.310	Trost 1972	n < 3
<i>Passer domesticus</i>	25.5	.334	Kendeigh 1944	Not BMR
<i>Anthus pratensis</i>	18.9	.300	Kendeigh et al. 1977	n?

Table A1 (Continued)

Species	Body Mass (g)	Metabolic Rate (W)	Reference	Classification
<i>Anthus trivialis</i>	19.7	.339	Kendeigh et al. 1977	<i>n?</i>
<i>Anthus campestris</i>	21.8	.383	Kendeigh et al. 1977	<i>n?</i>
<i>Motacilla alba</i>	18	.300	Gavrilov 1974	<i>n</i> < 3
<i>Motacilla flava</i>	14.7	.257	Kendeigh et al. 1977	<i>n?</i>
<i>Prunella modularis</i>	16.8	.324	Kendeigh et al. 1977	<i>n?</i>
<i>Vidua paradisaea</i>	10.5	.194	Terroine and Trautmann 1927	Conditions ns
<i>Lonchura fuscans</i>	9.5	.097	Weathers 1977	BMR
<i>Lonchura malacca</i>	11.8	.140	Hails 1983	BMR
<i>Lonchura maja</i>	12.8	.150	Hails 1983	BMR
<i>Arachnothera longirostra</i>	13	.189	Hails 1983	<i>n</i> < 3
<i>Aethopyga christinae</i>	5.2	.118	Prinzinger et al. 1989	BMR
<i>Fringilla coelebs</i>	21	.373	Gavrilov 1974	<i>n</i> < 3
<i>Fringilla montifringilla</i>	21	.383	Kendeigh et al. 1977	<i>n?</i>
<i>Carduelis pinus</i>	14	.291	Gavrilov 1974	<i>n?</i>
<i>Carduelis tristis</i>	13.6	.334	Dawson and Carey 1976	BMR
<i>Carpodacus erythrinus</i>	21.6	.358	Gavrilov 1974	<i>n?</i>
<i>Carpodacus mexicanus</i>	20.4	.310	Weathers 1981	BMR
<i>Carpodacus cassinii</i>	27.4	.339	Weathers 1981	BMR
<i>Vestiaria coccinea</i>	16.9	.349	MacMillen 1981	Not BMR
<i>Himatione sanguinea</i>	13.5	.300	Weathers et al. 1983	BMR
<i>Junco hyemalis</i>	18	.295	Weathers and Sullivan 1993	BMR
<i>Pooectes gramineus</i>	21.5	.271	Yarbrough 1971	BMR
<i>Spizella arborea</i>	16.6	.329	Lasiewski and Dawson 1967	Conditions ns
<i>Spizella passerina</i>	11.9	.194	Yarbrough 1971	BMR
<i>Calamospiza melanocoryx</i>	32.6	.455	Wunder 1979	Not BMR
<i>Emberiza schoeniclus</i>	17.6	.300	Kendeigh et al. 1977	<i>n?</i>
<i>Emberiza hortulana</i>	27	.407	Gavrilov 1974	<i>n</i> < 3
<i>Emberiza citrinella</i>	26.8	.436	Gavrilov 1974	<i>n</i> < 3
<i>Protonotaria citrea</i>	12.8	.199	Yarbrough 1971	BMR
<i>Vermivora pinus</i>	7.8	.150	Yarbrough 1971	<i>n</i> < 3
<i>Dendroica dominica</i>	9.8	.160	Yarbrough 1971	BMR
<i>Dendroica palmarum</i>	9.8	.155	Yarbrough 1971	BMR
<i>Dendroica coronata</i>	11.5	.189	Yarbrough 1971	BMR
<i>Dendroica pinus</i>	12	.179	Yarbrough 1971	<i>n</i> < 3
<i>Icterus galbula</i>	37.5	.504	Rising 1969	BMR
<i>Agelaius phoeniceus</i>	56.7	.833	Lewies and Dyer 1969	Conditions ns
<i>Cardinalis cardinalis</i>	41	.504	Hinds and Calder 1973	BMR
<i>Cardinalis sinuata</i>	32	.392	Hinds and Calder 1973	BMR

Note. Data for 248 species were classified according to our criteria for basal metabolic rate (BMR; see "Material and Methods"). Data were classified as follows: BMR = met criteria for BMR and measured in at least three individuals; not BMR = not measured under suitable experimental conditions; conditions ns = measured under experimental conditions that were not fully specified; *n* < 3 = met criteria for BMR but measured in fewer than three individuals; *n?* = met criteria for BMR, but sample size not specified.

<sup>a</sup> Erroneously listed as *Pterocles orcenbalis* in the appendix to Reynolds and Lee (1996).

