Phenotypic plasticity in the scaling of avian basal metabolic rate

Andrew E. McKechnie[1,*]**, Robert P. Freckleton**[2] **and Walter Jetz**[3]

[1]*DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, School of Animal, Plant and Environmental Sciences,
University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa*
[2]*Department of Zoology, University of Oxford, South Parks Road, Oxford OX13PS, UK*
[3]*Division of Biological Sciences, University of California, San Diego, La Jolla, CA 92093-0116, USA*

Many birds exhibit short-term, reversible adjustments in basal metabolic rate (BMR), but the overall contribution of phenotypic plasticity to avian metabolic diversity remains unclear. The available BMR data include estimates from birds living in natural environments and captive-raised birds in more homogenous, artificial environments. All previous analyses of interspecific variation in BMR have pooled these data. We hypothesized that phenotypic plasticity is an important contributor to interspecific variation in avian BMR, and that captive-raised populations exhibit general differences in BMR compared to wild-caught populations. We tested this hypothesis by fitting general linear models to BMR data for 231 bird species, using the generalized least-squares approach to correct for phylogenetic relatedness when necessary. The scaling exponent relating BMR to body mass in captive-raised birds (0.670) was significantly shallower than in wild-caught birds (0.744). The differences in metabolic scaling between captive-raised and wild-caught birds persisted when migratory tendency and habitat aridity were controlled for. Our results reveal that phenotypic plasticity is a major contributor to avian interspecific metabolic variation. The finding that metabolic scaling in birds is partly determined by environmental factors provides further support for models that predict variation in scaling exponents, such as the allometric cascade model.

Keywords: metabolic scaling; captivity; allometry; basal metabolic rate

1. INTRODUCTION

Physiological diversity arises from several fundamental sources of phenotypic variation. Most analyses of metabolic diversity in endotherms have focused on the allometric scaling of metabolic traits with body mass (M_b; Lasiewski & Dawson 1967; McNab 1988; Lovegrove 2000; White & Seymour 2003; Savage *et al*. 2004) and/or metabolic adaptation to physical and/or biotic characteristics of environments (Scholander *et al*. 1950; McNab 1986; Lovegrove 2000, 2003; Tieleman & Williams 2000; Mueller & Diamond 2001; Wikelski *et al*. 2003; Anderson & Jetz 2005). Recently, however, there has been increasing interest in phenotypic plasticity as an additional source of metabolic variation. Phenotypic plasticity may involve phenotypic flexibility (short-term, reversible changes within an individual) and/or developmental plasticity (irreversible changes that result from developmental processes; Piersma & Drent 2003). In birds, there is increasing evidence for considerable phenotypic flexibility in metabolic rates (Tieleman *et al*. 2003; Swanson in press) and in several digestive and thermoregulatory traits (Martinez del Rio *et al*. 1995; Karasov 1996; Levey *et al*. 1999; Tieleman & Williams 2002; McKechnie & Wolf 2004*b*). Avian metabolic flexibility appears to be most pronounced in long-distance migrants and year-round residents at high latitudes (Piersma *et al*. 1995;

Dawson & O'Conner 1996; Swanson & Olmstead 1999; Battley *et al*. 2001; Lindström & Klaassen 2003; Swanson in press), but is also evident in non-migrant species from the tropics and sub-tropics (Ambrose & Bradshaw 1988; Tieleman *et al*. 2003). Many mammals exhibit quantitatively similar phenotypic flexibility, with the seasonal direction of metabolic adjustments varying with M_b (Lovegrove 2005).

