



Ecological factors affect the level and scaling of avian BMR

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ARTICLE INFO

Article history:

Received 26 May 2008

Received in revised form 14 August 2008

Accepted 20 August 2008

Available online 27 August 2008

Keywords:

Avian flight
Ecological factors
Energetics
Geography
Mammalian flight
Migration
Non-passerines
Passerines
Phylogeny

ABSTRACT

The basal rate of metabolism (BMR) in 533 species of birds, when examined with ANCOVA, principally correlates with body mass, most of the residual variation correlating with food habits, climate, habitat, a volant or flightless condition, use or not of torpor, and a highland or lowland distribution. Avian BMR also correlates with migratory habits, if climate and a montane distribution is excluded from the analysis, and with an occurrence on small islands if a flightless condition and migration are excluded. Residual variation correlates with membership in avian orders and families principally because these groups are behaviorally and ecologically distinctive. However, the distinction between passerines and other birds remains a significant correlate of avian BMR, even after six ecological factors are included, with other birds having BMRs that averaged 74% of the passerine mean. This combination of factors accounts for 97.7% of the variation in avian BMR. Yet, migratory species that belong to Anseriformes, Charadriiformes, Pelecaniformes, and Procellariiformes and breed in temperate or polar environments have mass-independent basal rates equal to those found in passerines. In contrast, penguins belong to an order of polar, aquatic birds that have basal rates lower than passerines because their flightless condition depresses basal rate. Passerines dominate temperate, terrestrial environments and the four orders of aquatic birds dominate temperate and polar aquatic environments because their high BMRs facilitate reproduction and migration. The low BMRs of tropical passerines may reflect a sedentary lifestyle as much as a life in a tropical climate. Birds have BMRs that are 30–40% greater than mammals because of the commitment of birds to an expensive and expansive form of flight.

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1. Introduction

A variety of approaches have been used to analyze avian basal rates of metabolism (BMR), which are the minimal rates in the zone of thermoneutrality when birds do not increase heat production for temperature regulation. The argument to be made here is that avian BMR varies with a variety of factors, especially body mass, but also with avian behavior and conditions in the environment, a pattern that was seen in a recent analysis of BMR in mammals (McNab, 2008). This pattern has ecological consequences for birds.

Analyses of avian BMR began with Brody and Procter (1932), who described the combined BMR of birds and mammals as a power function of body mass, an approach partially followed by Benedict (1938), even though he argued that the use of logarithms diminished species differences. King and Farner (1961) subsequently demonstrated that birds have higher basal rates than mammals of the same mass, especially at masses less than 100 g.

Lasiewski and Dawson (1967) found that passerines had basal rates, corrected for body mass, that were 65% greater than those of

other birds, which in turn had basal rates that were approximately 11% greater than mammals. Then, Aschoff and Pohl (1970a,b) noted that thermoneutral rates of metabolism in birds and mammals were minimal during the period of inactivity, a condition that since has been incorporated into the definition of basal rate of metabolism. They also showed that passerines during the rest period have basal rates that averaged 65% greater than other birds. The Aschoff–Pohl relationship has been widely used as the standard scaling relationship for birds, but it was derived from only 17 species, 3 of which were domesticated and many repeatedly measured, for a total of 31 measurements. Kendeigh et al. (1977), using data from 172 species, demonstrated that basal rate in birds is 15–25% greater in winter than summer and that passerines have basal rates that are 57–70% greater than non-passerines. Thus, the consensus until the mid-1990s was that passerines have appreciably higher basal rates than other birds of the same mass and that birds collectively have higher basal rates than mammals.

The conclusion that birds have higher basal rates than mammals was challenged by Gillooly et al. (2001) and White and Seymour (2004), who argued that birds and mammals have the same basal rates after their rates were ‘corrected’ through the use of a Q_{10} function for their difference in body temperature (T_b), birds generally having higher body temperatures than mammals. Even if this argument were correct, it does not account for the higher body

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temperatures of birds, and thus represents an incomplete analysis. A more fundamental criticism is that this proposition confuses endothermy with ectothermy: the heat content of endotherms and therefore the temperature differential ($\Delta T = T_b - T_a$) maintained with the environment (T_a) is a product of the balance between heat gained from metabolism (M) and heat lost through thermal conductance (C): $\Delta T = M/C$ (Scholander et al., 1950). *Birds have higher body temperatures than mammals because birds have higher rates of metabolism*, not *visa versa*, just as mammals with high basal rates have higher body temperatures. Birds also have lower conductances than mammals (Lasiewski et al., 1967), which further contributes to their larger ΔT s and higher body temperatures. This view, of course, raises the question why birds have higher BMRs than mammals, which shall be addressed later in this article.

A new approach to the analysis of basal rates of metabolism has recently appeared. Like the analyses of Lasiewski and Dawson and those who followed, it tried to account for the residual variation in the BMR–mass relationship. Whereas the earlier analyses described much of the residual variation in terms of a passerine/non-passerine dichotomy, the new approach incorporates a cladogram and gives preference to phylogeny as an explanation for the variation in BMR beyond that associated with body mass. For example, Reynolds and Lee (1996), using such an analysis, found no difference in BMR between passerines and non-passerines in 254 species. Rezende et al. (2002), using a similar technique on 32 species, agreed with this conclusion. The emphasis on the passerine/non-passerine dichotomy in earlier studies actually was a type of phylogenetic analysis: passerines have high BMRs presumably *because* they are passerines, whatever that may mean, but those analyses did not have the formality of an included cladogram.

Reynolds and Lee's analysis was criticized by McKechnie and Wolf (2004), who argued that many of the data that were used did not conform to the conditions required for basal rates, maintaining that "...good predictions need good data." They appropriately discarded some of the data used by Reynolds and Lee, but added an arbitrary criterion for data acceptance, requiring at least three individuals to be measured for a species to be included. Consequently, they discarded data on 187 species, but added 59 others from recent literature for a total of 126 species. When they used a conventional ANCOVA analysis, McKechnie and Wolf demonstrated that passerines indeed had higher basal rates than non-passerines, but this difference disappeared when a phylogenetically-based technique was used, so they concluded that passerines and non-passerines have indistinguishable BMRs.

In an attempt to simplify the analysis, I (2005a), using all available data on tropical frugivores, demonstrated that 7 passerines (5 birds-of-paradise [Paradisaeidae] and 2 manakins [Pipridae]) had mass-independent basal rates that averaged 57% greater than 26 non-passerines (3 mousebirds [Coliidae], 15 pigeons [Columbidae], 7 toucans [Ramphastidae], and a hornbill [Bucerotidae]), a difference similar to that found by Lasiewski and Dawson (1967) and Kendeigh et al. (1977). That is, when frugivorous passerines were directly compared to non-passerines with the same food habits, *uncompromised by theoretical assumptions*, these passerines had higher basal rates.

Much ambiguity still exists as to the factors responsible for the variation in avian BMR and how it should be analyzed: good predictions indeed need good data *and* good analytical techniques. Here I shall try to account for the variation in the BMR of birds and to explain why birds have higher basal rates than mammals. For this analysis, I have accumulated data on BMR from 533 species that belong to 97 families and 26 orders, which are organized by the widely used classification of Dickinson (2003). The foods consumed, habitats used, climates occupied, their volant or flightless condition, use or not of torpor, their use or not of migration, and restriction or not to mountains and to islands are indicated for each species, as is time of measurement (see the Appendix). The reason to think that these

factors might influence BMR is that most behaviors and responses to conditions in the environment require an expenditure of energy, which makes them likely candidates to influence the level of energy expenditure.

This analysis is offered as an alternative to those proposed by Reynolds and Lee (1996), Rezende et al. (2002), and McKechnie and Wolf (2004). Most of the variation in avian BMR will be accounted for, but we will still have large gaps in our knowledge, especially with regard to species and families endemic to the tropics, where the greatest species diversity is found. Data need to be obtained from these species before we can feel confident that we understand the degree to which avian BMR varies, as well as determining the causes and consequences of this variation. Two recent studies, Wiersma et al. (2007) on 69 lowland Panamanian species and McNab (in prep.) on 46 highland New Guinean species, have significantly increased our knowledge of tropical bird energetics, although they represent only a small fraction of tropical endemics. For example, we have almost no data on the energetics of birds from the South American (except as they are shared with Panama), African, and Asian tropics. Even when the correlation among BMR, body mass, and other factors is high, an appreciable inability to account for the variation in BMR will remain.

2. Data and methods

2.1. Data

As pointed out by McKechnie and Wolf (2004), the selection of data is an important criterion if the sources of variation in avian BMR are to be understood. The criteria generally accepted to define BMR are that the measurements must be made 1) in post-absorptive adults, 2) in the zone of thermoneutrality, 3) while the birds are thermoregulating, and 4) when they are inactive during the period of inactivity (McNab, 1997). These criteria give assurance that the differences in rate of metabolism reflect the species, not the conditions under which they are measured.

Given the observations of Kendeigh et al. (1977), measurement in summer or possibly autumn should probably be another criterion for basal rate, at least in polar and temperate species, as long as reproduction is not occurring, when rate of metabolism might be higher. In species measured in several seasons, winter values were chosen only when they were the lowest seasonal measurements. Of measurements on 96 species derived from V.M. Gavrillov and V.R. Dol'nik (Kendeigh et al., 1977; Gavrillov and Dol'nik, 1985; Gavrillov, 1996), 56 were measured in summer, 20 in autumn, and 20 in winter. A similar concern may exist with respect to a wet–dry seasonality in tropical species. For example, a study of seasonal variation in the BMR of a scrub-wren, *Sericornis frontalis*, in western Australia indicated that BMR was lower in a xeric than in a semi-xeric or mesic environment, but only in summer when the rainfall and insect abundance was very low (Ambrose and Bradshaw, 1988).

Measurements that do not meet these criteria generally should not be counted as estimates of BMR, although some studies (MacMillen and Trost, 1967; Wijnandts, 1984; Gabrielsen et al., 1991; Grajal, 1991; McNab and Salisbury, 1995; Ellis and Jehl, 2003; McNab, 2003a, 2005; McNab and Ellis, 2006) have demonstrated no difference in rate of metabolism between day and night. Large species may be less prone to show a circadian rhythm in standard rate of metabolism: 26 of 33 species in the Appendix with no temporal difference in metabolism weigh more than 120 g. Consequently, data on 15 diurnal species that weigh more than 250 g, six of which weigh more than 1.7 kg and are polar, are included, even though they were measured in daytime while inactive. Time of measurement, considered either as during the inactive or active period (including measurements that may have been in the active period [indicated by ? in the Appendix]), demonstrated no correlation ($F_{1,528} = 0.94$, $P = 0.42$) with \log_{10} BMR when combined with \log_{10} mass.

Some conditions required for BMR are difficult to evaluate, especially the criterion for being post-absorptive. Individuals usually were not fed for several hours before measurement to ensure that they were post-absorptive, which probably is adequate in small species. The time required for a sufficient food deprivation undoubtedly increases with body mass, if only because a large gut can contain more food. The greatest difficulty, however, is encountered in herbivores, especially in those that depend on microbial fermentation in the gut, a problem more widespread in mammals than birds. The takahe (*Porphyrio hochstetteri*), a 2.8 kg fermenting herbivorous rallid from New Zealand, however, had a lower thermoneutral rate of metabolism after food was withdrawn for a day compared to when it was deprived food for only a few hours (McNab and Ellis, 2006).

Restriction of measurements to the zone of thermoneutrality is an important criterion for BMR. The lower limit of thermoneutrality is often as high as 30–32 °C in species that weigh <15 g; room-temperature measurements will not suffice for these species. A gray area of judgment is found in polar species at cool temperatures in summer. In many cases the measurements were made at ambient temperatures between 7 and 15 °C, which probably are in thermoneutrality if the birds weighed over 200 g.

McKechnie and Wolf (2004) were sensitive to these criteria, but they excluded all Russian data reported in Kendeigh et al. (1977) and Gavrilo and Dol'nik (1985) because the number of individuals used was unreported and may have been <3 (McKechnie, pers. com.). Nevertheless, the time of day, season, and range of ambient temperatures used were indicated for these measurements, as was an estimate of the limits of thermoneutrality; they undoubtedly used many individuals in most species. (As an example of the thoroughness of their measurements, see Gavrilo (1995).) By excluding the work of Gavrilo and Dol'nik, McKechnie and Wolf rejected the most complete picture of the energetics of a continental avifauna, thereby greatly diminishing the diversity in measured avian BMRs. I included these data, subject to the above criteria.

Several individuals should represent a species to be sure that the variation in a population is included in the estimate of a species' basal rate, but as a practical matter many species are difficult to obtain. When birds are obtained by mist-netting, some species are readily captured, whereas others are captured only now and then, even if the mist-netting occurs over an extended period. A decision then has to be made whether to report data when only one, two, or three individuals are captured. This becomes a problem in small species that cannot be easily kept in captivity because their reluctance to feed reduces the number of measurements (n), which makes it difficult to define their narrow zones of thermoneutrality. Two sample sizes therefore are important, both the number of individuals (N) and n . In the study of Wiersma et al. (2007), only N is given without any indication of n : it is one condition to have a small N and another to have a small n , the latter being a greater difficulty.

Availability should not be the basis for the exclusion of species, especially if endangered, rare, or secretive species are physiologically distinctive (see McNab, 2006); that is, species personality may be an important variable influencing availability as well as rate of metabolism (Careau et al., 2008). With the permission of the New Zealand Department of Conservation, I was able to make extensive measurements on two takahe (McNab and Ellis, 2006), which represented 1% of the world's population. The data from these individuals agreed with each other. To exclude these measurements because only two individuals of this remarkable endangered species were available is unconscionable. (If we had measurements on one *Archeopteryx lithographica*, would that not be intensively informative?) My experience indicates that an extensive set of data from one or two individuals usually gives a result similar to measurements on several individuals from the same population. Besides, if only one or two individuals of an uncommon species are measured, these data can potentially be replaced or supplemented should more data become

available. However, the possibility exists that more data on some species will never become available and these few measurements would then become invaluable. Research, like life, is bounded by opportunity.

Another potential concern is that the basal rates of populations within a species may reflect the environmental conditions in which they live, as has been often seen (Ambrose and Bradshaw, 1988; Klaassen, 1995; Piersma et al., 1996; Merola-Zwartjes and Ligon, 2000; Williams and Tieleman, 2000; Wikelski et al., 2003). If several populations of a species are included in an analysis, these species will have a greater influence than those represented by one population (e.g., Aschoff and Pohl, 1970a,b). However, if data from only one population is used to characterize a species that has had populations from several environments measured, the basis for its selection is unclear. Sometimes the values from several populations are averaged, but I preferentially chose those that gave the lowest estimate of BMR, because higher measurements are potentially due to activity, anxiety, personality, or season and the validity of low rates can be checked if body temperature is reported (to eliminate torpor values).

McKechnie et al. (2006) indicated that the basal rates of wild-caught birds are higher than those obtained from captives. They suggested that this difference may reflect a change of diet in captivity, which may lead to changes in body composition, especially in the gut. Higher rates in newly captured birds may also represent bird anxiety. As a practical matter, some species are not likely to be captured in the field, including endangered, evasive, and large species, which is why we usually must rely on captives in these species. (I would never have obtained permission to capture takahas in the field: they were measured at Mt. Bruce Wildlife Centre.) The comparison between wild-caught and captive individuals is best accomplished within a species to avoid differences among species that may reflect factors other than their source, including ecology, behavior, and climate. I have measured basal rate in captive and field-caught Loria's birds-of-paradise (*Cnemophilus loriae*), finding no difference, and Papuan boobook (*Ninox theomacha*), with slightly lower rates in captives, but I have also found that captive amakihi (*Hemignathus virens*) had higher BMRs than wild-caught individuals. Weathers et al. (1983) found no difference in BMR between captive and wild-caught apananes (*Himatione sanguinea*). So, the effect of captivity may be complex and species specific.

Rates of metabolism are expressed as kJ/h, which are converted from mL_O₂/h, the usual units of measurement, by multiplying those values by 0.020 kJ/mL_O₂ (=20.08 kJ/LO₂)/(1000 mL/L).

2.2. Ecological factors

Describing the ecological characteristics of species is complicated. For example, species were assigned to 26 food habits, 20 habitats, 5 climates, 2 flight conditions, 4 torpor states, 2 migratory categories, and 6 distributional states (see Appendix). As a result, 249,600 potential combinations exist for the 533 species. Data for the ecological characteristics came mainly from the first 12 volumes of the Handbook of the Birds of the World (del Hoyo et al., 1992–2007), as well as from handbooks on several passerine families not yet included in the HBW.

In the case of torpor, some species that had their basal rates measured were not demonstrated to enter torpor, but they were closely related to species that have been shown to enter torpor with similar behaviors and living in similar environments. Therefore, the question whether these species use torpidity is unclear, so they were indicated in the Appendix by?

2.3. Statistical methods

The analytical method used here is the analysis of covariance (ANCOVA), which permits an estimate of the BMR–mass power

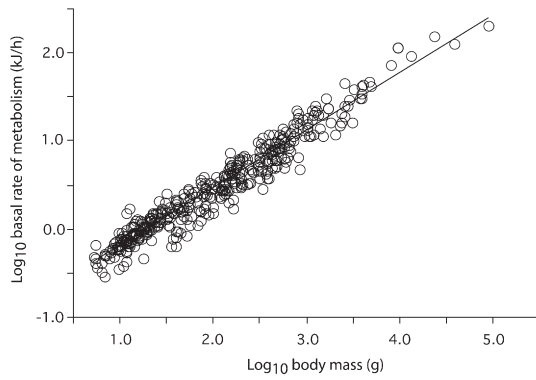


Fig. 1. \log_{10} basal rate of metabolism as a function of \log_{10} body mass in 533 species of birds (data taken from Appendix).

function to be calculated with the inclusion of taxonomic affiliations and various qualitative ecological variables. The variables were directly entered into the analysis, not as dummy variables. The statistical program used was SuperANOVA. BMR was first examined alone with respect to body mass and then with the presence of the passerine/non-passerine dichotomy, avian orders, avian families, and various ecological/behavioral factors. Each of these analyses requires one power for mass, which facilitates comparisons among the various alternate states, but in the case of avian orders, a better representation of the data are curves fitted individually for each order, when the powers of body mass are not required to be equal. An examination of the ecological/behavioral characters often found that the various conditions for one factor had statistically indistinct BMRs, which permitted them to be combined until the largest set of conditions with statistically distinct BMRs are determined for each factor (see Table 3). As a result, the potential combinations are reduced to no more than 432, only 44 of which were found.

