BRIEF COMMUNICATION

Associations between Resting, Activity, and Daily Metabolic Rate in Free-Living Endotherms: No Universal Rule in Birds and Mammals

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ABSTRACT

Energy management models provide theories and predictions for how animals manage their energy budgets within their energetic constraints, in terms of their resting metabolic rate (RMR) and daily energy expenditure (DEE). Thus, uncovering what associations exist between DEE and RMR is key to testing these models. Accordingly, there is considerable interest in the relationship between DEE and RMR at both inter- and intraspecific levels. Interpretation of the evidence for particular energy management models is enhanced by also considering the energy spent specifically on costly activities (activity energy expenditure [AEE] = DEE − RMR). However, to date there have been few intraspecific studies investigating such patterns. Our aim was to determine whether there is a generality of intraspecific relationships among RMR, DEE, and AEE using long-term data sets for bird and mammal species. For mammals, we use minimum heart rate (f_H), mean f_H, and activity f_H as qualitative proxies for RMR, DEE, and AEE, respectively. For the birds, we take advantage of calibration equations to convert f_H into rate of oxygen consumption in order to provide quantitative proxies for RMR, DEE, and AEE. For all 11 species, the DEE proxy was significantly positively correlated with the RMR proxy. There was also evidence of a significant positive correlation between AEE and RMR in all four mammal species but only in some of the bird species. Our results indicate there is no universal rule for birds and mammals governing the relationships among RMR, AEE, and DEE. Furthermore, they suggest that birds tend to have a different strategy for managing their energy budgets from those of mammals and that there are also differences in strategy between bird species. Future work in laboratory settings or highly controlled field settings can tease out the environmental and physiological processes contributing to variation in energy management strategies exhibited by different species.

Keywords: energy management model, energy expenditure, heart rate, intraspecific, oxygen consumption.

Introduction

Knowledge of energy budgets underlies our understanding of processes operating at every level of biological organization from the subcellular to entire communities. At the whole-organism

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level, energy use is typically quantified in terms of daily energy expenditure (DEE; a proxy for the total amount of energy used by an animal during a typical day of typical activities in the field) or basal metabolic rate (BMR; the metabolic rate of an inactive adult nonreproductive, postabsorptive endotherm in its thermoneutral zone). Data for rates of energy expenditure, including DEE and BMR, are now available for more than 1,000 species of birds and mammals (McNab 2008, 2009; Speakman and Król 2010). At the intraspecific (interindividual) level, these rates of energy expenditure have been related to other measures such as behavior, reproductive output, fitness, and survival (Jackson et al. 2001; Blackmer et al. 2005; Bochdansky et al. 2005; Artacho and Nespolo 2009; Boratyński et al. 2010; Larivée et al. 2010). Meanwhile, at the interspecific level, variation in these rates has been hypothesized to underlie a range of ecological patterns (Allen et al. 2002; Brown et al. 2004; Meehan et al. 2004; Meehan 2006; Buckley et al. 2008; Munch and Salinas 2009). As such, there has been considerable interest in the effect of broadscale environmental characteristics on both DEE and BMR (e.g., McNab and Morrison 1963; Mueller and Diamond 2001; Lovegrove 2003; Anderson and Jetz 2005; Humphries et al. 2005; Jetz et al. 2007; White et al. 2007; Speakman and Król 2010). For example, these interspecific comparative studies have revealed that both BMR and DEE are negatively associated with mean habitat temperature.

There is also interest in the relationship between DEE and BMR (Daan et al. 1990; Koteja 1991; Ricklefs et al. 1996; White and Seymour 2004). Once the effect of body mass is accounted for, BMR and DEE are positively correlated across eutherian mammals but not significantly correlated across birds or across marsupials (Koteja 1991; Ricklefs et al. 1996; White and Seymour 2004). Intraspecific studies of the relationship between DEE and BMR are less common because both of these quantities have been measured on the same individuals only for a small number of species. Collectively, these investigations yielded equivocal results regarding the relationship between DEE and BMR. While some studies reported a significant correlation between DEE and BMR (Nilsson 2002; Tieleman et al. 2008; Rezende et al. 2009), other studies reported a nonsignificant correlation after correcting for various intrinsic and extrinsic factors (Meerlo et al. 1997; Peterson et al. 1998; Fyhn et al. 2001; Speakman et al. 2003). Moreover, some studies found that the association between DEE and BMR can change from one context to another. For example, DEE and resting metabolic rate (RMR) were positively correlated in free-living chipmunks during the reproductive season, but this correlation did not persist during other periods of the year (Careau et al. 2013). The opposite was found in captive zebra finches, where DEE and RMR were positively correlated at the nonbreeding stage but not correlated during reproduction (at the one-egg stage, the relationship is dependent on the context under which it is examined, i.e., reproductive season; Vézina et al. 2006; Careau et al. 2013).