Most comparative analyses of avian metabolic rate have examined variation in basal metabolic rate (BMR), the lower limit of avian metabolic heat production (e.g. Weathers 1979; Daan *et al*. 1990; Rezende *et al*. 2002). BMR is a standardized baseline metabolic parameter and represents maintenance energy demand in the absence of increases in metabolism associated with thermoregulation, digestion, activity or circadian rhythms (McNab 1997; Swanson in press). Although there is evidence that at least some free-ranging birds adjust their BMR over relatively short time-scales, these phenotypic adjustments have been investigated in too few species to reveal the nature of BMR reaction norms (*sensu* Schlichting & Pigliucci 1998). Quantitative variation in the capacity for phenotypic adjustments among taxa remains unclear, as do the ways in which natural selection acts on the capacity to adjust BMR in response to fluctuating environmental conditions (Tieleman *et al*. 2003). The realization that phenotypic plasticity greatly complicates the identification of metabolic adaptation has led to some authors employing common-garden experimental designs. Wikelski *et al*. (2003), for instance, recently partitioned intraspecific BMR variation in stonechats (*Saxicola torquata*) into

* Author for correspondence (mckechnie@gecko.wits.ac.za).

phenotypic plasticity and genotypic adaptation by raising birds from geographically distinct populations under identical conditions before comparing metabolic and behavioural parameters among populations.

The short-term adjustments in BMR exhibited by many birds (e.g. Piersma *et al.* 1995; Tieleman *et al.* 2003; Klaassen *et al.* 2004) raise the possibility that scaling relationships between BMR and M_b are influenced by phenotypic flexibility and/or developmental plasticity in the individuals used for metabolic measurements. Although short-term adjustments in BMR have been examined in relatively few species, the signal of phenotypic plasticity can potentially be identified in avian BMR data sets by accounting for the origins of populations used for metabolic measurements. In some species, BMR was measured in individuals that had recently been caught from free-ranging populations, but in other cases BMR estimates were obtained from individuals that had been bred and/or raised in captivity. Hence, the available avian BMR data permit a comparative analysis of the BMR of birds from natural environments and that of captive-raised birds. Compared to populations in natural environments, birds raised in captivity can be viewed as belonging to experimental populations maintained under conditions of reduced thermal variability, greater quantitative and qualitative homogeneity of energy, nutrient and water resources and reduced levels of activity. We hypothesized that captive-raised birds exhibit general metabolic differences to individuals from natural environments, manifested either as differences in the allometric scaling coefficients for BMR, or as M_b-independent differences in BMR magnitude. Because several factors associated with captive conditions could potentially lead to metabolic adjustments, it is difficult to make specific predictions concerning the direction of differences in BMR between wild-caught and captive-raised birds. For instance, the available evidence suggests that increased food intake can be expected to lead to increases in the mass of metabolically active organs such as the stomach, liver and intestines, and hence elevated BMR (Karasov 1996; Mueller & Diamond 2001). In contrast, more moderate minimum environmental temperatures in captivity can be expected to result in reduced BMR (Tieleman *et al.* 2003; Swanson in press).

2. MATERIAL AND METHODS

(a) *Basal metabolic rate data*

We obtained BMR (W) and M_b (g) data for 231 avian species from the literature (Appendix 1, electronic supplementary material). Observed metabolic rates were included if they were measured during the rest phase of the circadian cycle at thermoneutral air temperatures in resting individuals that could reasonably be assumed to be postabsorptive (i.e. data that met inclusion criteria 1–3 in McKechnie & Wolf 2004*a*). We opted to include data irrespective of sample size, since this approach approximately doubled the size of our data set. Although some of the data we included represented means for only one or two individuals, the BMR of an individual is equally likely to be above or below the population mean. Hence, it is improbable that our conclusions were significantly affected by the inclusion of these data. All M_b and BMR data were log-transformed prior to analysis. For each datum, we consulted the original source and classified the

population in which BMR was measured as wild-caught (birds obtained from wild populations, and which typically spent periods ranging from several days to weeks in captivity before BMR measurements) or captive-raised (birds that hatched in captivity and/or spent most of their lives in captivity). We excluded several taxa with large M_b that were represented in only the wild-caught category, namely the ostrich (*Struthio camelus*) and members of the Procellaridae, Laridae and Spheniscidae.