3. Results

3.1. Scaling

\log_{10} BMR of the 533 species correlated with \log_{10} mass ($F_{1,531} = 8694.21$, $P < 0.0001$); $r^2 = 0.942$ (Fig. 1). When this relationship is taken out of logarithms, BMR scales according to the relationship

$$\text{BMR}(\text{kJ}/\text{h}) = 0.145m^{0.652 \pm 0.007}, \quad (1)$$

where m is mass in grams, and Eq. (1) has an $r^2 = 0.906$. The units of this equation can be converted into mLO_2/h by multiplying the coefficient 0.145 by 50 ($=1/0.020$), which then becomes 7.25. An examination of Fig. 1 indicates that an appreciable variation (5.8%) occurs around the mean logged curve. Even more variation occurs in the unlogged relationship (9.4%). The question therefore is whether any factors other than body mass account for the remaining variation in BMR. For example, is there a difference between passerines and non-passerines, as has been both claimed and denied?

3.2. Passerines vs. non-passerines

When the distinction between passerines and non-passerines is introduced into the analysis, \log_{10} BMR correlates both with \log_{10} mass ($F_{1,530} = 6484.97$, $P < 0.0001$) and the passerine/non-passerine dichotomy ($F_{1,530} = 118.22$, $P < 0.0001$); $r^2 = 0.953$ (Fig. 2). Then,

$$\text{BMR}(\text{kJ}/\text{h}) = 0.127(P)m^{0.721 \pm 0.009}, \quad (2)$$

where P is a non-dimensional coefficient, which when taken out of logarithms equals 1.00 in passerines ($n = 272$) and 0.71 in non-passerines ($n = 261$). Passerines have basal rates that averaged

141% ($=100/0.71$) of non-passerines, the coefficient in Eq. (2) now being 0.127 in passerines and $0.127 \times 0.71 = 0.090$ in other birds (compare Fig. 2a and b). This reconfirms the conclusion that has been made many times, namely that passerines have higher basal rates than the non-passerine collective and confirms the approximate magnitude of this difference. If Eq. (2) is used as a standard for oxygen consumption, the coefficient would be 4.50 for non-passerines and 6.35 for passerines, which are similar to the resting phase curves described by Aschoff and Pohl (1970), whose coefficients were 4.00 and 6.60, respectively, when the exponent was 0.730. Notice that with the increase in number of species measured, the mean passerine curve decreased (as we shall see, a result of including more tropical species) and the mean non-passerine curve increased (by including more polar species).

Another way to approach the difference between passerines and non-passerines is to scale BMR in each group independently, which unlike the analysis that led to Eq. (2), does not require these groups to have the same scaling exponent. Then,

$$\text{BMR}(\text{kJ}/\text{h}) = 0.089m^{0.724 \pm 0.013} \quad (3)$$

for non-passerines ($r^2 = 0.927$ for the logged curve) and

$$\text{BMR}(\text{kJ}/\text{h}) = 0.130m^{0.713 \pm 0.013} \quad (4)$$

for passerines ($r^2 = 0.919$ for the logged curve). Whether the difference in BMR between passerines and other birds is due to “phylogeny” or not, their means are different.

The difficulty with a comparison of passerines with non-passerines, given the array of ca. 28 avian orders, is that it is hard to see what non-passerines share, except that all *are* birds and they *are not* passerines. It would do well, then, to examine the extent to which non-passerine orders are similar to each other and to passerines. Does the BMR of avian orders share any patterns? And how distinct is avian BMR with regard to familial affiliation?

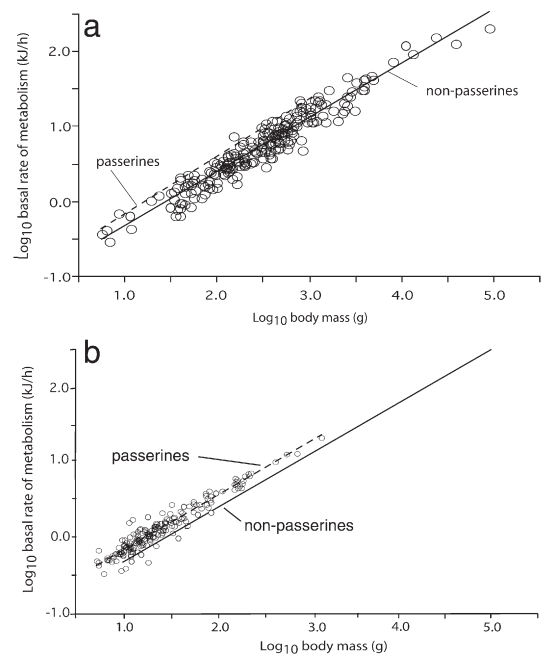


Fig. 2. \log_{10} basal rate of metabolism as a function of \log_{10} body mass a) in 261 birds other than passerines, 43 (16.5%) of which have a mass equal or greater than a mass of 1 kg. The passerine curve is indicated by a dashed curve. b) in 272 passerines, only one (0.4%) of which has a mass greater than 1 kg. The curve for birds other than passerines is indicated by a solid curve.

Table 1
Mean BMR in avian orders and the probability that they differ from that of Passeriformes

| Order | N | Coefficient O^a (Eq. (5)) | Least squares mean BMR (kJ/h) | P^b |
|-------------------|-----|--------------------------------|----------------------------------|---------|
| Anseriformes | 30 | 1.48 | 2.75 | 0.20 |
| Apodiformes | 6 | 1.24 | 2.31 | 0.0057 |
| Apterygiformes | 3 | 0.85 | 1.59 | <0.0001 |
| Caprimulgiformes | 8 | 0.70 | 1.30 | <0.0001 |
| Casuariiformes | 1 | 0.87 | 1.61 | 0.0072 |
| Charadriiformes | 25 | 1.56 | 2.90 | 0.81 |
| Ciconiiformes | 4 | 1.00 | 1.87 | <0.0001 |
| Coliiformes | 4 | 0.70 | 1.31 | <0.0001 |
| Columbiformes | 40 | 0.98 | 1.82 | <0.0001 |
| Coraciiformes | 9 | 1.06 | 1.98 | <0.0001 |
| Cuculiformes | 5 | 1.23 | 2.29 | 0.0099 |
| Falconiformes | 16 | 1.02 | 1.91 | <0.0001 |
| Gabuliformes | 1 | 0.95 | 1.77 | 0.016 |
| Galliformes | 14 | 1.27 | 2.37 | 0.0005 |
| Gruiformes | 15 | 1.01 | 1.89 | <0.0001 |
| Passeriformes | 272 | 1.58 | 2.94 | – |
| Pelecaniformes | 4 | 1.58 | 2.94 | 1.00 |
| Piciformes | 13 | 1.10 | 2.05 | <0.0001 |
| Podicipediformes | 1 | 1.57 | 2.93 | 0.99 |
| Procellariiformes | 13 | 1.46 | 2.72 | 0.26 |
| Psittaciformes | 21 | 1.43 | 2.65 | 0.041 |
| Pteroclidiformes | 1 | 1.24 | 2.32 | 0.26 |
| Sphenisciformes | 9 | 1.22 | 2.26 | 0.0028 |
| Strigiformes | 16 | 1.00 | 1.86 | <0.0001 |
| Struthioniformes | 1 | 0.79 | 1.46 | 0.0020 |
| Tinamiformes | 1 | 1.00 | 1.86 | 0.032 |

^a $BMR(kJ/h) = 0.085(O)m^{0.705}$.

^b Probability that the equation differs from that of Passeriformes.

3.3. Avian orders and families

To determine whether the BMRs of avian orders share any pattern, ANCOVA was run again, but this time \log_{10} BMR was examined with respect to \log_{10} mass and the 26 orders for which data are available. The result was that \log_{10} BMR correlated with \log_{10} mass ($F_{1,506} = 5303.62$, $P < 0.0001$) and order affiliation ($F_{25,506} = 17.67$, $P < 0.0001$); $r^2 = 0.969$. Consequently,

$$BMR(kJ/h) = 0.085(O)m^{0.705 \pm 0.010}, \quad (5)$$

where O is a coefficient for order affiliation. Note that because of the distinctiveness of the orders in terms of BMR, the unexplained variation in \log_{10} BMR is now down to 3.1%.

Each order has its distinctive coefficient and least squares mean basal rate (Table 1), the lowest basal rates occurring in Caprimulgiformes (frogmouths, goatsuckers) and the Coliiformes (mousebirds).

Table 2
Fitted curves for basal rate of metabolism in various avian orders

| Order | N | Δ mass | Coefficient | Power | r^2 |
|-------------------|-----|---------------|-------------|-------|-------|
| Anseriformes | 30 | 23.0 | 0.082 | 0.767 | 0.866 |
| Apodiformes | 6 | 7.9 | 0.091 | 0.761 | 0.813 |
| Caprimulgiformes | 8 | 9.5 | 0.052 | 0.731 | 0.923 |
| Charadriiformes | 25 | 32.2 | 0.075 | 0.807 | 0.922 |
| Columbiformes | 40 | 64.3 | 0.106 | 0.657 | 0.897 |
| Coraciiformes | 9 | 282.8 | 0.123 | 0.628 | 0.970 |
| Falconiformes | 16 | 28.9 | 0.132 | 0.636 | 0.905 |
| Galliformes | 14 | 86.9 | 0.079 | 0.759 | 0.968 |
| Gruiformes | 15 | 70.0 | 0.098 | 0.681 | 0.889 |
| Passeriformes | 272 | 231.3 | 0.130 | 0.713 | 0.919 |
| Piciformes | 11 | 25.0 | 0.123 | 0.639 | 0.903 |
| Procellariiformes | 13 | 182.3 | 0.135 | 0.691 | 0.982 |
| Psittaciformes | 21 | 31.0 | 0.137 | 0.678 | 0.940 |
| Sphenisciformes | 9 | 21.2 | 0.032 | 0.844 | 0.986 |
| Strigiformes | 16 | 45.0 | 0.077 | 0.723 | 0.889 |

Δ mass = maximal mass/minimal mass.

Passerines have a mean BMR that is 2.25 times that of caprimulgiformes and coliiformes. (Because ANCOVA forced each order to have the same power [slope on a log–log plot], these curves are not necessarily the best representatives of these orders as when examined individually, but they facilitate interordinal comparisons; see Table 2 for the best-fit relationships for orders with >5 species measured.)

What is most interesting about this analysis is that several orders have mean basal rates that are not significantly different from that of Passeriformes, including Anseriformes ($N=30$, $P=0.20$ [also see Miller and Eadie, 2006]), Procellariiformes ($N=13$, $P=0.26$), Charadriiformes ($N=25$, $P=0.81$) and Pelecaniformes ($N=4$, $P=1.00$), ignoring orders with only one species studied. These orders share being aquatic (pelagic, marine, or freshwater) and highly mobile, often in association with a polar or cold-temperate breeding distribution. The ‘aquatic’ orders that have a significantly lower BMR than passerines are the generally low-latitude Ciconiiformes ($N=4$, $P < 0.0001$) and the high-latitude Sphenisciformes ($N=9$, $P=0.0028$).

After orders were dropped from the analysis, familial affiliation was added to \log_{10} body mass. Then \log_{10} BMR correlated with \log_{10} mass ($F_{1,435} = 3195.73$, $P < 0.0001$) and family ($F_{96,435} = 7.44$, $P < 0.0001$); $r^2 = 0.978$. Thus, the inclusion of family affiliation further increases the ability to account for the variation in \log_{10} BMR with only 2.2% of the variation unaccounted for, an improvement over the inclusion of orders. However, given that data have been accumulated on species that belong to 97 families, further analysis would be exceedingly complex. A better strategy would be to analyze the factors that might be responsible for the diversity in BMR at the familial and ordinal levels, which will be examined by bringing ecological factors into the analysis, as was implied by the correlation of high BMR, non-passerine orders with aquatic habits, high mobility, and a temperate or polar breeding distribution.

3.4. Ecological factors

When all eight ecological factors were combined with \log_{10} mass, \log_{10} BMR correlated with \log_{10} mass, food habits, climate, habitat, the restriction or not to mountains, the use or not of torpor, and a volant or flightless condition, but not with the restriction to islands ($P=0.10$) or the use of migration ($P=0.16$). However, restriction to islands becomes a significant ($P=0.0024$) correlate of \log_{10} BMR when a flightless condition and migration are dropped, which reflects the common occurrence of a flightless condition in island endemics, as well as the sedentary nature of flighted island endemics. Migration is a significant ($F_{2,523} = 12.04$, $P < 0.0001$) correlate of \log_{10} BMR, if climate and mountains are dropped from the analysis because most migrants have a polar or temperate breeding distribution and most montane endemics live in the tropics. A difficulty is that far too many categories

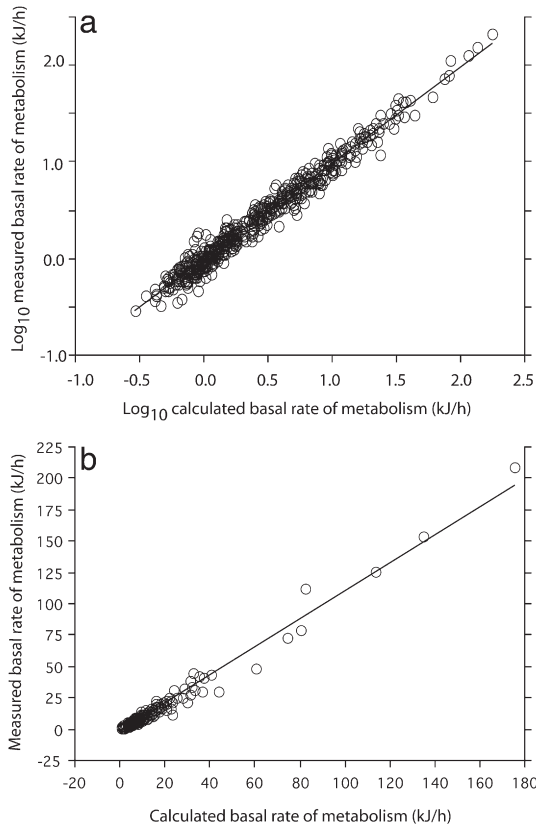


Fig. 3. a. \log_{10} measured basal rate of metabolism in 533 species of birds as a function of \log_{10} basal rate of metabolism calculated from Eq. (6). b. Measured basal rate of metabolism of birds as a function of basal rate calculated from Eq. (6).

in food habits and habitat exist for this relationship to be of any practical value because, even with the migration and island factors dropped, there still were 41,600 categorical combinations of ecological factors for the 533 species. These must be simplified.

The categories for a particular ecological factor can be combined when they have mean BMRs that are not statistically different. For example, the four torpor categories condense into two, the BMR of species that use torpor not being different ($P=0.067$) from the BMR of those related species that might use torpor (represented by ?), which was not different ($P=0.23$) from the BMR of the one species known to enter hibernation (*Phalaenoptilus nuttallii*). After this condensation, species that do not use torpor had higher basal rates ($F_{1,484}=40.22$, $P<0.0001$) than those that use, or may use, torpor.

Climate, when combined with \log_{10} mass, condensed torpor, and the other factors, condensed into three distinct categories, “polar,” “temperate,” and “tropical,” “temperate/tropical” being indistinguishable ($P=0.15$) from “tropical” and clearly different from ($P<0.0001$) from “temperate.” When temperate/tropical species were combined with tropical species, polar species had higher basal rates than temperate species ($t=3.25$, $P=0.0012$) and temperate species had higher basal rates than tropical species ($t=5.83$, $P<0.0001$).

When the categories for habitat were examined with the other factors, the 20 combinations reduced to three. One combined pelagic and marine species, a combination that was seen in non-passerine orders that had high basal rates. One of the other two habitat categories combined deserts, grasslands, savannahs, with tundra, whereas the other combined forests, alpine, open, with disturbed areas. Then each of the categories had a mean BMR that was different from the others, with “marine/pelagic” species greater than “forest”

species ($t=4.78$, $P<0.0001$), which in turn was greater than “desert/grassland” species ($t=5.83$, $P<0.0001$).

The greatest difficulty was to condense the 26 (=12 simple and 14 combined) food habits. Ultimately, they condensed into three categories: species with a nectar/pollen, nut diet, or aquatic vegetation diet had higher basal rates ($t=3.35$, $P=0.0009$) than omnivores, those feeding on grass, insects, and vertebrates, which collectively had higher basal rates ($t=3.35$, $P=0.0009$) than species committed to feeding on fruit or fruit mixed with vertebrates, leaves, or seeds.

When the complete analysis was re-examined, \log_{10} BMR correlated with \log_{10} mass and six ecological/behavioral factors, including torpor and mountains; $r^2=0.966$, which is appreciably better than with \log_{10} mass alone (when $r^2=0.942$). As effective as was this analysis in accounting for the variation in avian BMR, 3.5% variation in \log_{10} BMR remained. When a similar analysis was made on 639 species of mammals (McNab, 2008), the dichotomy between eutherians and other mammals retained significance, even though seven ecological and behavioral factors were included. This raises the question whether the dichotomy between passerines and other birds that was shown to exist (Eq. (2)) was accounted for by the ecological and behavioral differences between these two groupings.

When the passerine/non-passerine dichotomy was added, \log_{10} BMR now correlated with \log_{10} mass ($F_{1,521}=6968.62$, $P<0.0001$), food habits ($F_{2,521}=30.69$, $P<0.0001$), mountains ($F_{1,521}=6.73$, $P=0.0097$), climate ($F_{2,521}=43.91$, $P<0.0001$), torpor ($F_{1,521}=35.34$, $P<0.0001$), passerine/non-passerine dichotomy ($F_{1,521}=107.69$, $P<0.0001$), habitat ($F_{2,521}=38.47$, $P<0.0001$), and flight ($F_{1,521}=37.97$, $P<0.0001$); $r^2=0.972$ (Fig. 3a). When taken out of logarithms:

$$\text{BMR(kj/h)} = 0.139(F \cdot A \cdot C \cdot E \cdot T \cdot U \cdot S)m^{0.689 \pm 0.008}, \quad (6)$$

where the non-dimensional coefficients F stands for food, A for altitude, C for climate, E for passerine/non-passerine, T for torpor, U for habitat, and S for flight; $r^2=0.977$ (Fig. 3b). This equation accounts for 97.7% of the variation in BMR in all 533 species. It represents a great increase in the ability to account for the variation in avian BMR compared to Eq. (1) in which body mass alone accounted for 90.6% of the variation in BMR, realizing that a great increase in information is required for r^2 to approach the asymptote of 1.00. Time of measurement was added to Eq. (6) to determine whether BMR now correlated with it after the various behavioral/ecological factors were included: time of measurement still was not a significant correlate ($P=0.63$) of \log_{10} BMR.