Our understanding of how animals manage their energy budget assuming they have energetic constraints is intimately linked to the way in which DEE and RMR relate to each other at the intraspecific level. However, significant insight may be gained by looking at not only the BMR (or RMR) and DEE of an animal but also the energy spent specifically on energetically costly activities (Ricklefs et al. 1996). This quantity can be described as activity energy expenditure (AEE; $=\text{DEE} - \text{RMR}$; White et al. 2011). Considering RMR, DEE, and AEE allows us to distinguish among three different conceptual models of energy budgets. (1) The performance model (Careau et al. 2008), also referred to as the increased-intake hypothesis (Nilsson 2002), assumes that the capacity to expend energy at a high rate during activity requires greater maintenance costs (i.e., AEE and RMR should be positively correlated). In this case, higher RMR is predicted to be positively related to DEE with a slope >1 (Mathot and Dingemanse 2015). (2) The allocation model (Careau et al. 2008) sets DEE as a fixed amount, and, thus, it does not vary with RMR, while AEE decreases with increasing RMR. In this case, the slope of the DEE-RMR relationship is predicted to be zero (Mathot and Dingemanse 2015). (3) The independent model (Careau and Garland 2012) describes RMR and AEE as independent of each other such that, for example, increases in RMR do not result in changes to energy spent on other processes. Increases in RMR are nonetheless predicted to have a positive relation with DEE, since the former is a component of the latter, but with a slope no greater than unity since there is no relationship between RMR and AEE (Mathot and Dingemanse 2015).

An example of the application of such analysis is demonstrated in a study of Australasian gannets *Morus serrator* by Green et al. (2013) using heart rate (f_H) as a calibrated proxy for metabolic rate. The positive correlation between RMR and DEE in this species reflects variation in the magnitude of RMR, but there is no variation in AEE with RMR, suggesting the independent model of energy management. These findings for gannets contrast with the only comparable interspecific study, in which Ricklefs et al. (1996) found that birds showed no significant correlation between BMR and DEE, as well as no significant correlation between BMR and AEE, whereas mammals showed a positive correlation between BMR and both DEE and AEE. However, whether the findings of interspecific studies are comparable to those of intraspecific studies is questionable. Certainly, if we wish to study the consistency/variability of relationships across species, comparisons must be made of multiple intraspecific analyses.

In this study, we expand on the limited intraspecific data previously analyzed and examine the generality of the relationships among RMR, AEE, and DEE using long-term data sets for seven species of bird and four species of mammal. We investigate whether the strategy of energy management differs within or between these two taxa. Each of these data sets uses f_H as a proxy for metabolic rate, since heart rate and rate of oxygen consumption ($\dot{V}_{O_2}$) have been shown to be positively correlated in every endothermic species examined so far (Green 2011), in accordance with Fick's (1870) principle. For birds we use a quantitative approach (see Green 2011), since $\dot{V}_{O_2}$-f_H calibrations were available for each species, and also report the output resulting from the qualitative approach for comparative purposes. For mammals we used a qualitative approach (see Green 2011) where directional trends in f_H are used to infer directional trends in $\dot{V}_{O_2}$.