(b) *Data analyses*

We constructed a phylogeny (Appendix 2, electronic supplementary material) based primarily on Sibley & Ahlquist's (1990) DNA-hybridization data, using the phylogenies in Reynolds & Lee (1996), Tieleman & Williams (2000), McKechnie (2001), Schleucher (2002), Tieleman *et al.* (2002) and McKechnie & Wolf (2004*a*). We used a generalized least-squares (GLS) approach, using the phylogeny to account for covariance among the species (Pagel 1994; Martins & Hansen 1997; Pagel 1999; Freckleton *et al.* 2002). We assessed the need for phylogenetic correction by calculating the parameter λ for each model (Pagel 1999; Freckleton *et al.* 2002). The λ-statistic adjusts the phylogenetic correction according to the degree of phylogenetic dependence in the residuals of the linear model. A λ-value of zero indicates that the residuals show no phylogenetic structure, whilst a λ-value of one indicates that there is close phylogenetic dependence. We estimated λ using a maximum likelihood approach and used this value in the analysis. We then fitted general linear models to the data, using BMR as the continuous dependent variable and successively adding the following independent variables: M_b (continuous), passerine/non-passerine (categorical), population origin (categorical: wild-caught or captive-raised), migratory tendency (categorical: migrant or non-migrant) and habitat aridity (categorical: desert or non-desert). We added the latter two variables to control for potential bias in the data since several migratory species are known to exhibit large seasonal changes in BMR (Piersma *et al.* 1995; Battley *et al.* 2001; Lindström & Klaassen 2003), and birds inhabiting arid habitats have significantly lower BMR than their mesic counterparts (Tieleman & Williams 2000). We included a categorical variable for passerine or non-passerine membership for statistical reasons since there are significant differences in M_b (Garland & Ives 2000) and potential grade-shifts between the two clades. After adding each independent variable, we checked for changes in the Akaike Information Criterion (Sakamoto *et al.* 1986) and adjusted r^2-values, and tested for interaction terms indicating heterogeneity of slopes.

3. RESULTS

In the GLS framework accounting for phylogenetic relatedness, the overall relationship between BMR (W) and M_b (g) was best described by the linear regression $\log BMR = 0.623 \log M_b - 1.371$. However, the overall scaling exponent was affected by the inclusion of non-passerine species with larger M_b than any of the passerines, and the significantly higher absolute BMR of passerines compared to non-passerines ($F_{1,230} = 183.04$, $p < 0.001$; figure 1). When we controlled for non-passerine/passerine membership, the scaling exponent shifted to 0.707, reflecting the slopes calculated separately for passerines (0.717, 95% CI: 0.047) and non-passerines (0.699, 95%
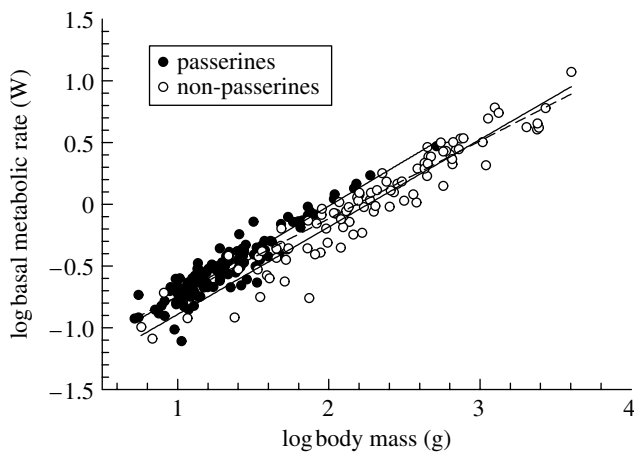
Figure 1. The relationship between basal metabolic rate (BMR) and body mass (M_b) in passerine birds (upper solid line), non-passerine birds (lower solid line) and across both clades (dashed line). The lines are generalized least-squares regressions controlling for phylogeny (see table 1). The inclusion of non-passerine species with M_b greater than the range of passerine M_b affects the overall slope.