Table 3
Coefficients for various ecological characteristics in Eq. (6)

| Character state | Condition | Coefficient |
|-----------------------|---|-------------|
| F (food habits) | Fruit | 0.69 |
| | Insects/seeds/omnivores/aquatic vegetation/ | |
| | Aquatic invertebrates/vertebrates | 0.74 |
| A (altitude) | Nut/nectar/pollen | 1.00 |
| | Lowlands | 0.93 |
| | Mountains | 1.00 |
| C (climate) | Tropical | 1.00 |
| | Temperate | 1.16 |
| | Polar | 1.41 |
| U (habitat) | Deserts/grasslands/savannahs/tundra | 0.70 |
| | Forests/open/disturbed/lakes/wetlands | 0.80 |
| | Marine/pelagic | 1.00 |
| T (torpor) | Torpor/?/HIB | 1.00 |
| | No torpor | 1.28 |
| E (passerine/nonpass) | Non-passerines | 0.76 |
| | Passerines | 1.00 |
| S (flight) | Flightless | 1.00 |
| | Flighted | 1.35 |

The non-dimensional coefficients in Eq. (6) are given in Table 3. Note that some modification of the values has occurred in the complete analysis (e.g., the non-passerine coefficient was 0.71 in Eq. (2), but 0.76 in Eq. (6)). For example, a volant non-passerine that feeds on aquatic invertebrates and lives in a lowland, temperate, marine environment, and does not enter torpor would be expected to have a basal rate estimated by Eq. (6), when the coefficient equaled 0.139 ($0.74 \times 0.93 \times 1.16 \times 1.00 \times 1.28 \times 0.76 \times 1.35$) = 0.146. Consequently, a wandering albatross (*Diomedea exulans*) weighing 8130 g would be expected to have a basal rate equal to 72.2 kJ/h, a value that is 99% of the measured value of 73.2 kJ/h. The frugivorous/insectivorous emerald toucanet (*Aulacorhynchus prasinus*) at 175 g would be expected from Eq. (6) to have a basal rate equal to 3.5 kJ/h, when the coefficient is 0.139 ($0.74 \times 0.93 \times 1.28 \times 1.00 \times 0.80 \times 0.76 \times 1.35$) = 0.101, which is 16% higher than the measured basal rate, 3.0 kJ/h. The house sparrow (*Passer domesticus*), a seed-eating passerine that weighs 23.0 g, had a measured basal rate equal to 1.3 kJ/h and one predicted by Eq. (6), when the coefficient is 0.153, equal to 1.3 kJ/h. When the basal rates of all 533 species are compared to the values expected from Eq. (6), the mean \pm S.E. is $101.6 \pm 0.88\%$, which is not different from 100% (Fig. 3), and $r^2 = 0.977$.

4. Discussion

This analysis of the factors influencing avian BMR has implications for phylogenetically-based analyses, scaling, taxonomic affiliation, the effect of food habits, and geographical ecology, as well as raising some questions why this model is unable to account completely for the variation in avian BMR. It also permits a comparison of the energetics of birds with that of the other endothermic vertebrate class, Mammalia.

4.1. Phylogenetic analyses

ANCOVA analyses assume that the datum from each species is independent of the data from other species, which raises a fundamental question: can similar characteristics in two related species truly be considered to be ‘independent’? This question was raised by Felsenstein (1985), which caused a mass movement to ‘correct’ all analyses of the evolution of phenotypes for the effects of phylogeny.

The answer to this question depends on what is meant by independent: if the evolution of character states is considered, then they may not be independent if two species with a particular character state has a common ancestor that show that state. However, if physiological rates are considered, then it may not make any difference whether they were attained by ancestry or convergence because they must be in sufficient harmony with conditions in the environment and the species’ behavior to permit the survival of species having these character states, at least as long as the function does not depend on a unique morphological structure. Thus, a vertebrate cannot persistently expend energy at rates that are unattainable from the resources exploited, irrespective of ancestry. As was clearly stated by Westoby et al. (1995, p. 728): “...if...the reason for similarity were ecological factors acting after the [related] species had become reproductively isolated and had separate opportunities for extinction or trait-change, then each species would be an *independent* [my italics] item of evidence, adding to our confidence that ... ecological factors did indeed cause those outcomes.” The highly flexible relationship of quantitative physiological rates to conditions in the environment is what is analyzed here.

Furthermore, phylogenetically-based analyses suffer from their dependence on cladograms. This is especially a problem when, as encountered here, an analysis is attempted for a large taxonomic unit, such as a class of vertebrates. No cladogram for a class exists today that is both complete and acceptable without controversy. For example, the cladogram invariably used in the analysis of BMR in the Class Aves

by Reynolds and Lee (1996), Rezende et al. (2002), McKechnie and Wolf (2004), and Wiersma et al. (2007) was derived (with various selective additions) from Sibley and Ahlquist (1990), which was based on the temperature at which hybrid DNA molecules derived from pairs of species showed 50% dissociation.

Few avian taxonomists accept the Sibley–Ahlquist classification (David Steadman, pers. com.), which is a radical classification compared to those based on morphology. In it the family Fringillidae contains blackbirds, New World sparrows, New World warblers, tanagers, two kinds of honeyeaters, cardinals, and New World orioles; passerines are grouped with Columbiformes, Gruiformes, and Ciconiiformes; and Ciconiiformes, besides the usual herons, storks, and ibises, contains the Charadriiformes, Falconiformes, Podicipediformes, Procellariiformes, Sphenisciformes, Gaviiformes, and the Pelicaniiformes. This grouping is responsible for the inability of Sibley–Ahlquist-based analyses to find that Passeriformes has a higher BMR than the collective of other birds because of dumping the Charadriiformes, Procellariiformes, and the Pelecaniformes, all orders with high BMRs, into one order that was closely allied with the Passeriformes.

Genomics is drastically, if somewhat chaotically, modifying our understanding of avian relationships. Recent analyses of the evolution of birds, based primarily on DNA base sequences by Barker et al. (2004), Fain and Houde (2004), Ericson et al. (2006), and Hackett et al. (2008), are very different from that proposed by Sibley and Ahlquist. Barker et al. (p. 11042) “...suggest not only that the DNA hybridization hypothesis [of Sibley and Ahlquist] is problematic, but also that use of the revised taxonomy based partially on it...as a proxy for evolutionary relationship is also questionable...” For example, Barker et al. concluded that the three species belonging to the bird-of-paradise subfamily Cnemophilinae are not paradisaeids (see also Cracraft and Feinstein, 2000), but are related to the Callaeatidae, the New Zealand wattlebirds! And many classically defined avian orders apparently are not monophyletic, including Falconiformes, Pelecaniformes, Ciconiiformes, and Gruiformes, whereas Apodiformes was combined with Caprimulgiformes (Hackett et al., 2008). With such flux, we are far from any consensus on avian phylogeny, which indicates that the description of order BMRs seen in Tables 1 and 2 will need to be revised, subject to subsequent revisions of avian taxonomy. Thus, if Falconiformes is broken into a narrowly defined Falconiformes, which among measured species includes the Falconidae, and ‘Accipitriiformes,’ which includes the Accipitridae, Falconiformes would have a mean BMR equal to 1.95 kJ/h and ‘Accipitriiformes’ 1.89 kJ/h.

Phylogeny and the environment influence phenotype in different ways and at different times (McNab, in press). Phylogeny influences the evolution of character states as a result of commitments made to solve problems previously encountered, sometimes restricting future possibilities and sometimes opening new opportunities, but they do not normally influence directly the narrow adjustments in physiology that connect behavior to conditions in the environment. That is, phylogeny may indicate whether a clade could evolve a particular food habit, but if that food habit evolves, energy expenditure reflects it and the environment in which the species lives. Two examples in birds of early commitments that opened new opportunities, the evolution of endothermy and the evolution of avian flight (see later), have had a radical impact on energy expenditure. Nevertheless, the refined adjustment of energy expenditure in these two cases is under the control of conditions in the environment, which are never part of any cladogram. Besides, the most adamant supporters of phylogenetic analyses of physiological character states admit the direct impact of body mass on energy expenditure. My view is that some factors other than mass have the same effect, including at least food habits and climate (McNab, 2003b).

The best means of controlling for phylogeny, when analyzing the impact of phylogenetic commitments on character states, should that be necessary, is obtained by comparing populations within a species

(e.g., Ambrose and Bradshaw, 1988; Klaassen, 1995; Wikelski et al., 2003), species within a genus (e.g., McNab, 2000, 2003a, 2005; Tieleman et al., 2002; McNab and Ellis, 2006), and genera within a family (e.g., Williams and Tieleman, 2000; McNab, 2005). As analyses move from populations to species, genera, families, orders, and classes, phylogenetic uncertainty increases.

4.2. Scaling

Body mass has the greatest impact on avian BMR of all effective factors because of its great range, in this study by a factor of $10^{4.2}$ -fold, i.e., the largest species (*Struthio camelus*) has a mass that is 17,300 times that of the smallest species (*Aethopyga christanae*). However, the addition or subtraction of various factors other than mass in an analysis influences the power of mass in the fitted scaling relationship of BMR, if the factors correlate with mass. When mass is the only factor used, the power of body mass describing BMR in birds is 0.652 ± 0.007 , whereas when the dichotomy between passerines and non-passerines is added, the power becomes 0.721 ± 0.009 , or 0.705 ± 0.010 when all 26 orders are incorporated into the analysis. When six ecological factors and the passerine/non-passerine dichotomy are added, the power equaled 0.689 ± 0.008 . This variation in the power reflects the correlation of various factors with mass, including the passerine/non-passerine dichotomy ($P=0.0019$), orders ($P<0.0001$), families ($P<0.0001$), and flight ($P<0.0001$). This flexibility raises a doubt that a “universal” value exists (Glazier, 2005; Bokma, 2004; McNab, 2008), as has been advocated in mammals by MacMahon (1973), Heusner (1982), West et al. (1999), and White and Seymour (2003), although White et al. (2006, 2007) appear to have changed their minds. All advocates of a universal power for metabolism ignore its residual variation, as if it were simply experimental error or inconvenient.

4.3. Taxonomic affiliations

The higher BMR of passerines than the pooled mean of other birds is reconfirmed here, although more important is the observation that ‘non-passerines’ is not a uniform category, as should be expected from the morphological, ecological, and behavioral diversities among these orders. Especially interesting is the observation that orders that share aquatic habits, a polar or temperate breeding distribution, and a mobile lifestyle have basal rates that do not differ from those of passerines. (This probably should also apply to the Podicipediformes, as it does with the one species studied, the eared grebe [*Podiceps nigricollis*].)

The mobility of these orders possibly influences BMR through a variation in body composition (Daan et al., 1990). Daan et al. emphasized the correlation of BMR with the sum of heart and kidney masses, which are only a small proportion of body mass, so this correlation may represent a correlation with the capacity for maximal metabolic output. McNab and Ellis (2006) showed that the reduction of BMR in flightless rails correlated with a reduction in pectoral muscle mass. Piersma et al. (1996) demonstrated a correlation of BMR with lean body composition in two subspecies of the migratory shorebird *Calidris canutus*.

The observation that penguins belong to the only aquatic, high-latitude order with basal rates that were lower than those of passerines reflects their flightless condition, given that flightless birds have lower basal rates than flighted species. Flightless birds collectively have basal rates that averaged 74% of flighted species, penguins have basal rates that averaged 78% of flighted species, their slightly higher basal rates probably reflecting an adaptation to cold-water. If the mean basal rate of penguins (2.26 kJ/h; Table 1) is adjusted for their flightless condition, their mean rate would be $(2.26/0.78)=2.89$ kJ/h, which is indistinguishable from that of passerines (2.94 kJ/h). The use of phylogenetic analyses in this case would be unable to distinguish a flightless condition from

membership in the Sphenisciformes, which represents the ultimate failure of phylogenetic analyses—the inability to dissect causative relationships.

Familial affiliation accounted for more of the variation in BMR when combined with body mass than ordinal affiliation probably because families are more uniform in their ecological and behavioral characteristics than orders, and consequently there are greater ecological, behavioral, and their associated physiological differences among families than among orders.

4.4. Food habits

Most of the variation in BMR that correlates with orders or families is associated with their ecological characteristics. Given that species feeding only on fruit, flying insects, or vertebrates have low basal rates, it is not surprising that the orders with the lowest mean basal rates (Table 1) include the Caprimulgiformes (insects), Coliiformes (fruit), Columbiformes (fruit, seeds), Coraciiformes (insects, fruit), Gruiformes (vertebrates, insects), Piciformes (insects, fruit), Falconiformes (insects, vertebrates), and Strigiformes (insects, vertebrates). This conclusion, of course, is sample dependent in that it reflects the species that were measured: although most temperate columbids are seed eaters, the majority (19/36) of measured species were tropical frugivores, which led to the low basal rate seen in the sample representing this order. A trophically balanced sample from this order might well have a higher basal rate.

Whether these avian orders have low basal rates because they have these food habits, or whether these food habits are correlated with low BMRs because they are found in these orders, may be subject to contention. However, the latter view is unintelligible in that it advocates a vague historical argument without any functional basis, whereas the former suggestion reflects an ecophysiological basis that will account for the consistencies seen among many phylogenetic units. For example, the similarly low mass-independent basal rates in frugivores that belong to the Columbidae, Coliidae, Bucerotidae, Ramphastidae, Pipridae, Paradisaeidae, and Pycnonotidae (McNab, 2005) cannot be the product of an immediate shared ancestry.

Why should BMR correlate with food habits? Note that feeding on insects or fruit alone is associated with intermediate basal rates, whereas the combination of insects with seeds or fruit correlates with some of the highest basal rates (McNab, 1988). Indeed, this pattern was seen in birds-of-paradise (McNab, 2005), all of which are to some extent frugivorous. Possibly the consumption of carbohydrates (seeds, fruit) or protein (insects) alone is inadequate to sustain a high BMR, whereas their mixture is associated with high BMRs. Or this difference in metabolism may reflect the temporal availabilities of foods, a combination of fruits and insects reducing periods of food shortage in the tropics, whereas BMR may be lower in species specializing on foods that are highly seasonal in availability, such as flying insects.

The analysis of the effect of food habits on the energetics of endotherms would be best accomplished by a detailed examination of the effects of digestibility of foods, their available energy contents, and the occurrence of secondary compounds (Cruz-Neto and Bozinovic, 2004), but we are presently a long way from this capacity. The correlation of BMR with food habits should remind us that we are dealing with associations and not necessarily directly with causative factors, which may be delineated only by careful, detailed experimental studies. This analysis, at best, is a preliminary step in the delineation of causative agencies.

4.5. Geographical ecology

The analysis represented by Eq. (6) demonstrated that the 262 temperate bird species have basal rates that averaged 116% of those

in 246 tropical species (Table 3). This difference is also found in 272 passerines, 144 of which are tropical: \log_{10} BMR correlates with \log_{10} mass ($F_{1,269}=3328.02$, $P<0.0001$) and climate ($F_{1,269}=31.15$, $P<0.0001$); $r^2=0.927$:

$$\text{BMR(kJ/h)} = 0.125(C)m^{0.708 \pm 0.012}, \quad (7)$$

where the log-transformed climate coefficient C equals 1.00 in tropical and temperate/tropical species and 1.13 in one polar (*Carduelis flammea*) and 127 temperate passerines. Temperate passerines therefore have basal rates that are 13% greater than tropical species, a smaller difference than in birds generally, but still conforming to the avian pattern. The greater difference in birds other than passerines may be related to the marine and pelagic habits of many temperate and polar species.

These observations are relevant to the conclusions of Gavrillov (1995, 1998, 1999), who attributed the dominance of temperate, terrestrial environments by passerines to their high basal rates. He argued that: 1) the high BMRs of temperate passerines were correlated with high potential energy and productive expenditures and 2) these two capacities permit temperate passerines to expend more energy on temperature regulation (and therefore tolerate lower ambient temperatures), reproduction, and migration than other birds, but 3) this advantage disappears at masses greater than 150 g. Furthermore, Lindström and Kvist (1995) showed that the maximal rate of energy intake is proportional to basal rate in temperate passerines. As a result, passerines dominate temperate, terrestrial environments at masses between 5 and 150 g. In the data assembled for this analysis, only 9 of 127 temperate passerines weigh more than 150 g, all of which are corvids. Gavrillov's analysis may explain why the largest passerine, the raven (*Corvus corax*), has a mass of only 1.2 kg and is sedentary.

As was suggested by Gavrillov for temperate passerines, the high BMRs of Anseriformes, Charadriiformes, Pelicaniformes, and Procellariiformes may be a means of ensuring a high reproductive output to compensate for a high mortality in cool to cold environments and to facilitate long distance migration. This pattern permits passerines to dominate temperate and polar terrestrial environments and the four high-latitude 'aquatic' orders to dominate temperate and polar aquatic environments. Sedentary species belonging to these orders, then, might be expected to have low BMRs, which may also explain why tropical passerines have low BMRs, rather than as an adaptation to a warm climate. Few sedentary species belonging to these aquatic orders have been measured, but compatible with the suggestion that they should be characterized by low basal rates, flighted and flightless anatids endemic to New Zealand have low basal rates (McNab, 2003a). New Zealand, in fact, has many sedentary aquatic birds, including the charadriiform wrybill (*Anarhynchus frontalis*), dotterels (*Charadrius* spp.), New Zealand snipe (*Coenocorypha* spp.), and black stilt (*Himantopus novaezelandiae*), and the pelicaniform shags *Phalacrocorax* [*Stictocarbo*] *punctatus* and *P.* [*Leucocarbo*] spp., which should be measured to test this hypothesis. Given the pelagic habits of procellariiforms, however, there may be no sedentary species and therefore none with low basal rates. Yet, the distinction between migratory and sedentary species is not absolute: some semi-sedentary or locally migratory shorebirds, like the Wilson's plover (*Charadrius wilsoni*), and tropical passerines should be examined.

4.6. Complications

Because Eq. (6) has r^2 equal to 0.977 with only 2.3% of the variation in BMR unaccounted for, a temptation exists to think that this analysis is nearly complete. However, when individual measurements are compared to the basal rates expected from Eqs. (1) and (6), the confidence associated with a high r^2 disappears. If we first

examine the distribution of BMR, expressed as a percentage of the mean—the "raw data"—262 of the 533 species (49.2%) have values <30%, which reflects the fact that 194 of the species (36.1%) weigh <30 g (Fig. 4). The great spread in these data (from 4.8 to 3442.7% of the mean) is greatly reduced when the data are represented relative to the value expected from mass by Eq. (1), which reemphasizes the determinative power of mass on BMR; then the mean ratio \pm S.E. of measured to calculated BMR is $104.0 \pm 1.22\%$, which ranged from 40.0 to 225.6%, i.e., a 5.6 fold variation in residuals. These ratios conform to a normal distribution truncated at 40% (Fig. 4). As expected, Eq. (6) further improves the ability to account for the variation in BMR with the mean \pm S.E. equal to $101.6 \pm 0.88\%$ and range from 50.5 to 205.3%, still a 4.1-fold variation (Fig. 4). Yet, both of these equations leave a remarkable variation in BMR unaccounted for, even though Eq. (6) reduces the residual S.E. by 30% compared to Eq. (1).

One possible explanation for this failure is that although BMR in birds correlates with many factors, others that are important have been neglected. If that is the case, what might they be? One is that Ellis (1980) demonstrated that mass-independent BMR in four herons varies with plumage color: white egrets had higher BMRs than the dark little blue heron (*Egretta caerulea*), both selecting an exposed nesting site, whereas another dark heron (*E. tricolor*) selected a sheltered nesting site and had a high BMR.