## Appendix B

Table B1: Additional basal metabolic rate (BMR) and body mass ( $M_b$ ) obtained from the literature

Species	$M_b$ (g)	BMR (W)	Reference
<i>Dendragapus obscurus</i>	1,131	4.957	Pekins et al. 1992
<i>Coturnix chinensis</i>	44.9	.368	Roberts and Baudinette 1986
<i>Coturnix pectoralis</i>	95.8	.635	Roberts and Baudinette 1986
<i>Picoides pubescens</i>	21.7	.383	Liknes and Swanson 1996
<i>Phoeniculus purpureus</i>	74.07	.174	Boix-Hinzen and Lovegrove 1998
<i>Colius striatus</i>	51	.236	McKechnie and Lovegrove 2001b
<i>Colius colius</i>	35.1	.177	McKechnie and Lovegrove 2001a
<i>Cacatua galerita</i>	776.1	3.419	Williams et al. 1991b
<i>Cacatua tenuirostris</i>	549.9	3.168	Williams et al. 1991b
<i>Eolophus roseicapillus</i>	268.7	1.248	Williams et al. 1991b
<i>Barnardius zonarius</i>	137	.718	Williams et al. 1991b
<i>Neophema petrophila</i>	48.4	.634	Williams et al. 1991b
<i>Oreotrochilus estella</i>	8.4	.192	Carpenter 1976
<i>Sephanoides sephaniodes</i>	5.74	.102	Lopez-Calleja and Bozinovic 1995
<i>Strix occidentalis</i>	571	2.675	Ganey et al. 1993
<i>Podargus strigoides</i>	380.3	1.033	Bech and Nicol 1999
<i>Columba leucomela</i>	456	2.437	Schleucher and Withers 2002
<i>Ocyphaps lophotes</i>	187	1.085	Schleucher and Withers 2002
<i>Geophaps plumifera</i>	81	.394	Withers and Williams 1990
<i>Geophaps smithii</i>	198	.873	Schleucher and Withers 2002
<i>Phaps elegans</i>	190	1.238	Schleucher and Withers 2002
<i>Phaps chalcoptera</i>	304	1.529	Schleucher and Withers 2002
<i>Phaps histrionica</i>	257	1.297	Schleucher and Withers 2002
<i>Leucosarcia melanoleuca</i>	445	1.695	Schleucher and Withers 2002
<i>Geopelia cuneata</i>	39	.266	Schleucher and Withers 2002
<i>Geopelia placida</i>	52	.355	Schleucher and Withers 2002
<i>Chalcophaps inidica</i>	124	.793	Schleucher and Withers 2002
<i>Ptilinopus melanospila</i>	98	.488	Schleucher 2002
<i>Ptilinopus superbus</i>	120.4	.756	Schleucher 1999
<i>Scolopax minor</i>	156.7	1.066	Vander Haegen et al. 1994
<i>Calidris canutus</i>	130	.880	Piersma et al. 1995
<i>Haematopus ostralegus</i>	554	2.910	Daan et al. 1990
<i>Buteo lineatus</i>	658	2.110	Wasser 1986
<i>Meitihreptus lunatus</i>	14.3	.249	Vitali et al. 1999
<i>Acanthorhynchus tenuirostris</i>	9.7	.249	Weathers et al. 1996
<i>Pycnonotus finlaysoni</i>	26.3	.221	Hails 1983
<i>Phylidonyris novaehollandiae</i>	17.3	.317	Weathers et al. 1996
<i>Phylidonyris melanops</i>	18.8	.293	Vitali et al. 1999
<i>Zosterops lateralis</i>	11	.149	Maddocks and Geiser 1997
<i>Alauda arvensis</i>	31.7	.722	Tieleman et al. 2002
<i>Lullula arborea</i>	25.5	.572	Tieleman et al. 2002
<i>Eremalauda dunni</i>	20.6	.278	Tieleman et al. 2002
<i>Certhilauda erythrochlamys</i>	27.3	.412	Williams 1999
<i>Alaemon alaudipes</i>	37.7	.427	Tieleman et al. 2002
<i>Spermestes cucullatus</i>	10.62	.078	Lovegrove and Smith 2003
<i>Padda oryzivora</i> <sup>a</sup>	25.4	.308	Marschall and Prinzinger 1991

Table B1 (Continued)

Species	$M_b$ (g)	BMR (W)	Reference
<i>Amadina fasciata</i> <sup>a</sup>	17.2	.214	Marschall and Prinzinger 1991
<i>Amadina erythrocephala</i>	22.4	.213	McKechnie and Lovegrove 2003
<i>Estrilda melpoda</i> <sup>a</sup>	7.5	.131	Marschall and Prinzinger 1991
<i>Nectarinia venusta</i>	7.1	.140	Prinzinger et al. 1989
<i>Loxoides baileui</i>	36	.463	Weathers and van Riper 1982
<i>Amphispiza bilineata</i>	11.6	.197	Weathers 1981
<i>Passerculus sandwichensis</i>	15.9	.221	Williams and Hansell 1981
<i>Melospiza melodia</i>	19.1	.250	Yarbrough 1971
<i>Melospiza georgiana</i>	14.9	.211	Yarbrough 1971
<i>Zonotrichia querula</i>	33.3	.446	Yarbrough 1971
<i>Zonotrichia leucophrys</i>	26.1	.336	Yarbrough 1971
<i>Zonotrichia albicollis</i>	20.2	.278	Yarbrough 1971
<i>Ammodramus savannarum</i>	13.8	.178	Yarbrough 1971
<i>Coereba flaveola</i>	10	.215	Merola-Zwartjes 1998

<sup>a</sup> Not all experimental conditions were specified in the cited article, but they were confirmed by correspondence with the authors.

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