CI: 0.045; table 1). Next we tested for a difference in BMR between wild-caught ($N=137$) and captive-raised ($N=94$) birds. There was a significant effect of population origin on the slope of the M_b-dependence of BMR (table 1). Captive-raised birds showed a shallower scaling coefficient (0.670, 95% CI: 0.035) than wild-caught birds (0.744, 95% CI: 0.047) after passerine/non-passerine membership was controlled for (figure 2). The two regression lines intersect at $\log M_b = 2.284$ g and $\log$ BMR $= 0.029$ W. Interaction terms for (i) population origin and non-passerine/passerine membership and (ii) population origin, body mass and non-passerine/passerine membership were non-significant. The differences in scaling coefficients between wild-caught and captive-raised birds remained significant after migratory tendency and habitat aridity were controlled for (table 1).

The relationships between BMR and M_b and passerine/non-passerine membership showed significant phylogenetic dependences, with λ-values significantly different from zero (table 1). However, phylogenetic dependence decreased with the inclusion of additional independent variables, and λ-values reached zero after population origin, migratory tendency and desert/non-desert were each added to the model (table 1), indicating that identical parameter values would be estimated in a conventional analysis. Our analysis suggests that the phylogenetic dependence in BMR arose mainly as a consequence of phylogenetic dependence in the predictor variables, and that once these had been accounted for the residuals exhibited phylogenetic independence. The observation that the position of a species in a BMR–M_b relationship does not depend directly on phylogeny accords with the hypothesis that phenotypic plasticity is an important contributor to metabolic diversity.

4. DISCUSSION

By accounting for the historical origins of bird populations used for metabolic measurements, we have extracted a signal of phenotypic plasticity from a large avian BMR data set, and revealed interactions between two of the fundamental sources of avian metabolic variation. To the

Table 1. Generalized least-squares model for variation in avian basic metabolic rate (BMR). (Model results denote the intercept, the effect of body mass, passerine/non-passerine membership and the origin of populations used for BMR measurements, i.e. captive-raised or wild-caught (origin). For each variable, the parameter estimate (*b*) is provided. We also tested for the effects of migratory tendency (migrant or non-migrant) and habitat aridity (desert or non-desert environment). The parameter λ provides a measure of the phylogenetic dependence of BMR (see Freckleton *et al.* 2002), and can vary from zero to one, with higher values indicating an increasing degree of phylogenetic dependence. Statistical significance is indicated with asterices: statistical significance at $^*p<0.05$, $^{**}p<0.01$ and $^{***}p<0.001$.)

variable	λ	b	F	r^2 (adj)
intercept	0.130***	−1.371		0.916
body mass		0.623	2504.15***	
intercept	0.158***	−1.604		0.932
body mass		0.707	1993.27***	
passerine/non-passerine		0.158	57.10***	
intercept	0.000	−1.676		0.939
body mass		0.743	1489.80***	
passerine/non-passerine		0.160	61.69***	
origin		0.120	8.33***	
origin × body mass		−0.070	9.97***	
intercept	0.000	−1.665		0.944
body mass		0.727	1495.37***	
passerine/non-passerine		0.136	44.68***	
migratory tendency		0.067	20.54***	
origin		0.119	8.33**	
origin × body mass		−0.050	5.29*	
intercept	0.000	−1.706		0.940
body mass		0.741	1499.62***	
passerine/non-passerine		0.153	55.15***	
habitat aridity		0.045	2.07*	
origin		0.167	16.32***	
origin × body mass		−0.071	10.47**	

best of our knowledge, this is the first study to verify that phenotypic plasticity is a major contributor to M_b-dependent interspecific variation in an endotherm physiological trait.