Another approach to unexplained variation in BMR is to examine the species that have the extreme ratios of measured to calculated BMR to see if they share some common characteristic, as was found in a similar analysis in mammals (McNab, 2008). However, in this study no pattern appears either in the species over- or underestimated. Some of the species that are underestimated may represent measurements that were not standard. This might well be the case in the acrocephaline warbler *Hippolais icterina*, which has a reported BMR (192% of the value expected from Eq. (6)), almost twice those reported from other temperate sylvids (which were between 88 and 116%), and *S. frontalis* (188%), which is much higher than three New Guinean *Sericornis* (93, 103, and 124%). The greatest overestimated species (two owls, a swallow, and two finches) also demonstrate no clear pattern, unless the owls and the swallow have unusually low BMRs for undefined reasons.

The assumption in Eq. (6) that each factor acts independently is unacceptable, as was seen with the addition of migration or an island distribution to the analysis, which required the dropping of other factors. As reasonable as the possibility of factor interaction might be, a cursory examination of some of these possibilities in *food* \times *climate* ($P=0.28$), *migration* \times *climate* ($P=0.83$), *migration* \times *island* \times *climate* ($P=0.64$), and *migration* \times *food* \times *climate* ($P=0.084$) were not significant when added to Eq. (6). However, among mammals, the term *food* \times *substrate* \times *climate* \times *habitat* was a significant correlate of \log_{10} BMR (McNab, 2008), and its addition increased r^2 .

4.7. The comparative energetics of birds and mammals

This analysis and a similar one on mammals (McNab, 2008) permit a comparison of the factors that influence BMR in these two clades that independently evolved endothermy. As seen above, the combination of body mass, climate, habitat, food habits, a highland/lowland distribution, the use of torpor, the use of flight, and the passerine/non-passerine dichotomy accounted for 97.7% of the variation in the BMR of 533 species of birds. In mammals, a combination of body mass, climate, habitat, substrate, food habits, the use of torpor, an island/continental distribution, and a highland/lowland distribution, in addition to the unique reproductive dichotomy between eutherians and monotremes/marsupials, accounted for 98.8% of the variation in the BMR of 639 species.

These analyses obviously had very similar results, which suggests that both groups of endotherms have independently

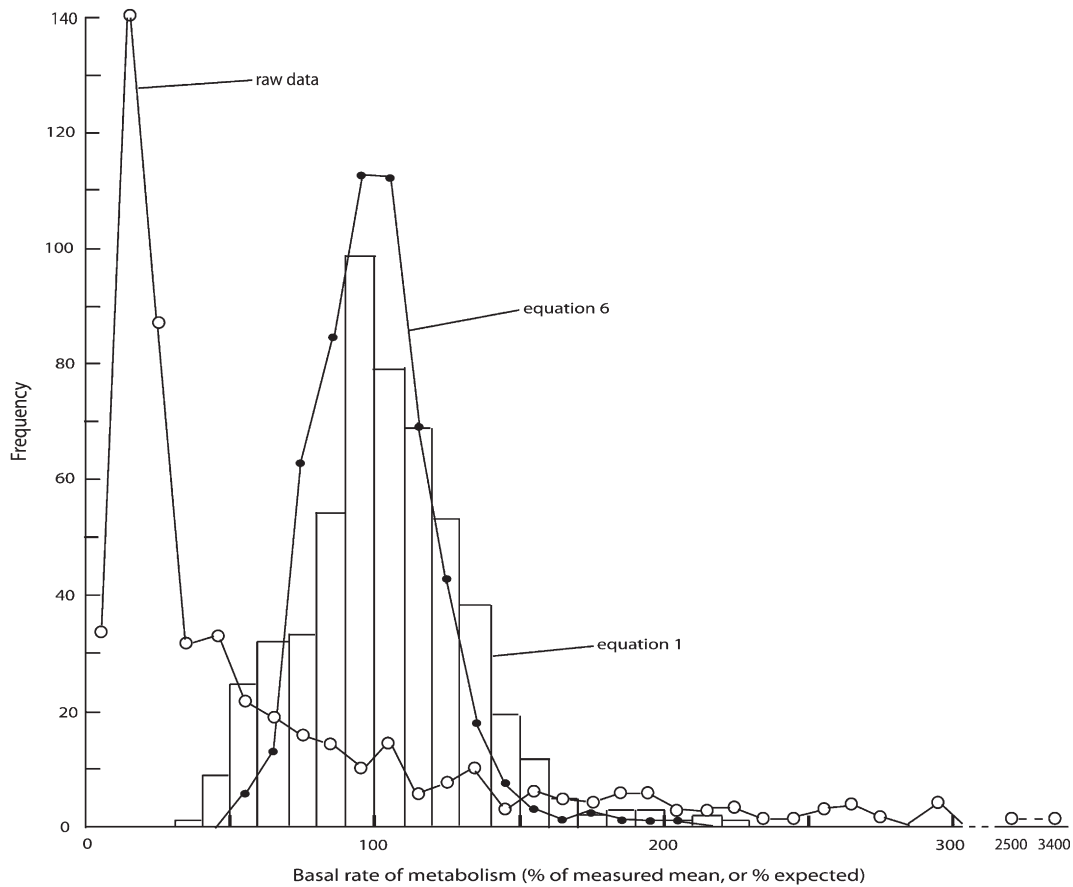


Fig. 4. The frequency distribution of basal rates of metabolism in 533 species of birds as a percentage of the basal rates expected from Eqs. (1) and (6).

responded to the same environmental factors since there is no evidence that birds and mammals had a shared endothermic ancestor. A close examination, however, demonstrates some fundamental differences in the energetics of birds and mammals, one of which is that birds collectively have BMRs that are much higher than those of mammals of the same mass (King and Farner, 1961; Aschoff and Pohl, 1970b).

Another notable difference is the response of birds and mammals to particular food habits. Although mammals and birds that feed on nectar have high basal rates, and those that feed on seeds or grass have intermediate BMRs, mammals and birds that feed on insects, vertebrates, or fruit have different basal rates. In mammals these foods are correlated with intermediate to high basal rates, whereas in birds they are associated with intermediate to low basal rates.

A complication in the comparison of birds and mammals is demonstrated in raptors: some (*Falco*, *Accipiter*, *Pandion*) have higher mass-independent basal rates than others (*Buteo*, *Parabuteo*, *Aquila*) (Wasser, 1986). The first group uses powered flight to capture vertebrate prey and has larger pectoral muscle masses, whereas the second group search for prey by soaring or using sit-and-wait tactics and has smaller pectoral muscle masses (Hartman, 1961). The reduction of BMR in flightless rails also correlates with a reduction in pectoral muscle mass compared to their flighted relatives (McNab and Ellis, 2006). Furthermore, birds that pursue insects in flight have higher basal rates than those that sit and wait for insect prey (Bonaccorso and McNab, 2003).

Flight, possibly as it reflects body composition, therefore, may be a factor pivotal to the difference in BMR between birds and mammals. Indeed, 22 species of flightless birds (3 kiwis, the emu, the ostrich, 2 ducks, 9 penguins, and 6 rails) have basal rates that

averaged $109.5 \pm 5.78\%$ of the values expected from mammals, whereas they averaged only 74% of volant birds. That is, the basal rates of flightless birds conform better to the mean mammal curve than to the mean bird curve (Fig. 5). The slightly higher basal rates (by mammalian standards) of some flightless birds reflect their cold-water distributions, namely penguins (105–160%), Auckland Island teal (*Anas aucklandica*, 135%), and Campbell Island teal (*A. nesiotis*, 119%).

As noted, birds generally have higher basal rates than mammals of the same mass. Because the mean mammalian scaling relation (McNab, 2008) is

$$\text{BMR}(\text{kJ}/\text{h}) = 0.070m^{0.721 \pm 0.006},$$

birds have BMRs that are approximately $0.145/0.070 = 2.1$ times those of mammals (at a mass of 1 g). But because the scaling power in birds is lower (0.652) than that of mammals (0.721), the difference in BMR between birds and mammals decreases with an increase in mass: these two equations reach equality at a mass of 38.3 kg (Fig. 5).

Two factors account for the lower power of the bird curve. One is that at masses >3 kg, 9 of 15 measured species are flightless and all 4 of those that weigh >10 kg are flightless (Fig. 5). That is, the accumulation of a flightless condition at intermediate and large masses pulls down the bird curve at higher masses, thereby contributing to its lower power. Another factor is the general commitment of small birds to continuous endothermy, which requires birds (and a few mammals) at masses <50 g to have increasingly high basal rates compared to a general mass standard as mass decreases (McNab, 1983, 1992). In contrast, only a minority of small mammals is committed to continuous endothermy (McNab, 2008).

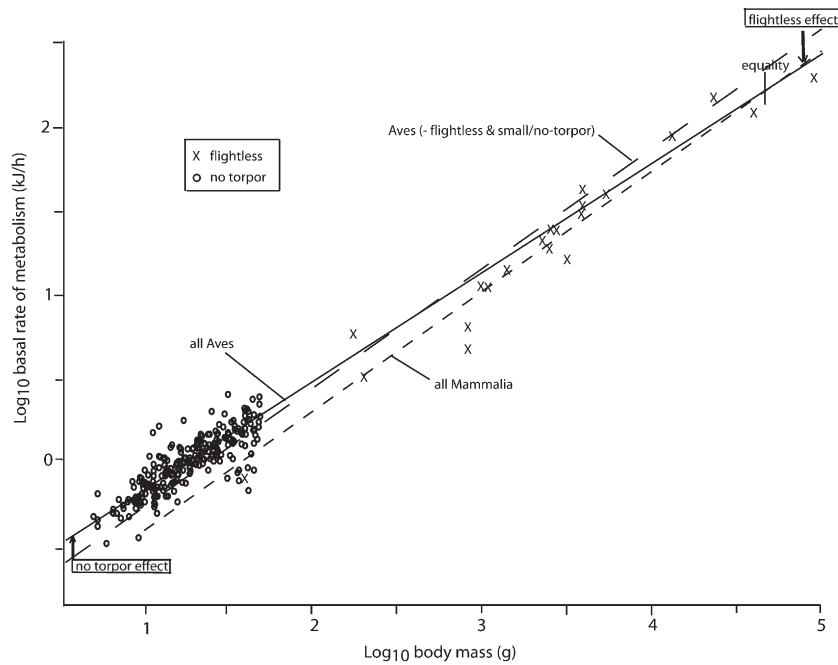


Fig. 5. \log_{10} mean basal rate of metabolism of birds and mammals as a function of \log_{10} body mass. Values for flightless birds and for birds that weigh <50 g that do not enter torpor are indicated and a resulting curve for birds with these values deleted is indicated.

When flightless birds and those continuously endothermic species that weigh <50 g are deleted from the bird curve, avian BMR now scales according to the relation ($N=277$):

$$\text{BMR}(\text{kJ}/\text{h}) = 0.105m^{0.708 \pm 0.014},$$

which is parallel to the mammal curve, the two powers, 0.721 and 0.730, being indistinguishable, as are the powers of the bird and mammal curves that incorporate all of the ecological factors (0.693 and 0.689, respectively). The modified bird curve is elevated compared to the mammal curve (Fig. 5): flighted birds that have not made a commitment to continuous endothermy at masses <50 g have a mean BMR that is 30–40% greater than that found in mammals.

One mammalian order, Chiroptera, is committed to flight: does the presence of flight in mammals have an impact on BMR similar to that in Aves? No: when flight is entered as the only factor with \log_{10} body mass, \log_{10} BMR in mammals correlates ($F_{1,629}=10.68$, $P=0.0011$) with flight, but non-flying mammals, unlike flightless birds, have higher basal rates (1.17:1) than fliers, which is opposite to the pattern in birds. A potential difficulty with this analysis is that most bats that belong to the suborder Microchiroptera feed on flying insects and enter torpor. So, to factor out the impacts of food habits and torpor, the analysis was rerun with the addition of condensed torpor and condensed food habits. Then, flight in bats remains a significant ($F_{1,626}=22.74$, $P<0.0001$) influence on \log_{10} BMR, but now with non-flying mammals having a mean BMR that is 1.24 times those of bats! As other factors are added to the analysis in various combinations, the effect of flight on BMR in mammals gains or loses significance. When added to the complete analysis in mammals (McNab, 2008), flight has no impact ($F_{1,618}=0.095$, $P=0.76$) on BMR.

This comparison of birds and mammals implies that the higher basal rates of birds reflect their commitment to a particular morphological form of flight and its absence in mammals. Hartman (1961) demonstrated in flighted birds that pectoral muscle mass varied from 9 to 36% of body mass, whereas the thoracic muscle masses in bats varied only from 7 to 12% (Hartman 1963). More

recently, Bullen and McKenzie (2004) reported that total flight muscle mass in bats varied from 9 to 23%, which is still less than the maximum seen in birds. The observation of Winter and Helversen (1998) that the cost of flapping flight in small bats is 20–25% less than the cost in small birds therefore is not surprising.

The correlation of basal rate in birds with pectoral muscle mass and the extent and type of flight appears to be the principal contributor to the difference in BMR between these classes. Whereas flight in birds is used for local, long distance, and pelagic movements, flight in bats is principally used for local movements. Temperate bats, which mainly feed on flying insects, usually respond to cold winters by hibernating in local caves. Temperate passerines with similar habits are migratory. The evolution of the avian form of flight clearly appears to have had an expansive impact on avian energetics, including the widespread occupation of polar and island environments. In contrast, the evolution of bat flight has had a more restricted influence, although a few temperate bats are migratory, especially species belonging to the genera *Lasiurus*, *Lasionycteris*, and *Nyctalus*, bats whose physiology (Genoud, 1993), large litter sizes (Banfield, 1974), and predatory behavior (Dondini and Vergari, 2000; Ibáñez et al., 2001; Popa-Lisseanu et al., 2007) are quite different from those characters in temperate *Myotis*. Other examples of the impact of history—i.e., phylogeny—on energy expenditure include the independent evolution of a commitment to endothermy in birds and mammals, and the evolution of a eutherian form of reproduction in mammals (McNab, 2008). As these cases demonstrate, the impact of a historical event on energy expenditure may be appreciable, if only occasional.

5. Conclusions

The analysis proposed here represents the most complete analysis of the standard energy expenditure of birds yet available, even given the difficulty accounting for the basal rates of individual species. When analyzing the factors responsible for the energy expenditure of birds, or any important component of the life history of a large assembly of species, we are trying to uncover the highly complex set of

factors responsible for that component. The ecological and behavioral factors influencing the BMR of birds and mammals are nearly identical, except as some historical adjustments in both clades were made that influenced energetics, including the evolution of endothermy and an avian form of flight in birds and endothermy and a eutherian form of reproduction in mammals.

These analyses are not easily accomplished. Organic nature is inherently complicated which permits organisms to survive by their opportunistic exploitation of resources, a behavior that leads to biological complexity and diversity. The persistent hope that organic nature is governed by a few simple rules is at best naïve;

there appear to be rules, but they usually consist of a series of conditional clauses. The greatest necessity today is to examine biological diversity, some of which will not persist due to a surplus of people.

Acknowledgements

I thank Harvey Lillywhite, Nathaniel Seavy, David Steadman, Charles Woods, and two anonymous reviewers for their critical evaluations of earlier versions of this article. I also thank Rebecca Kimball for her perspective on the phylogeny of birds.

Appendix A

A Basal rate of metabolism in birds

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|--------------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|---------------------------|
| Struthioniformes | | | | | | | | | | | | |
| Struthionidae | | | | | | | | | | | | |
| <i>Struthio camelus</i> | 92,400 | 209.66 | N | O | TR | G | O | O | O | O | + | Withers 1983 |
| Casuariiformes | | | | | | | | | | | | |
| Dromaiidae | | | | | | | | | | | | |
| <i>Dromaius novaehollandiae</i> | 38,900 | 126.04 | N | O | T | G | O | O | O | O | + | Maloney & Dawson 1994 |
| Apterygiformes | | | | | | | | | | | | |
| Apterygidae | | | | | | | | | | | | |
| <i>Apteryx owenii</i> | 1377 | 14.21 | D | I | T | F | O | O | L | O | + | McNab 1996 |
| <i>Apteryx haastii</i> | 2529 | 19.02 | D | I | T | F | O | O | L | O | + | McNab 1996 |
| <i>Apteryx australis</i> | 3137 | 16.60 | D | I | T | F | O | O | L | O | + | McNab 1996 |
| Tinamiformes | | | | | | | | | | | | |
| Tinamidae | | | | | | | | | | | | |
| <i>Nothoprocta perdicaria</i> | 458 | 6.35 | D | S | T | G | O | O | O | + | O | Withers et al. 1987 |
| Galliformes | | | | | | | | | | | | |
| Odontophoridae | | | | | | | | | | | | |
| <i>Callipepla gambelii</i> | 126.1 | 2.72 | N | S | T | D | O | O | O | O | O | Weathers 1981 |
| <i>Callipepla californica</i> | 137.1 | 2.76 | N | S/L | T | G | O | O | O | O | O | Hudson & Brush 1964 |
| Phasianidae | | | | | | | | | | | | |
| Tetraoninae | | | | | | | | | | | | |
| <i>Lagopus leucurus</i> | 326 | 8.50 | N | L | T | A | O | O | O | + | O | Johnson 1968 |
| <i>Lagopus mutus</i> | 465 | 9.86 | N | L | P | T | O | O | O | + | O | Mortensen & Blix 1986 |
| <i>Lagopus lagopus</i> | 658 | 10.10 | N | L | P | T | O | O | O | + | O | Mortensen & Blix 1986 |
| <i>Dendrogapus obscurus</i> | 1131 | 17.85 | N | L | T | F | O | O | O | + | O | Pekins et al. 1992 |
| <i>Tetrao urogallus</i> | 3900 | 42.92 | N | L | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| Perdicinae | | | | | | | | | | | | |
| <i>Coturnix chinensis</i> | 44.9 | 1.32 | N | S | TR | G | O | O | O | O | O | Roberts & Baudinette 1986 |
| <i>Coturnix pectoralis</i> | 95.8 | 2.29 | N | S | T | G | O | O | O | O | O | Roberts & Baudinette 1986 |
| <i>Coturnix coturnix</i> | 97 | 3.21 | N | S | T | G | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Coturnix japonica</i> | 115 | 3.52 | N | S | T | G | O | + | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Alectoris chukar</i> | 475 | 7.06 | D? | S | T | G | O | O | O | O | O | Marder & Bernstein 1983 |
| <i>Perdix perdix</i> | 501 | 7.75 | N | S/L | T | G | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Alectoris graeca</i> | 633 | 9.12 | N | S | T | G | O | O | O | + | O | Kendeigh et al. 1977 |
| Anseriformes | | | | | | | | | | | | |
| Anatidae | | | | | | | | | | | | |
| Ansirenae | | | | | | | | | | | | |
| <i>Branta bernicula</i> | 1253 | 21.82 | N | G | T | W | O | + | O | O | O | Daan et al. 1990 |
| <i>Anser canagicus</i> | 2609 | 32.25 | N | G | P | T | O | + | O | O | O | Gavrilov & Dolnik 1985 |
| <i>Chen^k caerulescens</i> | 2930 | 27.90 | D? | G | P | T | O | + | O | O | O | Boisemena et al. 1992 |
| <i>Anser anser</i> | 3250 | 39.01 | N | G | T | W | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Cygnus olor</i> | 8538 | 112.12 | D | AV | T | W | O | + | O | O | O | Bech 1980 |
| Tadorninae | | | | | | | | | | | | |
| <i>Hymenolaimus malacorhynchus</i> | 717.1 | 11.31 | D/N | AI | T | W | O | O | L | + | O | McNab 2003 |
| <i>Tadorna variegata</i> | 1193.6 | 12.04 | N | G | T | G | O | O | L | O | O | McNab 2003 |
| Anatinae | | | | | | | | | | | | |
| <i>Anas crecca</i> | 250 | 6.00 | N | AV | T | L | O | + | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Anas querquedula</i> | 289 | 8.04 | N | O | T | W | O | + | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Anas nesiotis</i> | 371.1 | 5.94 | D/N | AI | T | W | O | O | S | O | + | McNab 2003 |
| <i>Anas aucklandica</i> | 373.1 | 6.75 | D/N | AI | T | W | O | O | S | O | + | McNab 2003 |
| <i>Anas gracilis</i> | 393.7 | 11.98 | D/N | AV | T | W | O | O | O | O | O | McNab 2003 |
| <i>Lophodytes cucullatus</i> | 413.3 | 7.03 | D/N | V/AI | T | L | O | + | O | O | O | McNab 2003 |
| <i>Aythya nyroca</i> | 440 | 11.78 | N | AV | T | W | O | + | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Aix sponsa</i> | 448 | 8.09 | N | AV | T | W | O | + | O | O | O | Kendeigh et al. 1977 |