Methods

Heart rate was measured continuously using surgically implanted heart rate data loggers or transmitters or by ruminal devices administered orally (Signer et al. 2010), employed primarily to investigate other research questions. In total, data sets from seven bird and four mammal species were available for analysis (table 1). Information and details regarding the devices used, implantation and removal procedures, and data collection protocols are available from the following sources: great cormorants *Phalacrocorax carbo* (Grémillet et al. 2005), barnacle geese *Branta leucopsis* (Portugal et al. 2009), Australasian gannets (Green et al. 2013), little penguins *Eudyptula minor* (J. A. Green, L. R. Horne, P. Dann, P. J. Butler, and P. B. Frappell, unpublished data), king penguins *Aptenodytes patagonicus* (Halsey et al. 2010), macaroni penguins *Eudyptes chrysolophus* (Green et al. 2005), eider ducks *Somateria mollissima* (Guillemette et al. 2007), Przewalski horses *Equus ferus przewalksii* (Arnold et al. 2006), alpine ibex *Capra ibex* (Signer et al. 2011), red deer *Cervus elaphus* (Turbill et al. 2011), and roe deer *Capreolus capreolus* (W. Arnold and F. Schober, unpublished data). For alpine ibex and red deer, heart rate was determined from an accelerometer located in the reticulum, which accurately recorded heart rate when the instrumented animal was stationary and during relatively gentle activity. At higher levels of activity, however, heart rate was not discernible in the recorded acceleration data, and, thus, heart rate at high levels of activity is not included in the data sets for these two species.

For all individuals of each species, mean daily heart rate was calculated for each day (i.e., for each 24-h period). Minimum daily heart rate was determined by calculating mean f_H for consecutive short time intervals (5–15 min, depending on study) throughout the day and selecting the lowest of these values for each day. Activity daily f_H was then calculated as the difference between mean daily f_H and minimum daily f_H. A grand mean of all individuals was then calculated for each day of each study for all three variables. As the data are mean measures of heart rate from successive days, the degree of serial autocorrelation in the data was assessed before all statistical tests. The autocorrelation function in Minitab indicated, for each species, the number of data points between values of mean daily f_H, minimum daily f_H, and activity daily f_H required to produce nonsignificant levels of autocorrelation, i.e., the minimum interval necessary for time series data to be independent. See Guillemette and Butler (2012) for an alternative method. We then calculated means of each of the three variables for time periods equal to the largest of these three intervals for each species (see table 1) to give the following three variables: mean f_H, minimum f_H, and activity f_H. For birds, mean f_H and minimum f_H were converted into estimates of mean $\dot{V}_{O_2}$ and minimum $\dot{V}_{O_2}$, respectively, using calibration equations from the following sources: great cormorants (White et al. 2011), barnacle geese (Portugal et al. 2009), Australasian gannets (Green et al. 2013), little penguins (Green et al. 2008), king penguins (Halsey et al. 2007), macaroni penguins (Green et al. 2005), common eiders (Guillemette et al. 2007), and, where necessary, animal masses reported therein. Activity $\dot{V}_{O_2}$ was given as minimum $\dot{V}_{O_2}$ subtracted from mean $\dot{V}_{O_2}$. Therefore, for birds, mean $\dot{V}_{O_2}$, minimum $\dot{V}_{O_2}$, and activity $\dot{V}_{O_2}$ were quantitative proxies for DEE, RMR, and AEE, respectively, while for mammals, mean f_H, minimum f_H, and activity f_H were qualitative proxies for DEE, RMR, and AEE, respectively. Simple linear regressions conducted in SPSS v.21 examined the relationships between minimum f_H and mean f_H, between minimum f_H and activity f_H, between minimum $\dot{V}_{O_2}$ and mean $\dot{V}_{O_2}$, and between minimum $\dot{V}_{O_2}$ and activity $\dot{V}_{O_2}$. The *P* value associated with these tests is interpreted as a continuous variable indicating the strength of evidence against the null hypothesis (Fisher 1959; Lew 2012; Halsey et al. 2015).

These analyses have taken advantage of the $\dot{V}_{O_2}$-f_H calibration equations available for all species of bird in this study. For two of the bird species (great cormorants and Australasian gannets) these calibrations account for the curvilinear relationships in f_H and $\dot{V}_{O_2}$ observed in flying birds (White et al. 2011; Green et al. 2013). However, it has not yet been possible to account for this in the calibration equations available for barnacle geese or eider; it is known that calibrations based on walking may not accurately estimate $\dot{V}_{O_2}$ from f_H during flight in the geese at least (Ward et al. 2002). There is thus an argument to analyze f_H data for the bird species instead of estimates of $\dot{V}_{O_2}$. To investigate this, we repeated the $\dot{V}_{O_2}$-based analysis for birds on the underlying heart rate data (appendix).