Our results support the hypothesis that phenotypic adjustments to artificial environments lead to general metabolic differences between captive-raised birds and their wild-caught counterparts. Almost no data exist on the effects of captivity on avian metabolic parameters within species. In the only such study of which we are aware, the BMR of freshly caught apapanes (*Himatione sanguinea*) was similar to that of individuals that had been in captivity for one year (Weathers *et al.* 1983). For a few species, BMR estimates are available for captive-raised as well as wild-caught populations. For instance, the BMR of wild-caught speckled mousebirds (*Colius striatus*) was 0.236 W (McKechnie & Lovegrove 2001*a*),
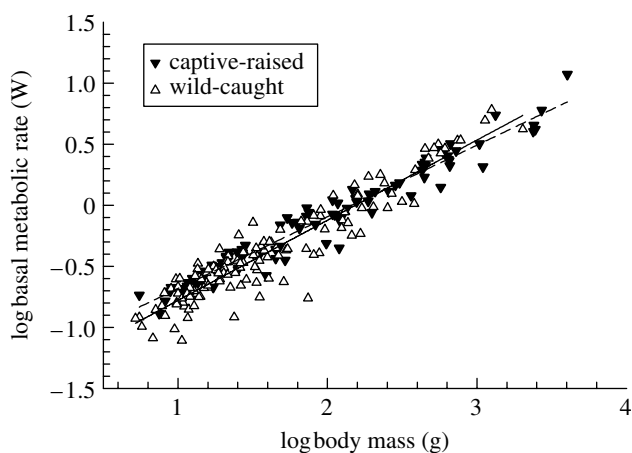
Figure 2. The scaling relationship between basal metabolic rate (BMR) and body mass (M_b) differs between birds from wild-caught and captive-raised populations. The dashed line is the scaling relationship (log BMR $= 0.670$ log $M_b - 1.501$ ($N = 94$)) for captive-raised birds calculated from a generalized least-squares model, which accounts for phylogenetic relatedness and M_b differences between passerines and non-passerines. The solid line is the corresponding relationship for wild-caught birds (log BMR $= 0.744$ log $M_b - 1.670$ ($N = 137$)).

equivalent to approximately 75% of that of second- and third-generation captives in an earlier study (Bartholomew & Trost 1970). The shallower scaling exponent for captive-raised birds reflects the fact that metabolic adjustments to artificial environments vary with M_b (figure 2). In general, small species upregulate BMR in captivity, whereas large species downregulate BMR (figure 2). The non-significance of interactions between population origin and non-passerine/passerine membership, and population origin, body mass and non-passerine/passerine membership, indicates that metabolic responses to captivity do not differ in a consistent way between passerines and non-passerines.

Metabolic adjustments to captive conditions are potentially driven by several fundamental differences between natural and artificial environments. One major category of differences concerns the availability and/or quality of food provided in captivity. The digestive tract morphology of many species is highly plastic, with large changes in organ masses occurring in response to variation in food intake and/or quality (Karasov 1996; Starck 1999; Dekinga *et al.* 2001). For instance, several species rapidly adjust gizzard mass in response to the fibre content of their diet (Starck 1999; Dekinga *et al.* 2001). The observation that the caeca and small intestines of red grouse (*Lagopus lagopus*) decreased in length when fed an artificial diet in captivity (Moss 1972) suggests that switches from natural to artificial diets may be accompanied by major changes in digestive tract morphology. In view of the phenotypic flexibility in body composition exhibited by many birds, it is likely that adjustments of organ masses are responsible for at least some of the metabolic variation observed in this study. Besides changes in organ masses, limited exercise in captivity could lead to reductions in the mass and/or metabolic intensity of flight muscles. Phenotypic flexibility in avian body composition, and the BMR variation that arises from changes in organ and/or muscle masses, results in the slopes of intraspecific BMR allometries generally

being steeper than those of interspecific scaling relationships (Kvist & Lindström 2001; Battley *et al.* 2001).