(continued on next page)

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|-------------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|----------------------------|
| Anseriformes | | | | | | | | | | | | |
| Anatidae | | | | | | | | | | | | |
| Anatinae | | | | | | | | | | | | |
| <i>Anas castanea</i> | 483.3 | 6.86 | D | O | T | W | O | O | O | O | O | McNab 2003 |
| <i>Aythya novaeseelandiae</i> | 488.4 | 8.40 | D/N | AI | T | L | O | O | L | O | O | McNab 2003 |
| <i>Anas rhynchotis</i> | 508.0 | 9.47 | D | AI | T | W | O | O | O | O | O | McNab 2003 |
| <i>Anas chlorotis</i> | 528.8 | 8.35 | D/N | AI | T | W | O | O | L | O | O | McNab 2003 |
| <i>Anas clypeata</i> | 554 | 13.96 | N | AI | T | W | O | + | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Aythya affinis</i> | 561.5 | 10.33 | N | O | T | L | O | + | O | O | O | McNab 2003 |
| <i>Aythya fuligula</i> | 574 | 9.73 | N | AV | T | L | O | O | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Aythya collaris</i> | 681.5 | 11.84 | N | O | T | W | O | + | O | O | O | McNab 2003 |
| <i>Anas acuta</i> | 721 | 15.71 | N | AV | T | W | O | + | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Anas penelope</i> | 723 | 10.15 | N | AV | T | W | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Anas strepera</i> | 791 | 22.33 | N | AV | T | W | O | + | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Aythya ferina</i> | 816 | 20.94 | N | AV | T | W | O | +/O | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Anas platyrhynchos</i> | 1020 | 14.64 | N | O | T | W | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Netta rufina</i> | 1237 | 25.56 | N | AV | T | L | O | + | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Somateria mollissima</i> | 1660 | 21.99 | D | AI | P | M | O | + | O | O | O | Jenssen et al. 1989 |
| Sphenisciformes | | | | | | | | | | | | |
| Spheniscidae | | | | | | | | | | | | |
| <i>Eudyptula minor</i> | 1100 | 11.49 | N | V | T | M | O | O | O | O | + | Baudinette et al. 1986 |
| <i>Eudyptes chrysocome</i> | 2330 | 21.00 | ? | AI | P | M | O | + | O | O | + | Gavrilov 1977; Brown 1984 |
| <i>Eudyptes pachyrhynchus</i> | 2600 | 24.92 | N | AI | T | M | O | + | O | O | + | Drent & Stonehouse 1971 |
| <i>Eudyptes chrysolophus</i> | 3870 | 31.13 | ? | AI | T | P | O | + | O | O | + | Gavrilov 1977; Brown 1984 |
| <i>Spheniscus humboldti</i> | 3870 | 34.14 | N | V | T | M | O | + | O | O | + | Drent & Stonehouse 1971 |
| <i>Pygoscelis adeliae</i> | 3970 | 44.04 | D? | AI | P | M | O | + | O | O | + | Kooyman et al. 1976 |
| <i>Megadyptes antipodes</i> | 4800 | 41.45 | N | V | T | M | O | O | O | O | + | Drent & Stonehouse 1971 |
| <i>Aptenodytes patagonicus</i> | 11,080 | 78.67 | ? | V | P | P | O | O | O | O | + | Gavrilov 1977 |
| <i>Aptenodytes forsteri</i> | 23,370 | 154.19 | D | V | P | P | O | + | O | O | + | Pinshow et al. 1976 |
| Procellariiformes | | | | | | | | | | | | |
| Diomedidae | | | | | | | | | | | | |
| <i>Phoebastria fusca</i> | 2875 | 29.79 | N | AI | T | P | O | + | O | O | O | Adams & Brown 1984 |
| <i>Diomedea chrysostoma</i> | 3753 | 30.63 | N | AI | T | P | O | + | O | O | O | Adams & Brown 1984 |
| <i>Diomedea exulans</i> | 8130 | 73.17 | N | AI | T | P | O | + | O | O | O | Brown & Adams 1984 |
| Procellariidae | | | | | | | | | | | | |
| <i>Halobaena caerulea</i> | 191 | 6.38 | N | AI | T | P | O | O | O | O | O | Brown 1988 |
| <i>Pterodroma mollis</i> | 274 | 6.29 | N | AI | T | P | O | + | O | O | O | Adams & Brown 1984 |
| <i>Pterodroma brevirostris</i> | 315 | 6.38 | N | AI | T | P | O | + | O | O | O | Brown & Adams 1984 |
| <i>Puffinus puffinus</i> | 367 | 8.38 | N | V | T | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Pterodroma macroptera</i> | 479 | 9.71 | N | AI | T | P | O | + | O | O | O | Brown 1988 |
| <i>Fulmarus glacialis</i> | 728 | 13.75 | N | AI | P | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Procellaria cinerea</i> | 1014 | 18.04 | N | AI | T | P | O | + | O | O | O | Brown & Adams 1984 |
| <i>Procellaria aequinoctialis</i> | 1287 | 22.71 | N | AI | T | P | O | + | O | O | O | Brown & Adams 1984 |
| <i>Macronectes giganteus</i> | 4780 | 48.08 | N | V | P | M | O | + | O | O | O | Brown & Adams 1984 |
| Hydrobatidae | | | | | | | | | | | | |
| Hydrobatinae | | | | | | | | | | | | |
| <i>Oceanodroma furcata</i> | 44.6 | 1.59 | N | AI | T | P | O | + | O | O | O | Vleck & Kenagy 1980 |
| Podicipediformes | | | | | | | | | | | | |
| Podicipedidae | | | | | | | | | | | | |
| <i>Podiceps nigricollis</i> | 317 | 7.71 | D/N | AI | T | W | O | + | O | O | O | Ellis & Jehl 2003 |
| Ciconiiformes | | | | | | | | | | | | |
| Ardeidae | | | | | | | | | | | | |
| <i>Egretta^k caerulea</i> | 290.3 | 3.59 | D | AI | T/TR | W | O | + | O | O | O | Ellis 1980 |
| <i>Bebulcus ibis</i> | 299.2 | 4.74 | D | O | T/TR | W/O | O | + | O | O | O | Ellis 1980 |
| <i>Egretta^k tricolor</i> | 309.0 | 6.12 | D | V | T/TR | W | O | + | O | O | O | Ellis 1980 |
| <i>Egretta thula</i> | 314.0 | 4.89 | D | V/AI | T/TR | W | O | + | O | O | O | Ellis 1980 |
| Pelecaniformes | | | | | | | | | | | | |
| Sulidae | | | | | | | | | | | | |
| <i>Morus bassanus</i> | 2574 | 44.96 | N | V | T | M | O | + | O | O | O | Bryant & Furness 1995 |
| Phalacrocoracidae | | | | | | | | | | | | |
| <i>Phalacrocorax auritus</i> | 1330 | 19.77 | N | V | T | M/L | O | + | O | O | O | Hennemann 1983 |
| <i>Phalacrocorax aristotelis</i> | 1619 | 30.79 | N | V | T | M | O | O | O | O | O | Bryant & Furness 1995 |
| Anhingidae | | | | | | | | | | | | |
| <i>Anhinga anhinga</i> | 1040 | 11.49 | N | V | TR | L/W | O | O | O | O | O | Hennemann 1983 |
| Falconiformes | | | | | | | | | | | | |
| Falconidae | | | | | | | | | | | | |
| Caracarinae | | | | | | | | | | | | |
| <i>Daptrius ater</i> | 362 | 4.32 | N | O | TR | F | O | O | O | O | O | Wasser 1986 |

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|---------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|----------------------------|
| Falconiformes | | | | | | | | | | | | |
| Falconidae | | | | | | | | | | | | |
| Falconinae | | | | | | | | | | | | |
| <i>Falco sparverius</i> | 116 | 2.38 | N | I | T | G | O | +/O | O | O | O | Wasser 1986 |
| <i>Falco tinnunculus</i> | 131 | 2.79 | N | V | T | G | O | +/O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Falco subbuteo</i> | 208 | 4.67 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Falco mexicanus</i> | 430 | 6.99 | N | V | T | D | O | O | O | O | O | Wasser 1986 |
| Accipitridae | | | | | | | | | | | | |
| Pandioninae | | | | | | | | | | | | |
| <i>Pandion haliaetus</i> | 1495 | 19.88 | N | V | T | L/W | O | O | O | O | O | Wasser 1986 |
| Accipitrinae | | | | | | | | | | | | |
| <i>Accipiter striatus</i> | 83 | 2.52 | N | V | T | F | O | + | O | O | O | Wasser 1986 |
| <i>Accipiter nisus</i> | 135 | 3.42 | N | V | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Ictinia mississippiensis</i> | 232 | 3.29 | N | FI | T | F | O | + | O | O | O | Wasser 1986 |
| <i>Accipiter cooperi</i> | 452 | 7.66 | N | V | T | F | O | +/O | O | O | O | Wasser 1986 |
| <i>Parabuteo unicinctus</i> | 572 | 5.07 | N | V | TR | D | O | O | O | O | O | Wasser 1986 |
| <i>Pernis apivorus</i> | 652 | 8.41 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Buteo lineatus</i> | 658 | 7.60 | N | V | T | F | O | O | O | O | O | Wasser 1986 |
| <i>Buteo buteo</i> | 1012 | 13.52 | N | V | T | G | O | + | O | O | O | Prinzinger & Hänssler 1980 |
| <i>Buteo jamaicensis</i> | 1475 | 11.43 | N | V | T | G | O | + | O | O | O | Wasser 1986 |
| <i>Aquila rapax</i> | 2398 | 16.27 | N | V | TR | G | O | O | O | O | O | Wasser 1986 |
| Gruiformes | | | | | | | | | | | | |
| Rallidae | | | | | | | | | | | | |
| <i>Atlantia rogersi</i> | 39.4 | 0.81 | N | O | T | G | O | O | S | O | + | Ryan et al. 1989 |
| <i>Porzana cinerea</i> | 47.9 | 1.78 | D/N | O | TR | W | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Crex crex</i> | 96 | 2.83 | N | O | T | G | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Gallirallus philippensis</i> | 171.7 | 3.51 | D/N | O | TR | G | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Gallirallus owstoni</i> | 198.8 | 3.30 | D/N | O | TR | F | O | O | S | O | + | McNab & Ellis 2006 |
| <i>Gallinula ventralis</i> | 309.2 | 5.81 | D/N | AV | T | W | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Aramides cajanea</i> | 374.3 | 5.55 | D/N | O | TR | F | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Fulica atra</i> | 412 | 7.36 | N | AV | T | L | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Gallinula tenebrosa</i> | 512.4 | 8.42 | D/N | AV | T | W | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Gallirallus australis</i> | 813.5 | 6.58 | D/N | O | T | F | O | O | L | O | + | McNab & Ellis 2006 |
| <i>Amaurornis ineptus</i> | 856.6 | 4.83 | N | O | TR | F | O | O | O | O | + | McNab & Ellis 2006 |
| <i>Porphyrio porphyrio</i> | 919.3 | 13.31 | D/N | AV | TR | W | O | O | O | O | O | McNab & Ellis 2006 |
| <i>Gallinula mortierii</i> | 954.4 | 11.47 | D/N | AV | T | G | O | O | O | O | + | McNab & Ellis 2006 |
| <i>Porphyrio hochstetteri</i> | 2758.3 | 24.79 | D | G | T | A | O | O | L | + | + | McNab & Ellis 2006 |
| <i>Turnix suscitator</i> | 58.1 | 1.39 | N | S | TR | G | O | O | O | O | O | Prinzinger et al. 1993 |
| Charadriiformes | | | | | | | | | | | | |
| Haematopodidae | | | | | | | | | | | | |
| <i>Haematopus ostralegus</i> | 554 | 10.48 | N | AI | T | M/L | O | + | O | O | O | Kersten & Piersma 1987 |
| Charadriidae | | | | | | | | | | | | |
| Pluvialinae | | | | | | | | | | | | |
| <i>Pluvialis apricaria</i> | 151 | 4.47 | N | AI | P | T | O | + | O | O | O | Daan et al. 1990 |
| <i>Pluvialis squatorola</i> | 226 | 6.41 | N | AI | P | T | O | + | O | O | O | Kersten & Piersma 1987 |
| <i>Charadrius dubius</i> | 36 | 1.50 | N | AI | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| Thinocoridae | | | | | | | | | | | | |
| <i>Thinocorus rumicivorus</i> | 55.5 | 1.12 | N | AI | T/TR | D | O | + | O | O | O | Ehlers & Morton 1982 |
| Jacanidae | | | | | | | | | | | | |
| <i>Jacana jacana</i> | 107.0 | 3.62 | N | AI | TR | W | O | O | O | O | O | Wiersma et al. 2007 |
| Scolopacidae | | | | | | | | | | | | |
| Scolopacinae | | | | | | | | | | | | |
| <i>Scolopax minor</i> | 156.7 | 3.85 | N | AI | T | F | O | + | O | O | O | Vander Haegen et al. 1994 |
| <i>Scolopax rusticola</i> | 430 | 7.78 | N | AI | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| Arenacinae | | | | | | | | | | | | |
| <i>Arenaria interpres</i> | 90 | 3.32 | N | AI | P | T/B | O | + | O | O | O | Kersten & Piersma 1987 |
| <i>Calidris canutus</i> | 130 | 3.17 | N | AI | P | T/B | O | + | O | O | O | Piersma et al. 1995 |
| Tringinae | | | | | | | | | | | | |
| <i>Tringa ochropus</i> | 90 | 3.32 | N | AI | T | F | O | + | O | O | O | Prinzinger & Hä |
| <i>Limosa lapponica</i> | 240 | 5.47 | N | AI | P | T | O | + | O | O | O | Daan et al. 1990 |
| Laridae | | | | | | | | | | | | |
| <i>Rhodostethia rosea</i> | 155 | 3.83 | N | AI | P | T | O | + | O | O | O | Gavrilov 1996 |
| <i>Rissa tridactyla</i> | 305 | 9.88 | N | AI | P | B | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Larus ridibundus</i> | 306 | 6.70 | N | AI | T | M/L | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Larus canus</i> | 431 | 8.10 | N | AI | T | M | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Larus argentatus</i> | 924 | 17.83 | N | O | T | M/L | O | + | O | O | O | Bryant & Furness 1995 |
| Stercorariidae | | | | | | | | | | | | |
| <i>Stercorarius parasiticus</i> | 351 | 8.29 | N | V | P | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Stercorarius skua</i> | 1159 | 22.42 | N | V | P | M | O | + | O | O | O | Bryant & Furness 1995 |

(continued on next page)