Results

Table 1 provides full details on the results of statistical analyses undertaken in this study. The duration of data collection varied between species from a few weeks to more than 2 yr. Conducting the statistical analysis on the data set for each species reduced to the size of the smallest data set did not change the overall findings of the study, and, thus, the statistical analyses reported here are based on the full data set available for each species. For all seven bird species, there was strong evidence that mean $\dot{V}_{O_2}$ was positively related to minimum $\dot{V}_{O_2}$ (fig. 1*A*), while in all four mammal species there was strong evidence that mean f_H was positively related to minimum f_H (fig. 1*C*). Only the data for macaroni penguins indicated strong evidence for a relationship between activity $\dot{V}_{O_2}$ and minimum $\dot{V}_{O_2}$, while there was some evidence for such a relationship in the little penguin data (fig. 1*B*). For all other bird species, there was no evidence of such a relationship. Analyzing the f_H data for birds, that is, using the qualitative approach, yielded broadly similar results with only one exception (appendix). All four mammal data sets provided strong evidence of a positive relationship between activity f_H and minimum f_H (fig. 1*D*).

Discussion

This study shows that qualitative (f_H) and quantitative ($\dot{V}_{O_2}$) proxies of RMR and DEE are positively related at the intraspecific level in all species of bird and mammal for which data

Table 1: Results of simple linear regressions between quantitative and qualitative proxies of resting metabolic rate (minimum $\dot{V}_{O_2}$ or f_H), daily metabolic rate (mean $\dot{V}_{O_2}$ or f_H), and activity metabolic rate (activity $\dot{V}_{O_2}$ or f_H) in 11 species of free-ranging birds and mammals

	Mean $\dot{V}_{O_2}$ ~ minimum $\dot{V}_{O_2}$				Activity $\dot{V}_{O_2}$ ~ minimum $\dot{V}_{O_2}$							Auto	
Species	Slope	95% CI	r^2	P	Slope	95% CI	r^2	P	Model supported	N	Duration	correlation	n
Great cormorant (G)	**1.12**	**[.55 to 1.64]**	**.66**	**.001**	.12	[−.50 to .63]	.02	.63	Independent	7	172	14	13
Barnacle goose (B)	**1.12**	**[.88 to 1.32]**	**.91**	**<.001**	.15	[−.07 to .34]	.17	.12	Independent	6	361	23	16
Australasian gannet (A)	**1.25**	**[1.01 to 1.38]**	**.82**	**<.001**	.26	[−.02 to .41]	.16	.11	Independent	6	237	14	17
Little penguin (L)	**1.22**	**[.89 to 1.39]**	**.86**	**<.001**	**.21**	**[−.17 to .41]**	**.15**	**.08**	Independent/ performance	5	208	10	21
King penguin (K)	**.58**[a]	**[.14 to .66]**	**.83**	**.01**	.38[a]	[−2.15 to .89]	.08	.32	Independent	6	30	2	15
Macaroni penguin (M)	**1.33**	**[1.08 to 1.75]**	**.88**	**<.001**	**.33**	**[.09 to .76]**	**.31**	**.03**	Performance	63	730	49	15
Eider duck (E)	**1.06**	**[.82 to 1.49]**	**.74**	**<.001**	.12	[−.14 to .53]	.03	.52	Independent	13	220	13	16
	Mean f_H ~ minimum f_H				Activity f_H ~ minimum f_H								
	Slope	95% CI	r^2	P	Slope	95% CI	r^2	P					
Przewalski horse (P)	**1.17**	**[1.08 to 1.49]**	**.97**	**<.001**	**.17**	**[.11 to .35]**	**.41**	**.01**	Performance	7	371	24	17
Alpine ibex (A)	**1.13**	**[1.04 to 1.31]**	**.98**	**<.001**	**.14**	**[.06 to .25]**	**.40**	**.01**	Performance	20	348	48	15
Red deer (R)	**1.07**	**[1.04 to 1.09]**	**1.00**	**<.001**	**.08**	**[.05 to .11]**	**.56**	**<.001**	Performance	15	771	24	24
Roe deer (RO)	**1.2**	**[1.05 to 1.34]**	**.83**	**<.001**	**.19**	**[.04 to .32]**	**.11**	**.03**	Performance	14	1,254	30	45

Note. Letters in parentheses that follow species names indicate abbreviation used in figure 1. Correlations indicating some degree of evidence of a relationship are indicated in bold. Also shown are the number of animals from which data were analyzed (N), the length of the data set in days (duration), the autocorrelation, and the resultant number of data points used in the analysis for each species (n). Values in brackets are bias-corrected accelerated 95% confidence intervals (CI) based on 10,000 bootstrapped iterations. f_H = heart rate.