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|----------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|---------------------------|
| Charadriiformes | | | | | | | | | | | | |
| Alcidae | | | | | | | | | | | | |
| <i>Alle alle</i> | 152.5 | 7.40 | D/N | AI | P | P | O | + | O | O | O | Gabrielsen et al. 1991 |
| <i>Fratercula arctica</i> | 329 | 9.25 | N | V | T | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Cephus grille</i> | 342.2 | 10.92 | D/N | AI | P | M | O | + | O | O | O | Gabrielsen et al. 1991 |
| <i>Alca torda</i> | 589 | 12.96 | N | V/I | T | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Uria aalge</i> | 771 | 16.25 | N | V | T | M | O | + | O | O | O | Bryant & Furness 1995 |
| <i>Uria lomvia</i> | 819 | 18.25 | N | V/I | P | M | O | + | O | O | O | Bryant & Furness 1995 |
| Pteroclidiformes | | | | | | | | | | | | |
| Pteroclididae | | | | | | | | | | | | |
| <i>Pterocles orientalis</i> | 386.4 | 7.01 | N | S | T | G | O | O | O | O | O | Hinsley et al. 1993 |
| Columbiformes | | | | | | | | | | | | |
| Columbidae | | | | | | | | | | | | |
| Columbinae | | | | | | | | | | | | |
| <i>Oena capensis</i> | 36 | 0.88 | N | S | T/TR | G | O | +/O | O | O | O | Schleucher 2001 |
| <i>Geopelia cuneata</i> | 39 | 0.96 | N | S | T/TR | G | + | O | O | O | O | Schleucher & Withers 2002 |
| <i>Columbina inca</i> | 41.5 | 0.94 | D/N | S | T | F | O | O | O | O | O | MacMillen & Trost 1967 |
| <i>Columbina talpacoti</i> | 45.7 | 1.49 | N | S | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Geopelia placida</i> | 52 | 1.28 | N | S | T/TR | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Gallicolumba beccarii</i> | 68.8 | 1.92 | N | F/S | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Geophaps plumifera</i> | 81 | 1.52 | N | S | TR | G | O | O | O | O | O | Withers & Williams 1990 |
| <i>Zenaida macroura</i> | 91.4 | 2.33 | N | S | T | G | O | +/O | O | O | O | Hudson & Brush 1964 |
| <i>Geotrygon montana</i> | 107.3 | 2.43 | N | F/S | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Streptopelia senegalensis</i> | 108 | 3.05 | N | S | TR | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Chalcophaps indica</i> | 124 | 2.85 | N | S | TR | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Leptotila verreauxi</i> | 131 | 3.19 | N | S | T | F | O | O | O | O | O | Vleck & Vleck 1979 |
| <i>Streptopelia turtur</i> | 154 | 4.10 | N | S | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Streptopelia decaocto</i> | 170 | 3.42 | N | S | T | B | O | O | O | O | O | Daan et al. 1990 |
| <i>Ocyphaps lophotes</i> | 187 | 3.91 | N | S | T/TR | G | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Phaps elegans</i> | 190 | 4.46 | N | S | T | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Geophaps smithii</i> | 198 | 3.14 | N | S | TR | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Columba leucocephala</i> | 251.9 | 4.84 | N | F | TR | F | O | O | I | O | O | McNab 2000 |
| <i>Phaps histrionica</i> | 257 | 4.67 | N | S | T/TR | G | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Phaps chalcoptera</i> | 304 | 5.50 | N | S | T | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Columba livia</i> | 368 | 5.97 | N | S | T | B | O | O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Columba leucomela</i> | 456 | 8.77 | N | F/S | T/TR | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Columba vitiensis</i> | 467.9 | 5.20 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Leucosarcia melanoleuca</i> | 468.0 | 6.02 | N | F/S | T | F | O | O | O | O | O | McNab 2000 |
| <i>Caloenas nicobarica</i> | 613.0 | 6.53 | N | N/F | TR | F | O | O | S | O | O | McNab 2000 |
| Gourinae | | | | | | | | | | | | |
| <i>Goura cristata</i> | 2313.4 | 15.36 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| Treroninae | | | | | | | | | | | | |
| <i>Ptilinopus melanospila</i> | 98 | 1.76 | N | F | TR | F | O | O | O | O | O | Schleucher & Withers 2002 |
| <i>Ptilinopus superbus</i> | 120.4 | 2.72 | N | F | TR | F | O | O | O | O | O | Schleucher 2002 |
| <i>Ptilinopus perlatus</i> | 196.0 | 3.82 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Drepanoptila holosericea</i> | 198 | 2.97 | N | F | TR | F | + | O | I | O | O | Schleucher 2002 |
| <i>Gymnophaps albertsii</i> | 241.6 | 3.40 | N | F | TR | F | O | O | O | + | O | McNab 2000 |
| <i>Ducula pacifica</i> | 333.4 | 2.86 | N | F | TR | F | O | O | S | O | O | McNab 2000 |
| <i>Ducula radiata</i> | 333.6 | 5.06 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Ducula rufigaster</i> | 376.7 | 4.58 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Ducula pistrinaria</i> | 394.2 | 3.86 | N | F | TR | F | O | O | S | O | O | McNab 2000 |
| <i>Ducula rubricera</i> | 418.8 | 4.91 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Hemiphaga novaeseelandiae</i> | 435.6 | 6.78 | N | F/L | T | F | O | O | L | O | O | McNab 2000 |
| <i>Ducula spilorrhoa</i> | 453.6 | 4.94 | N | F | TR | F | O | O | S | O | O | McNab 2000 |
| <i>Ducula zoeae</i> | 456.2 | 6.13 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| <i>Ducula pinon</i> | 583.8 | 6.41 | N | F | TR | F | O | O | O | O | O | McNab 2000 |
| Psittaciformes | | | | | | | | | | | | |
| Psittacidae | | | | | | | | | | | | |
| Nestorinae | | | | | | | | | | | | |
| <i>Nestor meridionalis</i> | 369.3 | 7.71 | D | F/I | T | F | O | O | L | O | O | McNab & Salisbury 1995 |
| <i>Nestor notabilis</i> | 836.9 | 15.98 | D/N | F/L | T | A | O | O | L | + | O | McNab & Salisbury 1995 |
| Cacatuinae | | | | | | | | | | | | |
| <i>Nymphicus hollandicus</i> | 85.6 | 2.48 | N | S | T/TR | F | O | O | O | O | O | Kendeigh et al. 1997 |
| <i>Cacatua roseicapilla</i> | 268.7 | 4.50 | N | S | T/TR | F/G | O | O | O | O | O | Williams et al. 1991 |
| <i>Calyptorhynchus banksii</i> | 535.3 | 10.68 | N | N | TR | F | O | O | O | O | O | Williams et al. 1991 |
| <i>Cacatua tenuirostris</i> | 549.9 | 11.40 | N | S | T | F/G | O | O | O | O | O | Williams et al. 1991 |
| <i>Cacatua galerita</i> | 776.1 | 12.30 | N | S | T/TR | F | O | O | O | O | O | Williams et al. 1991 |

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|-------------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|--------------------------------|
| Psittaciformes | | | | | | | | | | | | |
| Psittacidae | | | | | | | | | | | | |
| Loriinae | | | | | | | | | | | | |
| <i>Trichoglossus haematodus</i> | 137.1 | 4.30 | N | P | TR | F | O | O | O | O | O | Williams et al. 1991 |
| Psittacinae | | | | | | | | | | | | |
| <i>Loriculus galgulus</i> | 27 | 1.86 | N | F | TR | F | O | O | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Melopsittacus undulatus</i> | 33.7 | 1.33 | N | S | T/TR | F | O | O | O | O | O | Weathers & Schoenbaechler 1976 |
| <i>Neopsephotus bourkii</i> | 40 | 1.94 | N | S | T | F/G | O | O | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Neophema pulchella</i> | 40 | 2.09 | N | F/S | T | F/G | O | O | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Agapornis roseicollis</i> | 48.1 | 1.67 | N | S | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Neophema petrophila</i> | 48.4 | 2.28 | N | S | T | F/G | O | O | O | O | O | Williams et al. 1991 |
| <i>Cyanorhamphus auriceps</i> | 52.9 | 1.77 | D/N | S/L | T | F | O | O | L | O | O | McNab & Salisbury 1995 |
| <i>Cyanorhamphus novaezelandiae</i> | 56.1 | 2.24 | D/N | F/L | T | F | O | O | L | O | O | McNab & Salisbury 1995 |
| <i>Agapornis fischeri</i> | 56.7 | 1.90 | N | S | T | F/G | O | O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Brotogeris jugularis</i> | 63.5 | 2.07 | N | F/S | TR | G | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Myiopsitta monachus</i> | 80.4 | 1.89 | N | S | T | F/G | O | O | O | O | O | Weathers & Caccamise 1978 |
| <i>Cyanorhamphus unicolor</i> | 129.4 | 3.89 | D/N | L | T | G | O | O | S | O | O | McNab & Salisbury 1995 |
| <i>Barnardius zonarius</i> | 131.8 | 2.85 | N | F/S | T | F | O | O | O | O | O | Williams et al. 1991 |
| Cuculiformes | | | | | | | | | | | | |
| Opisthocomidae | | | | | | | | | | | | |
| <i>Opisthocomus hoazin</i> | 598 | 5.76 | D/N | L | TR | F | O | O | O | O | O | Grajal 1991 |
| Cuculidae | | | | | | | | | | | | |
| Cuculinae | | | | | | | | | | | | |
| <i>Cuculus canorus</i> | 111.6 | 3.02 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Eudynamys scolopacea</i> | 188 | 5.92 | N | F | T/TR | F | O | +/O | O | O | O | Prinzinger & Hänsler 1980 |
| Centropinae | | | | | | | | | | | | |
| <i>Centropus senegalensis</i> | 175 | 5.43 | N | I | TR | F/G | O | O | O | O | O | Prinzinger & Hänsler 1980 |
| Neomorphae | | | | | | | | | | | | |
| <i>Geococcyx californicus</i> | 294.6 | 4.55 | N | I/L | T | D | O | O | O | O | O | Ohmart & Lasiewski 1971 |
| Strigiformes | | | | | | | | | | | | |
| Tytonidae | | | | | | | | | | | | |
| <i>Tyto alba</i> | 533.2 | 6.46 | D | V | T/TR | G | O | O | O | O | O | Edwards 1987 |
| <i>Tyto tenebriosa</i> | 770.0 | 10.36 | D | V | TR | F | O | O | O | O | O | McNab, pers. obs. |
| Strigidae | | | | | | | | | | | | |
| Striginae | | | | | | | | | | | | |
| <i>Otus scops</i> | 78.9 | 1.70 | D | I | T | F | O | + | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Otus trichopsis</i> | 99.8 | 1.50 | D | I | TR | F | O | O | O | O | O | Ligon 1969 |
| <i>Otus asio</i> | 165.5 | 2.16 | D | V/I | T | F | O | O | O | O | O | Ligon 1969 |
| <i>Strix occidentalis</i> | 571 | 9.63 | D | V | T | F | O | O | O | O | O | Ganey et al. 1993 |
| <i>Bubo virginianus</i> | 1000 | 15.62 | D | V | T/TR | F | O | O | O | O | O | Ganey et al. 1993 |
| <i>Nyctea scandiaca</i> | 2026 | 11.84 | D | V | P | T | O | + | O | O | O | Gessaman 1972 |
| Surniinae | | | | | | | | | | | | |
| <i>Micrathene whitneyi</i> | 45 | 0.91 | D | I | T | D | O | + | O | O | O | Ligon 1968 |
| <i>Glaucidium gnoma</i> | 52.0 | 1.67 | D | I | T/TR | F | O | O | O | + | O | Ligon 1969 |
| <i>Aegolius acadicus</i> | 118.1 | 2.25 | D | V | T | F | O | + | O | O | O | Ligon 1969 |
| <i>Aegolius funereus</i> | 130.0 | 4.07 | D | V | T | F | O | O | O | + | O | Hohtola et al. 1994 |
| <i>Athene cunicularia</i> | 146.7 | 2.80 | D | V/I | T | G | O | +/O | O | O | O | Coulombe 1970 |
| <i>Ninox theomacha</i> | 151.4 | 3.77 | D | I | TR | F | O | O | O | O | O | McNab, pers. obs. |
| <i>Uroglaux dimorpha</i> | 245.3 | 5.27 | D | V/I | TR | F | O | O | O | O | O | McNab, pers. obs. |
| Asioninae | | | | | | | | | | | | |
| <i>Asio otus</i> | 252 | 3.43 | D/N | V | T | F/G | O | +/O | O | O | O | Wijnandts 1984 |
| Caprimulgiformes | | | | | | | | | | | | |
| Podargidae | | | | | | | | | | | | |
| Podarginae | | | | | | | | | | | | |
| <i>Podargus ocellatus</i> | 145 | 2.04 | D | FI | TR | F | ? | O | O | O | O | Lasiewski et al. 1970 |
| <i>Podargus papuensis</i> | 314.6 | 3.85 | D | FI | TR | F | ? | O | O | O | O | McNab & Bonaccorso 1995 |
| <i>Podargus strigoides</i> | 380.3 | 3.72 | D | FI | T/TR | F | + | O | O | O | O | Bech & Nichol 1999 |
| Caprimulginae | | | | | | | | | | | | |
| Chordeilinae | | | | | | | | | | | | |
| <i>Chordeilus minor</i> | 72 | 1.59 | D | FI | T | G | + | + | O | O | O | Lasiewski & Dawson 1964 |
| Eurostopodinae | | | | | | | | | | | | |
| <i>Eurostopodus argus</i> | 88 | 1.47 | D | FI | T/TR | F/G | ? | O | O | O | O | Dawson & Fisher 1969 |
| <i>Eurostopodus mystacalis</i> | 162 | 1.73 | D | FI | T/TR | F | ? | +/O | O | O | O | McNab & Bonaccorso 1995 |
| Caprimulginae | | | | | | | | | | | | |
| <i>Phalaenoptilus nuttalli</i> | 40 | 0.64 | D | FI | T | D | HIB | +/O | O | O | O | Bartholomew et al. 1962 |
| <i>Caprimulgus macrurus</i> | 68.6 | 1.12 | D | FI | TR | F | ? | O | O | O | O | McNab & Bonaccorso 1995 |
| Apodiformes | | | | | | | | | | | | |
| Apodidae | | | | | | | | | | | | |
| <i>Collocalia esculenta</i> | 6.8 | 0.29 | N | FI | TR | F | + | O | O | O | O | McNab & Bonaccorso 1995 |
| <i>Collocalia vanikorensis</i> | 11.6 | 0.43 | N | FI | TR | F | ? | O | O | O | O | McNab & Bonaccorso 1995 |
| <i>Apus apus</i> | 44.9 | 1.57 | N | FI | T | D/G | + | + | O | O | O | Kendeigh et al. 1977 |

(continued on next page)

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|---------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|--------------------------------|
| Apodiformes | | | | | | | | | | | | |
| Trochilidae | | | | | | | | | | | | |
| <i>Sephanoides sephanoides</i> | 5.7 | 0.37 | N | P | T | F | (+) | + | 0 | 0 | 0 | Lopez-Calleja & Bozinovic 1995 |
| <i>Oreotrochilus estella</i> | 8.4 | 0.69 | N | P | TR | A | + | 0 | 0 | 0 | 0 | Carpenter 1976 |
| <i>Patagona gigas</i> | 19.1 | 1.03 | N | P | TR | G/A | + | +/0 | 0 | + | 0 | Lasiewski et al. 1967 |
| Coliiformes | | | | | | | | | | | | |
| Coliidae | | | | | | | | | | | | |
| <i>Colius colius</i> | 35.1 | 0.64 | N | F | T | F | + | 0 | 0 | 0 | 0 | McKechnie & Lovegrove 2001b |
| <i>Colius striatus</i> | 51 | 0.85 | N | F | TR | F | + | 0 | 0 | 0 | 0 | McKechnie & Lovegrove 2001a |
| <i>Urocolius macrourus</i> | 51.3 | 0.86 | N | F | TR | F | + | 0 | 0 | 0 | 0 | Prinzinger 1988 |
| <i>Colius castanotus</i> | 69 | 1.66 | N | F | TR | F | + | 0 | 0 | 0 | 0 | Prinzinger et al. 1981 |
| Coraciiformes | | | | | | | | | | | | |
| Alcedinidae | | | | | | | | | | | | |
| Alcedininae | | | | | | | | | | | | |
| <i>Alcedo atthis</i> | 34.3 | 1.36 | N | V | T/TR | W | +/0 | 0 | 0 | 0 | 0 | Kendeigh et al. 1977 |
| <i>Dacelo novaeguineae</i> | 336 | 4.02 | N | V/I | T/TR | G | 0 | 0 | 0 | 0 | 0 | Buttemer et al. 2003 |
| Cerylinae | | | | | | | | | | | | |
| <i>Chloroceryle aenea</i> | 11.8 | 0.63 | N | V/I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| Todidae | | | | | | | | | | | | |
| <i>Todus mexicanus</i> | 6.3 | 0.41 | N | I | TR | F | + | 0 | I | 0 | 0 | Merola-Zwartjes & Ligon 2000 |
| Momotidae | | | | | | | | | | | | |
| <i>Momotus momota</i> | 102.4 | 1.77 | N | I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| Meropidae | | | | | | | | | | | | |
| <i>Merops viridis</i> | 33.8 | 1.07 | N | I | TR | G | 0 | 0 | 0 | 0 | 0 | Bryant et al. 1984 |
| Upupidae | | | | | | | | | | | | |
| <i>Upupa epops</i> | 67.0 | 1.99 | N | I | T/TR | G | 0 | +/0 | 0 | 0 | 0 | Prinzinger & Hänsler 1980 |
| Phoeniculidae | | | | | | | | | | | | |
| <i>Phoeniculus purpureus</i> | 74.1 | 1.25 | N | I | TR | G | 0 | 0 | 0 | 0 | 0 | Boix-Hinzen & Lovegrove 1998 |
| Bucerotidae | | | | | | | | | | | | |
| <i>Rhyticeros plicatus</i> | 1781.6 | 16.33 | N | F | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| Gabuliformes | | | | | | | | | | | | |
| Bucconidae | | | | | | | | | | | | |
| <i>Notharchus macrorhynchos</i> | 43.2 | 1.14 | N | I | TR | G | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| Piciformes | | | | | | | | | | | | |
| Ramphastidae | | | | | | | | | | | | |
| Ramphastinae | | | | | | | | | | | | |
| <i>Aulacorhynchus sulcatus</i> | 131.7 | 2.44 | N | F/I | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Bailloni bailloni</i> | 133.0 | 2.53 | N | F | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Aulacorhynchus prasinus</i> | 174.7 | 2.99 | N | F/I | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Pteroglossus aracari</i> | 200.7 | 3.20 | N | F/I | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Ramphastos dicolorus</i> | 328.9 | 4.55 | N | F/V | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Ramphastos tucanus</i> | 420.3 | 6.15 | N | F/V | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| <i>Ramphastos toco</i> | 582.0 | 8.72 | N | F/V | TR | F | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| Lybiinae | | | | | | | | | | | | |
| <i>Trachyphonus darnaudii</i> | 36.6 | 0.79 | N | O | TR | G | 0 | 0 | 0 | 0 | 0 | McNab 2001 |
| Picidae | | | | | | | | | | | | |
| Jygninae | | | | | | | | | | | | |
| <i>Jynx toquilla</i> | 31.8 | 1.29 | N | I | T | F | 0 | + | 0 | 0 | 0 | Kendeigh et al. 1977 |
| Picinae | | | | | | | | | | | | |
| <i>Picoides pubescens</i> | 23.3 | 1.19 | N | I | T | F | 0 | + | 0 | 0 | 0 | Liknes & Swanson 1996 |
| <i>Melanerpes rubricapillus</i> | 48.7 | 1.93 | N | I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Ceelus loricatus</i> | 83.1 | 2.47 | N | I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Dendrocopus major</i> | 98 | 3.22 | N | I | T | F | 0 | 0 | 0 | 0 | 0 | Kendeigh et al. 1977 |
| Passeriformes | | | | | | | | | | | | |
| Pittidae | | | | | | | | | | | | |
| <i>Pitta versicolor</i> | 83.1 | 2.04 | D/N | I | T/TR | F | 0 | + | 0 | 0 | 0 | McNab pers obs |
| Pipridae | | | | | | | | | | | | |
| <i>Lepidothrix coronata</i> | 9.2 | 0.54 | N | F/I | TR | F | ? | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Pipra mentalis</i> | 12.3 | 0.70 | N | F/I | TR | F | + | 0 | 0 | 0 | 0 | Bartholomew et al. 1983 |
| <i>Manacus vitellinus</i> | 15.5 | 0.84 | N | F/I | TR | F | + | 0 | 0 | 0 | 0 | Bartholomew et al. 1983 |
| <i>Chiroxiphia lanceolata</i> | 18.4 | 1.22 | N | F | TR | F | ? | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| Cotingidae | | | | | | | | | | | | |
| <i>Phytotoma rara</i> | 41.6 | 2.06 | N | L/G | T | G | 0 | +/0 | 0 | 0 | 0 | Rezende et al. 2001 |
| Tyrannidae | | | | | | | | | | | | |
| Elaeniinae | | | | | | | | | | | | |
| <i>Todirostrum cinereum</i> | 7.3 | 0.61 | N | I | TR | B | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Mionectes oleagineus</i> | 10.3 | 0.59 | N | F | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Camptostoma obsoletum</i> | 12.5 | 0.95 | N | I | TR | B | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Cnipodectes subbrunneus</i> | 20.5 | 0.99 | N | I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |
| <i>Rhynchocyclus olivaceus</i> | 21.0 | 1.08 | N | I | TR | F | 0 | 0 | 0 | 0 | 0 | Wiersma et al. 2007 |