[a] The relationships for king penguins were analyzed after a $\log_{10}$ transformation because the data clearly fitted a power relationship rather than a linear relationship. The way the exponent is interpreted is the same as for the linear relationships exhibited by all the other species.

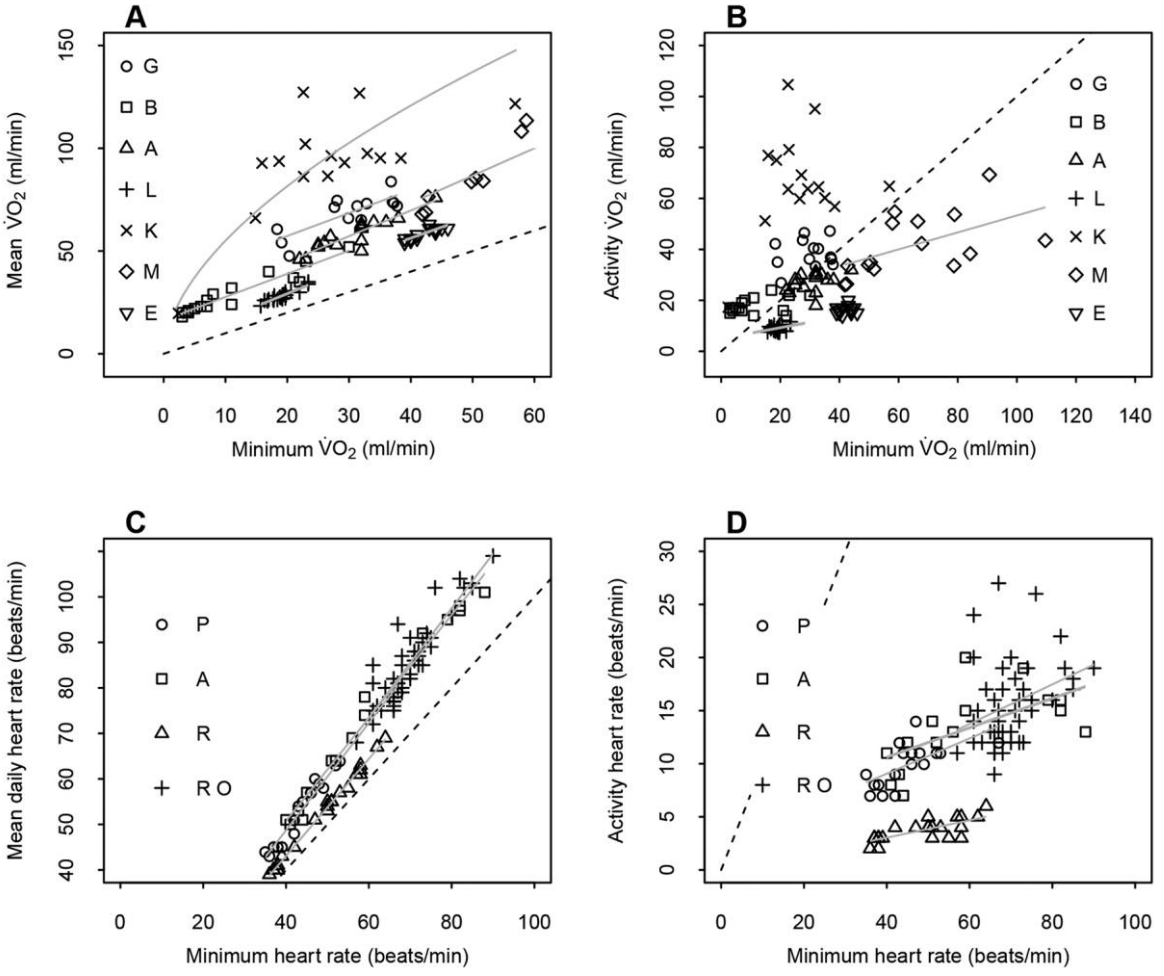

Figure 1. Relationships between quantitative proxies of metabolic rate in seven species of bird ($\dot{V}_{O_2}$; *A*, *B*) and between qualitative proxies of metabolic rate in four species of mammal (heart rate; *C*, *D*). Explanations for each measure are provided in the main text. Evidence for correlations is indicated by the presence of best-fit lines (all data points in *A*, *C*, and *D* have best-fit lines; the line for little penguins in *B* has been extended for clarity). Some data points are obscured behind others. The *Y*-axis of *C* does not include 0. In each panel the dashed line indicates the slope of unity. See table 1 for species name abbreviations. $\dot{V}_{O_2}$ = rate of oxygen consumption.