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|-------------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|-------------------------------|
| Tyrannidae | | | | | | | | | | | | |
| Fluvicolinae | | | | | | | | | | | | |
| <i>Empidonax virescens</i> | 12.3 | 0.64 | N | FI | T | F | O | + | O | O | O | Yarborough 1971 |
| <i>Contopus virens</i> | 13.9 | 0.93 | N | FI | T | F | O | + | O | O | O | Yarborough 1971 |
| <i>Sayornis phoebe</i> | 21.6 | 1.24 | N | FI | T | F | O | + | O | O | O | Yarborough 1971 |
| Tyranninae | | | | | | | | | | | | |
| <i>Myiarchus crinitus</i> | 33.9 | 1.38 | N | FI | T | F | O | + | O | O | O | Yarborough 1971 |
| <i>Tyrannus tyrannus</i> | 35.7 | 1.57 | N | FI | T | G | O | + | O | O | O | Yarborough 1971 |
| <i>Tyrannus melancholicus</i> | 38.0 | 1.31 | N | FI | TR | G | O | +/O | O | O | O | Wiersma et al. 2007 |
| <i>Myiodynastes maculatus</i> | 41.0 | 2.12 | N | FI | TR | F | O | +/O | O | O | O | Wiersma et al. 2007 |
| Furnariidae | | | | | | | | | | | | |
| <i>Xenops minutus</i> | 9.9 | 0.82 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| Dendrocolaptidae | | | | | | | | | | | | |
| <i>Glyphorhynchus spirurus</i> | 13.5 | 0.72 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Dendrocincla fuliginosa</i> | 39.0 | 1.77 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Xiphorhynchus guttatus</i> | 45.2 | 1.61 | N | I | TR | F | O | O | O | O | O | Vleck & Vleck 1979 |
| Thamnophilidae | | | | | | | | | | | | |
| <i>Myrmotherula axillaris</i> | 9.6 | 0.78 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Cercomacra tyrannina</i> | 15.4 | 0.68 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Hylophylax naevoides</i> | 16.1 | 0.86 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thamnophilus atrinuchus</i> | 20.5 | 1.01 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thamnophilus punctatus</i> | 21 | 1.24 | N | I | TR | F | O | O | O | O | O | Vleck & Vleck 1979 |
| <i>Thamnophilus doloiatus</i> | 26.2 | 1.03 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Mymeciza longipes</i> | 27.4 | 1.17 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Gymnopathys bicolor</i> | 27.7 | 1.20 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Myrmeciza exsul</i> | 28.3 | 1.04 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| Meliphagidae | | | | | | | | | | | | |
| <i>Lichmera indistincta</i> | 10.1 | 0.76 | N | P/I | T/TR | F | O | O | O | O | O | Vitali et al. 1999 |
| <i>Melithreptus lunatus</i> | 14.3 | 0.90 | N | I | T | F | O | O | O | O | O | Vitali et al. 1999 |
| <i>Phylidonyris melanops</i> | 18.8 | 1.05 | N | P/I | T | O | O | O | O | O | O | Vitali et al. 1999 |
| <i>Ptiloprora guisei</i> | 20.7 | 1.05 | N | F/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Lichenostomus virescens</i> | (25) | 1.07 | N | P/I | T/TR | D | O | O | O | O | O | Collins et al. 1980 |
| <i>Melipotes fumigatus</i> | 57.1 | 2.44 | N | F | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Melidectes rufocrissalis</i> | 62.8 | 2.80 | N | P/I | TR | B | O | O | O | + | O | McNab, pers. obs. |
| <i>Philemon buceroides</i> | 140.5 | 5.06 | N | O | TR | F | O | O | O | O | O | Bonaccorso & McNab pers. obs. |
| <i>Prothemadera novaeseelandiae</i> | 144.2 | 3.98 | D | F/I | T | F | O | O | L | O | O | McNab, pers. obs. |
| Pardalotidae | | | | | | | | | | | | |
| <i>Sericornis perspicillatus</i> | 8.8 | 0.78 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Sericornis papuensis</i> | 10.4 | 0.66 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Sericornis frontalis</i> | 11.0 | 0.66 | N | I | T/TR | B | O | O | O | O | O | Ambrose & Bradshaw 1988 |
| <i>Crateroscelis nigrorufa</i> | 14.6 | 0.74 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Sericornis nouhuysi</i> | 16.6 | 1.01 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Crateroscelis robusta</i> | 17.3 | 0.91 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Cinlosomatidae | | | | | | | | | | | | |
| <i>Ifrita kowaldi</i> | 28.9 | 1.13 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Rhipiduridae | | | | | | | | | | | | |
| <i>Rhipidura albolimbata</i> | 9.7 | 0.59 | N | FI | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Rhipidura atra</i> | 11.0 | 1.11 | N | FI | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Monarchidae | | | | | | | | | | | | |
| <i>Macheirhamphus nigripes</i> | 9.7 | 0.83 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Monarchus axillaris</i> | 17.5 | 1.81 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Petroicidae | | | | | | | | | | | | |
| <i>Microeca papuanus</i> | 12.5 | 1.11 | N | FI | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Peneothello sigillatus</i> | 21.6 | 1.12 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Peneothello cyanus</i> | 23.8 | 1.26 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Poecilodryas albonotata</i> | 36.4 | 1.62 | N | FI | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Pachycephalidae | | | | | | | | | | | | |
| <i>Eulacestoma nigropectus</i> | 19.9 | 1.24 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Pachycephala schlegelii</i> | 22.6 | 1.00 | N | F/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Pachycephala soror</i> | 23.3 | 1.31 | N | I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Pachycephala rufinucha</i> | 38.6 | 1.50 | N | F/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Pitohui nigrescens</i> | 70.5 | 2.27 | N | F/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Melanocharitidae | | | | | | | | | | | | |
| <i>Toxorhamphus poliopterus</i> | 13.2 | 0.69 | N | P/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Melanocharis versteri</i> | 13.6 | 0.88 | N | F/I | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Oreocharis arfaki</i> | 22.3 | 1.16 | N | F | TR | F | O | O | O | + | O | McNab, pers. obs. |
| <i>Paramythia montium</i> | 40.3 | 1.50 | N | F | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Laniidae | | | | | | | | | | | | |
| <i>Lanius collurio</i> | 27.0 | 1.38 | N | V/I | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Lanius excubitor</i> | 72.4 | 3.68 | N | V/I | T | O | O | +/O | O | O | O | Kendeigh et al. 1977 |
| Oriolidae | | | | | | | | | | | | |
| <i>Oriolus oriolus</i> | 64.9 | 2.34 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |

(continued on next page)

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|--|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|---------------------------|
| Tyrannidae | | | | | | | | | | | | |
| Corvidae | | | | | | | | | | | | |
| <i>Cyanocitta cristata</i> | 80.8 | 3.00 | N | O | T | O | O | O | O | O | O | Misch 1960 |
| <i>Nucifraga caryocatactes</i> | 147.0 | 4.85 | N | O | T | F | O | O | O | + | O | Kendeigh et al. 1977 |
| <i>Pica nuttalli</i> | 151.9 | 5.28 | N | O | T | O | O | O | O | O | O | Hayworth & Weathers 1984 |
| <i>Garrulus glandarius</i> | 153.0 | 4.99 | N | O | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Pica pica</i> | 158.9 | 4.31 | N | O | T | O | O | O | O | O | O | Hayworth & Weathers 1984 |
| <i>Corvus monedula</i> | 188 | 6.19 | N | O | T | O | O | O | O | O | O | Daan et al. 1990 |
| <i>Pyrrhocorax graculus</i> | 206.4 | 6.17 | N | O | T | O | O | O | O | + | O | Kendeigh et al. 1977 |
| <i>Corvus frugilegus</i> | 390.0 | 9.42 | N | O | T | F/O | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Corvus corone</i> | 518.0 | 11.93 | N | O | T | O | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Corvus ruficollis</i> | 660.0 | 12.23 | N | V/I | T | D | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Corvus corax</i> | 1203.0 | 19.80 | N | O | T | O | O | O | O | O | O | Kendeigh et al. 1977 |
| Artamidae | | | | | | | | | | | | |
| <i>Artamus maximus</i> | 60.0 | 1.99 | N | FI | TR | O | O | O | O | + | O | McNab, pers. obs. |
| Paradisaeidae | | | | | | | | | | | | |
| Cnemophilinae | | | | | | | | | | | | |
| <i>Cnemophilus loriae</i> | 78.1 | 2.38 | D/N+ | F | TR | F | O | O | O | + | O | McNab 2005 |
| <i>Cnemophilus macgregori</i> | 89.0 | 2.68 | N | F | TR | F | O | O | O | + | O | McNab, pers. obs. |
| Paradisaeinae | | | | | | | | | | | | |
| <i>Cicinnurus regius</i> | 54.0 | 2.10 | N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Lophorina superba</i> | 74.6 | 2.60 | D/N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Diphyllosdes^k magnificus</i> | 82.3 | 2.84 | N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Parotia lawesi</i> | 144.9 | 4.13 | N | F | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Astrapia stephaniae</i> | 148.2 | 5.80 | D/N | F/I | TR | F | O | O | O | + | O | McNab 2005 |
| <i>Paradisaea rudolphi</i> | 156.1 | 5.48 | N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Parotia wahnesi</i> | 164.2 | 4.64 | N | F | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Phonygamus^k keraudrenii</i> | 170.7 | 4.31 | N | F | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Manucodia chalybata</i> | 177.2 | 4.94 | N | F | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Ptiloris magnificus</i> | 179.4 | 5.40 | D/N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| <i>Epimachus meyeri</i> | 202.7 | 6.63 | D/N | F/I | TR | F | O | O | O | + | O | McNab 2005 |
| <i>Paradisaea raggiana</i> | 215.7 | 6.75 | D/N | F/I | TR | F | O | O | O | O | O | McNab 2005 |
| Bombycillidae | | | | | | | | | | | | |
| Bombycillinae | | | | | | | | | | | | |
| <i>Bombycilla garrulus</i> | 72.5 | 3.43 | N | F/I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| Paridae | | | | | | | | | | | | |
| <i>Parus caeruleus</i> | 9.6 | 0.60 | N | I/S | T | F | O | +/O | O | O | O | Lindström & Kvist 1995 |
| <i>Poecile atricapillus</i> | 10.3 | 0.91 | N | I/S | T | F/O | O | O | O | O | O | Rising & Hudson 1974 |
| <i>Parus ater</i> | 10.8 | 0.85 | N | I/S | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Parus montanus</i> | 11.6 | 0.99 | N | I/S | T | F | O | O | O | O | O | Reinertsen & Haftorn 1986 |
| <i>Parus major</i> | 16.5 | 1.26 | N | I/S | T | F | + | +/O | O | O | O | Reinertsen & Haftorn 1986 |
| Hirundinidae | | | | | | | | | | | | |
| <i>Tachycineta albilinea</i> | 11.7 | 0.90 | N | FI | TR | O | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Stegidopteryx ruficollis</i> | 11.9 | 0.57 | N | FI | TR | O | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Riparia riparia</i> | 13.6 | 0.84 | N | FI | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Hirundo tahitica</i> | 14.1 | 0.64 | N | FI | TR | O | O | O | O | O | O | Bryant et al. 1984 |
| <i>Tachycineta bicolor</i> | 16.4 | 1.03 | N | FI | TR | O | O | + | O | O | O | Wiersma et al. 2007 |
| <i>Delichon urbica</i> | 18.0 | 0.46 | N | FI | T | O | + | + | O | O | O | Prinzinger & Hänsler 1980 |
| <i>Hirundo rustica</i> | 18.4 | 1.08 | N | FI | T | O | + | + | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Progne chalybea</i> | 34.9 | 1.68 | N | FI | TR | O | O | +/O | O | O | O | Wiersma et al. 2007 |
| Aegithalidae | | | | | | | | | | | | |
| <i>Psaltriparus minimus</i> | 5.5 | 0.46 | N | I/S | T | F/O | O | O | O | O | O | Chaplin 1982 |
| <i>Aegithalos caudatus</i> | 8.9 | 0.72 | N | I | T | F | O | +/O | O | O | O | Gavrilov & Dol'nik 1985 |
| Alaudidae | | | | | | | | | | | | |
| <i>Eremalauda dunni</i> | 20.6 | 1.00 | N | I/S | TR | B | O | O | O | O | O | Tieleman et al. 2002 |
| <i>Lullula arborea</i> | 25.5 | 2.06 | N | I | T | B | O | +/O | O | O | O | Tieleman et al. 2002 |
| <i>Eremophila alpestris</i> | 26.0 | 1.19 | N | I | T | B/G | O | +/O | O | O | O | Trost 1972 |
| <i>Certhilauda erythroclamys</i> | 27.3 | 1.50 | N | I | T | D | O | O | O | O | O | Williams 1999 |
| <i>Alauda arvensis</i> | 31.7 | 2.60 | N | I/S | T | G | O | + | O | O | O | Tieleman et al. 2002 |
| <i>Alaemon alaudipes</i> | 37.7 | 1.54 | N | I | T | D | O | O | O | O | O | Tieleman et al. 2002 |
| Pycnonotidae | | | | | | | | | | | | |
| <i>Phyllastrephus hypochloris</i> | 18.9 | 0.95 | N | I | TR | F | O | O | O | + | O | Seavy & McNab 2007 |
| <i>Andropodus curvirostris</i> | 23.0 | 1.06 | N | F | TR | F | O | O | O | O | O | Seavy & McNab 2007 |
| <i>Andropodus virens</i> | 24.2 | 1.19 | N | F | TR | F | O | O | O | O | O | Seavy & McNab 2007 |
| <i>Andropodus latirostris</i> | 26.6 | 1.30 | N | F | TR | F | O | O | O | O | O | Seavy & McNab 2007 |
| <i>Pycnonotus barbatus</i> | 40.3 | 1.72 | N | F | TR | F | O | O | O | O | O | Seavy & McNab 2007 |
| Sylviidae | | | | | | | | | | | | |
| Acrocephalinae | | | | | | | | | | | | |
| <i>Acrocephalus palustris</i> | 10.8 | 0.73 | N | I | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Acrocephalus schoenobaenus</i> | 11.5 | 0.78 | N | I | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Hippolais icterina</i> | 12.5 | 1.69 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|---|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|-------------------------|
| Sylviidae | | | | | | | | | | | | |
| Phylloscopinae | | | | | | | | | | | | |
| <i>Phylloscopus collybita</i> | 8.2 | 0.59 | N | I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Phylloscopus sibilatrix</i> | 9.2 | 0.63 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Phylloscopus trochilus</i> | 10.7 | 0.75 | N | I | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| Sylviinae | | | | | | | | | | | | |
| <i>Sylvia curruca</i> | 10.6 | 0.72 | N | I | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Sylvia nisoria</i> | 21.3 | 1.38 | N | I | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Sylvia atricapilla</i> | 21.9 | 1.50 | N | I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Sylvia borin</i> | 24.8 | 1.50 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| Zosteropidae | | | | | | | | | | | | |
| <i>Zosterops lateralis</i> | 11.8 | 0.58 | N | O | T/TR | B | O | O | O | O | O | Maddocks & Geiser 1997 |
| Regulidae | | | | | | | | | | | | |
| <i>Regulus regulus</i> | 5.5 | 0.66 | N | I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| Troglodytidae | | | | | | | | | | | | |
| <i>Troglodytes troglodytes</i> | 8.9 | 0.60 | N | I | T | F | O | +/O | O | O | O | Lindström & Kvist 1995 |
| <i>Troglodytes aedon</i> | 10.2 | 0.75 | N | I | T | O | O | + | O | O | O | Wiersma et al. 2007 |
| <i>Troglodytes musculus</i> | 13.3 | 0.76 | N | I | TR | O | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thryothorus ludovicianus</i> | 14.9 | 1.29 | N | I | T | F | O | O | O | O | O | Eberhardt 1994 |
| <i>Thryothorus leucotis</i> | 18.0 | 0.76 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thryothorus rufalbus</i> | 22.6 | 1.07 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thryothorus fasciatoventris</i> | 27.2 | 1.12 | N | I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| Sittidae | | | | | | | | | | | | |
| <i>Sitta carolinensis</i> | 18.3 | 1.04 | N | I/S | T | F | O | O | O | O | O | Liknes & Swanson 1996 |
| Sturnidae | | | | | | | | | | | | |
| <i>Sturnus vulgaris</i> | 75.0 | 3.16 | N | O | T | O | O | O | O | O | O | Kendeigh et al. 1977 |
| Turdidae | | | | | | | | | | | | |
| Myiadestinae | | | | | | | | | | | | |
| <i>Sialia mexicana</i> | 27.5 | 1.52 | N | F/I | T | F | O | +/O | O | O | O | Mock 1991 |
| Turdinae | | | | | | | | | | | | |
| <i>Turdus iliacus</i> | 58.0 | 2.60 | N | F/I | T | F/O | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Turdus migratorius</i> | 62.4 | 2.74 | N | F/I | T | F/B | O | +/O | O | O | O | Wiersma et al. 2007 |
| <i>Turdus philomelos</i> | 62.8 | 2.61 | N | F/I | T | F | O | +/O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Turdus poliocephalus</i> | 66.1 | 2.56 | N | F/I | TR | F/O | O | O | O | + | O | McNab, pers. ob. |
| <i>Turdus grayi</i> | 77.9 | 2.44 | N | F/I | TR | F/O | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Turdus merula</i> | 82.6 | 3.34 | N | I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Turdus viscivorus</i> | 108.2 | 3.97 | N | F/I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| Saxicolinae | | | | | | | | | | | | |
| <i>Phoenicurus phoenicurus</i> | 13.0 | 0.84 | N | F/I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Phoenicurus ochruros</i> | 13.8 | 0.87 | N | F/I | T | O | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Saxicola rubetra</i> | 14.3 | 0.87 | N | I | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Tarsiger cyanurus</i> | 14.8 | 0.85 | N | I | T | F | O | + | O | + | O | Gavrilov & Dol'nik 1985 |
| <i>Saxicola torquata</i> | 16.5 | 0.92 | N | I | TR | D | O | +/O | O | O | O | Klaassen 1995 |
| <i>Erithacus rubecula</i> | 17.6 | 1.01 | N | F/I | T | F | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Luscinia svecica</i> | 20.8 | 1.29 | N | I | T | F/O | O | + | O | + | O | Kendeigh et al. 1977 |
| Mimidae | | | | | | | | | | | | |
| <i>Mimus polyglottus</i> | 44.2 | 2.44 | N | O | T | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Mimus gilvus</i> | 68.9 | 2.66 | N | O | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| Muscicapidae | | | | | | | | | | | | |
| <i>Ficedula hypoleuca</i> | 11.7 | 0.84 | N | I | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Muscicapa striata</i> | 14.4 | 0.89 | N | I | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| Nectariniidae | | | | | | | | | | | | |
| <i>Aethopyga christinae</i> | 5.2 | 0.48 | N | S | TR | F | O | O | O | O | O | Prinzinger et al. 1989 |
| <i>Cinnyris^k minimus</i> | 5.5 | 0.42 | N | P/I | TR | F | O | O | O | O | O | Seavy 2006 |
| <i>Cinnyris^k bifasciatus</i> | 6.2 | 0.33 | N | P/I | TR | B | O | +/O | O | O | O | Prinzinger et al. 1989 |
| <i>Cinnyris^k reichenowii^k</i> | 6.7 | 0.51 | N | P/I | TR | F | O | +/O | O | + | O | Seavy 2006 |
| <i>Cinnyris^k chloropygius</i> | 6.8 | 0.50 | N | P/I | TR | B | O | +/O | O | O | O | Seavy 2006 |
| <i>Aethopyga siparaja</i> | 6.8 | 0.53 | N | P/I | TR | F | O | +/O | O | O | O | Prinzinger et al. 1989 |
| <i>Cinnyris^k venustus</i> | 7.1 | 0.50 | N | P/I | TR | F | O | +/O | O | + | O | Prinzinger et al. 1989 |
| <i>Hedydipna^k collaris</i> | 8.3 | 0.61 | N | I | TR | F | O | O | O | O | O | Prinzinger et al. 1989 |
| <i>Cyanomitra^k veroxii</i> | 8.4 | 0.48 | N | I | TR | F | O | O | O | O | O | Prinzinger et al. 1989 |
| <i>Cinnyris^k cupreus</i> | 9.0 | 0.59 | N | P/I | TR | F/O | O | +/O | O | O | O | Seavy 2006 |
| <i>Chalcomitra^k adelberti</i> | 9.5 | 0.63 | N | P/I | TR | F | O | O | O | O | O | Prinzinger et al. 1989 |
| <i>Chalcomitra^k amethystina</i> | 10.0 | 0.63 | N | P/I | TR | F | O | +/O | O | O | O | Prinzinger et al. 1989 |
| <i>Chalcomitra^k rubescens</i> | 10.0 | 0.66 | N | P/I | TR | F | O | O | O | O | O | Seavy 2006 |
| <i>Chalcomitra^k obscura</i> | 11.2 | 0.72 | N | P/I | TR | F | O | O | O | O | O | Seavy 2006 |
| <i>Antheptes orientalis</i> | 11.8 | 0.55 | N | P/I | TR | O | O | O | O | O | O | Prinzinger et al. 1989 |
| <i>Nectarinia tacaze</i> | 13.5 | 0.88 | N | P/I | TR | O | + | O | O | + | O | Prinzinger et al. 1989 |
| <i>Chalcomitra^k senegalensis</i> | 13.7 | 0.86 | N | P/I | TR | F/O | O | +/O | O | O | O | Seavy 2006 |
| <i>Cyanomitra^k verticalis</i> | 14.1 | 0.90 | N | P/I | TR | F | O | O | O | O | O | Seavy 2006 |