are available (table 1; fig. 1*A*, 1*C*). This provides evidence that a relationship between RMR and DEE is a consistent feature of endothermic species. This study also shows that there is a positive intraspecific relationship between qualitative proxies of RMR and AEE in all examined mammals (table 1; fig. 1*D*). In contrast, for five of the seven species of bird examined in this study there was no evidence for a relationship between estimated RMR and AEE (table 1; fig. 1*B*).

Examination of the relationships between RMR, AEE, and DEE offers insight into the energy management strategies employed by each species. The key to this analysis is to partition DEE into RMR and AEE in order to test for evidence supporting each of the three theorized models (independent, allocation, performance). For five species of birds analyzed, the data suggest that they tend to employ the independent model of energy management; however, for the macaroni and little penguins, there is evidence of energy management based on the performance model.

Evidence of the energy management strategy employed by each of the mammal species represented in this study can also be obtained through the analysis of the f_H data. A relationship with a slope greater than 1 between activity f_H and minimum f_H supports the performance model; this was the case for all four species of mammal. Some variety in the energy utilization model apparently employed between bird species, in contrast to the consistency found within mammals, may at least in part be due to the broader taxonomic range of bird species analyzed, though there was a greater range of body masses in the mammals (roe deer, 25 kg; Przewalski horse, 300 kg) than in the birds (eider ducks, 2 kg; king penguins, 10 kg).

DEE and RMR were strongly correlated in all 11 species examined here. This is in stark contrast to many previous intraspecific studies that report nonsignificant results (Meerlo et al. 1997; Peterson et al. 1998; Fyhn et al. 2001; Speakman et al. 2003). Aside from one study, based on a low sample size ($n = 6$, $r^2 =$

0.70 in Nilsson 2002), the r^2 of all of the previously reported statistically significant correlations falls below the range observed in this study: $r^2 = 0.20$ in Tieleman et al. (2008), $r^2 = 0.23$ in Careau et al. (2013), $r^2 = 0.35$ in Vézina et al. (2006), and $r^2 = 0.50$ in Rezende et al. (2009). One noticeable difference is that our results are based on heart rate telemetry, whereas all of the studies listed above used doubly labeled water and respirometry techniques to estimate DEE and BMR. Moreover, most of the previous studies reported correlations on a mass-residual basis (Careau et al. 2013 also reported statistically significant correlations on a whole-animal basis), whereas our results are not adjusted for body mass differences between individuals. Previous studies investigated correlations across individuals, whereas in this study each data point is composed of the same set of animals. Variation in body mass within individuals over time may, at least in part, drive the relationships seen in this study between RMR, DEE, and AEE (Portugal et al. 2009).

RMR often shows substantial plasticity and can be higher in cold-acclimated animals than warm-acclimated ones (West 1972; McDevitt and Speakman 1994; Nespolo et al. 2001; McKechnie et al. 2007; McKechnie 2008; Smit and McKechnie 2010). Similarly, DEE is negatively related to ambient temperature in some studies (e.g., Tinbergen and Dietz 1994; Weathers et al. 1996; Speakman 2000) though not in others (e.g., Humphries et al. 2005). Where both DEE and RMR are negatively associated with temperature, variation in temperature during the long periods over which heart rate measurements can be made (e.g., 24–441 d in this study; table 1) will manifest as a positive association between DEE and RMR, which might spuriously indicate use of the independent model of energy management. Indeed, in macaroni penguins, which spend many months of their annual cycle continuously at sea, RMR will be higher during this period, as the animals are in water rather than air, which brings a substantial thermoregulatory challenge (Green et al. 2005). These days are likely to also be associated with high activity, as birds are continually diving and foraging. Thus, both RMR and AEE are elevated due to covarying environmental circumstances rather than physiological coupling. This may also be the case to a lesser extent for little penguins, which during their winter intersperse intermittent periods of several weeks at sea with periods of several days ashore (Ritchie et al. 2010). Alternatively, temperature-dependent changes in behavior may act to buffer or eliminate the effect of ambient temperature on DEE (Speakman 2000; Humphries et al. 2005), and these changes may act in opposition to extrinsically caused changes in RMR. In addition, substitution of the heat required for thermoregulation by the heat produced by activity introduces another potential route for compensation within AEE (Humphries and Careau 2011; see also substitution model; Careau and Garland 2012). Therefore, intraspecific associations among RMR, AEE, and DEE could be context dependent, as has also been suggested for the consequences of intraspecific variation in RMR (Burton et al. 2011). Thus, it is not clear whether the differences observed within the birds and between birds and mammals in this study result from differences among species in their (*a*) metabolic pathways contributing to RMR and DEE, (*b*) responses to environmental factors that act as extrinsic drivers of RMR and DEE, or (*c*) perhaps even locomotion types (all four mammals are terrestrial quadrupeds, while the species of bird are either predominantly flyers or swimmers).