(continued on next page)

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor ^g | Migration ^g | Islands ^h | Mountains ⁱ | Flightless ^j | Reference |
|---------------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|---------------------|------------------------|----------------------|------------------------|-------------------------|-----------------------------|
| Turdidae | | | | | | | | | | | | |
| Nectariniidae | | | | | | | | | | | | |
| <i>Cyanomitra</i> ^k | 15.8 | 0.98 | N | P/I | TR | F | O | O | O | O | O | Seavy 2006 |
| <i>cyanolema</i> | | | | | | | | | | | | |
| <i>Nectarinia kilimensis</i> | 16.2 | 0.94 | N | P/I | TR | F | O | O | O | + | O | Seavy 2006 |
| Passeridae | | | | | | | | | | | | |
| <i>Erythrura trichroa</i> | 15.1 | 0.86 | N | F/S | TR | B | O | O | O | + | O | McNab, pers. obs. |
| <i>Oreostruthus fuliginosus</i> | 16.0 | 0.59 | N | F/S | TR | B | O | O | O | + | O | McNab, pers. obs. |
| <i>Passer montanus</i> | 22.3 | 1.46 | N | I/S | T | O | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Passer domesticus</i> | 23.0 | 1.32 | N | S/L | T | O | O | O | O | O | O | Kendeigh et al. 1977 |
| Estrildidae | | | | | | | | | | | | |
| Estrildinae | | | | | | | | | | | | |
| <i>Estrilda melpoda</i> | 7.5 | 0.47 | N | I/S | TR | O | O | O | O | O | O | Marschall & Prinzinger 1991 |
| <i>Estrilda troglodytes</i> | 7.5 | 0.54 | N | S | TR | O | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Uraeginthus bengalis</i> | 9.2 | 0.59 | N | S | TR | F/O | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Chloebia gouldiae</i> | 15.5 | 0.78 | N | S | T | G | O | O | O | O | O | Marschall & Prinzinger 1991 |
| <i>Amadina fasciata</i> | 17.2 | 0.77 | N | S/I | T/TR | O | O | O | O | O | O | Marschall & Prinzinger 1991 |
| <i>Amadina erythrocephala</i> | 21.7 | 0.76 | N | S/I | T/TR | G | O | O | O | O | O | McKechnie & Lovegrove 2003 |
| Poepphilinae | | | | | | | | | | | | |
| <i>Taeniopygia guttata</i> | 11.7 | 0.74 | N | I/L | T/TR | O | O | O | O | O | O | Calder 1964 |
| Lonchurinae | | | | | | | | | | | | |
| <i>Lonchura fuscans</i> | 9.5 | 0.36 | N | S | TR | O | O | O | O | O | O | Weathers 1977 |
| <i>Lonchura striata</i> | 10.3 | 0.77 | N | S | TR | B | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Lonchura^k cucullata</i> | 10.6 | 0.39 | N | S | T/TR | O | O | O | O | O | O | Lovegrove & Smith 2003 |
| <i>Lonchura^k oryzivora</i> | 25.4 | 1.11 | N | O | T | F/G | O | O | O | O | O | Marschall & Prinzinger 1991 |
| Prunellidae | | | | | | | | | | | | |
| <i>Prunella modularis</i> | 16.8 | 1.17 | N | I | T | B | O | +O | O | O | O | Kendeigh et al. 1977 |
| Motacillidae | | | | | | | | | | | | |
| <i>Motacilla flava</i> | 14.7 | 0.93 | N | I | T | G | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Motacilla alba</i> | 18.0 | 1.08 | N | I | T | O | O | +O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Anthus pratensis</i> | 18.9 | 1.08 | N | I | T | O | O | +O | O | O | O | Kendeigh et al. 1977 |
| <i>Anthus trivialis</i> | 19.7 | 1.22 | N | I | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Anthus campestris</i> | 21.8 | 1.38 | N | I | T | O | O | + | O | O | O | Kendeigh et al. 1977 |
| Fringillidae | | | | | | | | | | | | |
| Fringillinae | | | | | | | | | | | | |
| <i>Fringilla coelebs</i> | 21.0 | 1.34 | N | S | T | F | O | +O | O | O | O | Gavrilov & Dol'nik 1985 |
| <i>Fringilla montifringilla</i> | 21.0 | 1.38 | N | O | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| Carduelinae | | | | | | | | | | | | |
| <i>Carduelis tristis</i> | 12.8 | 1.09 | N | S | T | F/O | O | +O | O | O | O | Dawson & Carey 1976 |
| <i>Carduelis spinus</i> | 14.0 | 1.05 | N | S | T | F | O | +O | O | O | O | Kendeigh et al. 1977 |
| <i>Carduelis flammea</i> | 14.7 | 1.25 | N | S | P | O | O | + | O | O | O | Reinertsen & Haftorn 1986 |
| <i>Carduelis carduelis</i> | 16.5 | 1.25 | N | S | T | O | O | +O | O | O | O | Kendeigh et al. 1977 |
| <i>Carduelis cannabina</i> | 16.9 | 1.22 | N | S | T | B | O | +O | O | O | O | Kendeigh et al. 1977 |
| <i>Carpodacus mexicanus</i> | 20.4 | 1.12 | N | S | T | O | O | O | O | O | O | Weathers 1981 |
| <i>Carpodacus erythrinus</i> | 21.2 | 1.33 | N | S/L | T | B | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Carpodacus cassinii</i> | 27.4 | 1.22 | N | S | T | F | O | +O | O | + | O | Weathers 1981 |
| <i>Carduelis chloris</i> | 28.2 | 1.71 | N | S | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Loxia leucoptera</i> | 29.8 | 1.67 | N | S | T | F | O | +O | O | + | O | Dawson & Tordoff 1964 |
| <i>Pyrrhula pyrrhula</i> | 30.4 | 1.99 | N | L | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Loxia curvirostra</i> | 39.4 | 2.16 | N | S | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Coccothraustes coccothraustes</i> | 48.3 | 2.51 | N | O | T | F | O | O | O | O | O | Kendeigh et al. 1977 |
| <i>Loxia pytyopsittacus</i> | 53.7 | 2.87 | N | S | T | F | O | + | O | O | O | Kendeigh et al. 1977 |
| <i>Coccothraustes vespertina</i> | 54.5 | 2.71 | N | S/N | T | F | O | +O | O | + | O | West & Hart 1966 |
| <i>Pinicola enucleator</i> | 78.4 | 3.91 | N | L | T | F | O | +O | O | + | O | Gavrilov & Dol'nik 1985 |
| Drepanidinae | | | | | | | | | | | | |
| <i>Himatione sanguinea</i> | 13.5 | 1.08 | N | P | TR | F | O | O | I | O | O | Weathers et al. 1983 |
| <i>Telespiza cantans</i> | 31.6 | 1.53 | N | O | TR | G | O | O | I | O | O | Weathers & van Riper 1982 |
| <i>Loxioides bailleui</i> | 34.8 | 1.61 | N | S | TR | F | O | O | I | O | O | Weathers & van Riper 1982 |
| Vireonidae | | | | | | | | | | | | |
| <i>Vireo flavoviridis</i> | 15.9 | 1.01 | N | I | TR | B | O | + | O | O | O | Wiersma et al. 2007 |
| <i>Vireo olivaceus</i> | 16.2 | 0.86 | N | I | T | B | O | + | O | O | O | Wiersma et al. 2007 |
| Parulidae | | | | | | | | | | | | |
| <i>Vermivora pinus</i> | 7.8 | 0.54 | N | I | T | F/O | O | + | O | O | O | Yarbrough 1971 |
| <i>Dendroica palmarum</i> | 9.8 | 0.56 | N | I | T | O | O | + | O | O | O | Yarbrough 1971 |
| <i>Dendroica dominica</i> | 9.8 | 0.58 | N | I | T | F | O | + | O | O | O | Yarbrough 1971 |
| <i>Dendroica coronata</i> | 11.5 | 0.68 | N | F/I | T | F | O | + | O | O | O | Yarbrough 1971 |
| <i>Dendroica pinus</i> | 12.0 | 0.64 | N | I | T | F | O | +O | O | O | O | Yarbrough 1971 |
| <i>Dendroica petechia</i> | 12.2 | 0.50 | N | I | TR | F | O | + | O | O | O | Wiersma et al. 2007 |
| <i>Protonotaria citrea</i> | 12.8 | 0.72 | N | I | T | F | O | + | O | O | O | Yarbrough 1971 |

Appendix A (continued)

| Species | Mass ^a (g) | BMR (kJ/h) | Time ^b | Food ^c | Climate ^d | Habitat ^e | Torpor? ^f | Migration ^g | Islands? ^h | Mountains? ⁱ | Flightless? ^j | Reference |
|----------------------------------|-----------------------|------------|-------------------|-------------------|----------------------|----------------------|----------------------|------------------------|-----------------------|-------------------------|--------------------------|--------------------------|
| Estrildidae | | | | | | | | | | | | |
| Parulidae | | | | | | | | | | | | |
| <i>Seiurus novaeboracensis</i> | 18.7 | 1.01 | N | I | T | F | O | + | O | O | O | Yarborough 1971 |
| <i>Seiurus aurocapillus</i> | 19.0 | 0.87 | N | I | T | F | O | + | O | O | O | Yarborough 1971 |
| Icteridae | | | | | | | | | | | | |
| <i>Icterus bullocki</i> | 34 | 1.81 | N | F/I | T | F | O | + | O | O | O | Rising 1969 |
| <i>Icterus galbula</i> | 34 | 1.81 | N | F/I | T | F | O | + | O | O | O | Rising 1969 |
| <i>Sturnella militaris</i> | 38.2 | 1.59 | N | I | TR | G | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Agelaius phoeniceus</i> | 43.1 | 1.74 | N | I/S | T | W | O | +/O | O | O | O | Weathers 1981 |
| <i>Quiscalus quiscula</i> | 92.2 | 3.56 | N | O | T | B | O | +/O | O | O | O | Wiersma et al. 2007 |
| <i>Quiscalus mexicanus</i> | 137.3 | 4.06 | N | O | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| Coerebidae | | | | | | | | | | | | |
| <i>Coereba flaveola</i> | 10.0 | 0.77 | N | P | TR | F | O | O | I | O | O | Merola-Zwartjes 1998 |
| Thraupidae | | | | | | | | | | | | |
| <i>Cyanerpes cyaneus</i> | 13.5 | 0.98 | N | F/P | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Euphonia laniirostris</i> | 13.5 | 1.06 | N | F | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Tanagra larvata</i> | 16.2 | 0.85 | N | F/I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Rhamphocelus dimidiatus</i> | 26.4 | 1.32 | N | F/I | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thraupis episcopus</i> | 30.4 | 1.44 | N | F/I | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Eucometis penicillata</i> | 30.7 | 1.42 | N | F/I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Rhamphocelus flammigerus</i> | 32.0 | 1.50 | N | F/I | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Thraupis palmarum</i> | 32.6 | 1.42 | N | F/I | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Habia fuscicauda</i> | 40.0 | 1.28 | N | F/I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| Emberizidae | | | | | | | | | | | | |
| <i>Sporophila americana</i> | 10.2 | 0.71 | N | S | TR | O | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Amphispiza bilineata</i> | 11.6 | 0.71 | N | I/S | T | D | O | +/O | O | O | O | Weathers 1981 |
| <i>Spizella passerina</i> | 11.9 | 0.70 | N | I/S | T | F | O | + | O | O | O | Yarborough 1971 |
| <i>Oryzoborus angolensis</i> | 12.3 | 0.72 | N | S | TR | B | O | + | O | O | O | Wiersma et al. 2007 |
| <i>Ammodramus savannarum</i> | 13.8 | 0.64 | N | I/S | T | G | O | + | O | O | O | Yarborough 1971 |
| <i>Melospiza georgiana</i> | 14.9 | 0.76 | N | I/S | T | B | O | + | O | O | O | Yarborough 1971 |
| <i>Passerculus sandwichensis</i> | 15.9 | 0.80 | N | I/S | T | G | O | + | O | O | O | Williams & Hansell 1981 |
| <i>Emberiza schoeniclus</i> | 17.6 | 1.08 | N | S | T | O | O | +/O | O | O | O | Kendeigh et al. 1977 |
| <i>Melospiza melodia</i> | 19.1 | 0.90 | N | I/S | T | B | O | + | O | O | O | Yarborough 1971 |
| <i>Zonotrichia albicollis</i> | 20.2 | 1.00 | N | F/S | T | B | O | + | O | O | O | Yarborough 1971 |
| <i>Pooectes gramineus</i> | 21.5 | 0.98 | N | I/S | T | G | O | + | O | O | O | Yarborough 1971 |
| <i>Emberiza hortulana</i> | 24.3 | 1.50 | N | I | T | O | O | + | O | O | O | Gavrillov & Dol'nik 1985 |
| <i>Zonotrichia leucophrys</i> | 26.1 | 1.21 | N | F/S | T | B | O | + | O | O | O | Yarborough 1971 |
| <i>Emberiza citrinella</i> | 26.8 | 1.57 | N | S | T | O | O | +/O | O | O | O | Gavrillov & Dol'nik 1985 |
| <i>Zonotrichia querula</i> | 33.3 | 1.77 | N | I/S | T | B | O | + | O | O | O | Yarborough 1971 |
| <i>Arremonops conirostris</i> | 39.7 | 1.63 | N | S | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| Cardinalidae | | | | | | | | | | | | |
| <i>Cyanocopsa cyanoides</i> | 27.9 | 1.35 | N | F/S | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Cardinalis sinuatus</i> | 32.0 | 1.41 | N | I/S | T | B | O | O | O | O | O | Hinds & Calder 1973 |
| <i>Saltator orenocensis</i> | 32.7 | 1.13 | N | F/L | TR | B | O | O | O | O | O | Bosque et al. 1999 |
| <i>Cardinalis cardinalis</i> | 41.0 | 1.81 | N | I/S | T | B | O | O | O | O | O | Hinds & Calder 1973 |
| <i>Saltator striatipectus</i> | 42.1 | 1.83 | N | F/I | TR | B | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Saltator maximus</i> | 44.8 | 1.97 | N | F/I | TR | F | O | O | O | O | O | Wiersma et al. 2007 |
| <i>Saltator coerulescens</i> | 47.0 | 1.40 | N | F/L | TR | B | O | O | O | O | O | Bosque et al. 1999 |

^aMass: (), intermediate within mass range.

^bTime of measurement: D, daytime in nocturnal species; N, night in diurnal species; D/N, rates equal day and night.

^cFood: A, aquatic invertebrates; AV, aquatic vegetation; F, fruit; Fl, flying insects; G, grass; L, leaves; I, insects and arthropods; N, nuts; O, omnivore; P, pollen and nectar; S, seeds; V, vertebrates.

^dClimate: P, polar; T, temperate; TR, tropical.

^eHabitat: A, alpine; B, bare or disturbed grounds, brush; D, desert; F, forests, woodlands; G, grasslands and savannahs; L, lakes; M, marine; O, open; P, pelagic; T, tundra; W, wetlands.

^fTorpor?: O, no torpor; +, torpor; HIB, hibernation.

^gMigration?: O, no; +, yes.

^hIslands?: S, small island; I, intermediate island; L, large island; O, not an island endemic.

ⁱMountains?: +, mountain endemic; O, not a mountain endemic.

^jFlightless?: +, yes; O, no.

^kGeneric or specific name changes from the original report.

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