Complex interactions among components of energy budgets can obfuscate associations among RMR, AEE, and DEE. Moreover, even if the performance model is strongly supported at the among-individual level (i.e., slope of the DEE-RMR relationship is >1), this does not rule out the possibility that some form of allocation is occurring within individuals (see fig. 1*B* in Careau and Garland 2015). Furthermore, AEE is often a broad category encompassing a number of behaviors including feeding, preening, fighting, and various types of locomotion that can differ greatly in terms of energy expenditure, and, thus, further understanding of an animal's energy management strategy may be obtained by investigating the heart rate of various activity subcategories. Finally, it may be the case that some animals alter their energy management strategy during different periods of their breeding or life cycles. For example, during molting, the energy costs of feather production may increase the RMR of birds without affecting their AEE (as shown in eider ducks; Guillemette and Butler 2012; the independent model), while during hyperphagia before migration, as their muscles and organs grow, they could in theory exhibit both an increase in RMR and a correlated increase in AEE (the performance model; cf. Guillemette and Butler 2012). Future within-species research involving (1) environmentally controlled scenarios, (2) repeated measures of DEE and RMR on multiple individuals and during different seasons, and, perhaps, (3) the analysis of metabolic rate for different activity types will be necessary to uncover any intrinsically driven physiological processes contributing to variation in these traits among and within individuals.

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APPENDIX

Qualitative Analysis of Metabolic Rates in Birds

We repeated the analysis between resting metabolic rate (RMR), activity energy expenditure (AEE), and daily energy expenditure (DEE) using heart rate (minimum f_H, activity f_H, and mean f_H, respectively) for each of these bird species under consideration (fig. A1). For most correlations for the seven species of bird, the conclusion does not change whether interpreting the data quantitatively ($\dot{V}_{O_2}$ data) or qualitatively (f_H data; see table A1). However, the relationship between activity f_H and minimum f_H for Australasian gannets is significantly negative. This is a product of the curvilinear relationship between $\dot{V}_{O_2}$ and f_H (Green et al. 2013) and the greater proportion of the day spent in flight by this species (25%–35%; Green et al. 2013) compared to the other volant bird species included in this study (usually $<5\%$; Grémillet et al. 2005; Pelletier et al. 2008; Portugal et al. 2012). For any species, a curvilinear relationship results in the difference in heart rate between minimum f_H and mean f_H, equating to a greater difference in $\dot{V}_{O_2}$ at higher heart rates than at lower heart rates. However, for the geese, eider, and cormorants, there is no difference in interpretation between the qualitative and quantitative analyses, since on a typical day high heart rates associated with flight are recorded only rarely. In contrast, for the gannets, the high heart rates associated with flight are recorded often, and these have a disproportionately large effect on DEE. Thus, the lack of a relationship between AEE and RMR in Australasian gannets presents as a negative relationship between activity f_H and minimum f_H. Overall, this then supports the use of the quantitative approach where possible, since it incorporates the maximum amount of information that we have about the respiratory and cardiovascular physiology of these birds. While $\dot{V}_{O_2}$-f_H calibrations were not available for the four mammal species in this study, calibrations for other terrestrial mammals have been reported as linear relationships (Green 2011). Assuming this holds for the mammal species presently under consideration, we would expect the conclusions formed from the f_H relationships to hold for those data when converted to $\dot{V}_{O_2}$.

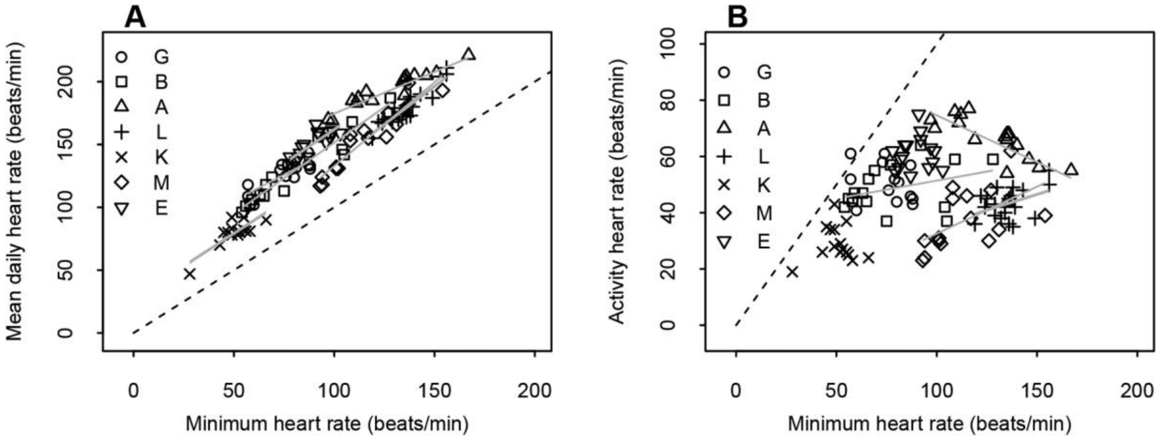

Figure A1. Relationships between qualitative proxies of metabolic rate (heart rate) in seven species of birds. Evidence for correlations is indicated by the presence of best-fit lines (all data points in *A* have best-fit lines). Some data points are obscured behind others. In each panel the dashed line indicates the slope of unity. See table A1 for species name abbreviations.

Table A1: Results of simple linear regressions between qualitative proxies of resting metabolic rate (minimum f_H), daily metabolic rate (mean f_H), and activity metabolic rate (activity f_H) in seven species of free-ranging birds

	Mean f_H ~ minimum f_H				Activity f_H ~ minimum f_H								
Species	Slope	95% CI	r^2	P	Slope	95% CI	r^2	P	Model supported	N	Duration	Autocorrelation	n
Great cormorant (G)	**.83**	**[.47 to 1.14]**	**.70**	**<.001**	−.17	[−.54 to .15]	.08	.34	Independent	7	172	14	13
Barnacle goose (B)	**1.13**	**[.91 to 1.31]**	**.92**	**<.001**	.13	[−.09 to .32]	.13	.17	Independent	6	361	23	16
Australasian gannet (A)	**.66**	**[.53 to .75]**	**.79**	**<.001**	**−.33**	**[−.46 to −.25]**	**.49**	**<.01**		6	237	14	17
Little penguin (L)	**1.21**	**[.90 to 1.40]**	**.86**	**<.001**	**.23**	**[−.10 to .41]**	**.18**	**.06**	Independent/ performance	5	208	10	21
King penguin (K)	**1.04**	**[.27 to 1.36]**	**.67**	**<.001**	.04	[−.75 to .36]	.00	.85	Independent	6	30	2	15
Macaroni penguin (M)	**1.33**	**[1.06 to 1.79]**	**.87**	**<.001**	**.33**	**[.08 to .76]**	**.31**	**.03**	Performance	63	730	49	15
Eider duck (E)	**1.08**	**[.79 to 1.50]**	**.68**	**<.001**	.05	[−.28 to .59]	.00	.81	Independent	13	220	13	16

Note. Letters in parentheses that follow species names indicate abbreviation used in figure A1. Correlations indicating some degree of evidence of a relationship are indicated in bold. Also shown are the number of animals from which data were analyzed (N), the length of the data set in days (duration), the autocorrelation, and the resultant number of data points used in the analysis for each species (n). Values in brackets are bias-corrected accelerated 95% confidence intervals (CI) based on 10,000 bootstrapped iterations. f_H = heart rate.

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