The M_b-dependence of metabolic responses to captivity and the consequent differences in metabolic scaling between birds from wild-caught and captive-raised populations reveal that the origins of study populations need to be taken into account when testing hypotheses concerning metabolic adaptation. Analyses testing for metabolic divergence among taxa may produce misleading results if the BMR of wild-caught populations is compared to that of captive-raised populations, or vice versa. The assumption that the BMR of captive-raised individuals is representative of wild individuals is widespread in comparative studies, and may be explicit (e.g. Schleucher & Withers 2002) or implicit (e.g. McNab 2001).

Our results call into question whether adaptive variation in endotherm metabolic traits reflects adaptation through natural selection, phenotypic plasticity, or some combination of these two sources of phenotypic variation. Many studies have implicitly assumed that inter- and/or intraspecific metabolic variation constitutes adaptation, both in phylogenetically independent and conventional analyses (Lovegrove 2000, 2003; Merola-Zwartjes & Ligon 2000; McNab 2003). In the case of avian BMR, this assumption is unjustified, since phenotypic adjustments contribute significantly to phylogenetically independent variation. In view of our results, we suggest that attempts to correlate avian BMR with ecological factors should focus on the BMR of wild-caught birds. However, caution needs to be exercised in inferring adaptation, unless inter- and/or intraspecific data are collected under carefully controlled common garden conditions (Wikelski *et al.* 2003; Broggi *et al.* 2005). Another approach to identifying physiological adaptation while explicitly accounting for phenotypic plasticity has been employed by Tieleman *et al.* (2003), who hypothesized that larks (Alaudidae) inhabiting unpredictable arid habitats have evolved greater phenotypic flexibility in BMR than species in mesic habitats. These authors tested their hypothesis by comparing BMR adjustments in response to thermal acclimation among four species of larks (Tieleman *et al.* 2003).

We have assumed that the differences in BMR between wild-caught and captive-raised birds reflect phenotypic adjustments, and not genotypic divergence. Captive populations presumably experience some degree of artificial selection favouring individuals that breed under captive conditions, and/or selection for particular traits such as plumage colour. However, we consider it unlikely that captive-raised birds experience strong enough selection on metabolic traits to cause the fundamental differences in the scaling of BMR demonstrated here. Metabolic adjustments to captive conditions could potentially involve developmental plasticity and/or phenotypic flexibility, but our analyses do not allow us to distinguish between these two forms of phenotypic plasticity. Avian BMR can be significantly adjusted over time-scales of days to weeks (Lindström 1997; Battley *et al.* 2001; Tieleman *et al.* 2003), and the fact that many of the wild-caught populations included in this analysis spent several weeks in captivity before BMR measurements (e.g. McKechnie & Lovegrove 2001*b*, 2003) suggests that the differences between wild-caught and captive-raised birds partly reflect developmental effects.

The fractal geometry and allometric cascade models proposed by West *et al.* (1997) and Darveau *et al.* (2002), respectively, have rekindled the long-standing debate surrounding the processes underlying allometric scaling patterns, and specifically the exponent(s) relating metabolic rate to body size (Banavar *et al.* 2002; West *et al.* 2003; White & Seymour 2003; Savage *et al.* 2004). Our finding that avian BMR scales differently depending on the origins of populations used for metabolic measurements has important implications for this debate, since it reveals (i) that BMR–M_b relationships in birds cannot be described by a single, universal scaling exponent, and (ii) that scaling exponents are environment-dependent. The scaling model of West *et al.* is based on general physical properties of resource distribution networks and, under the commonly used assumptions and optimal conditions, predicts an exponent of 0.75 for the scaling of whole-organism metabolic rate (West *et al.* 1997; Savage *et al.* 2004). Banavar *et al.* (2002) proposed a similar model that predicts limited variation in scaling exponents around 0.75, arising from inefficiencies in resource distribution networks or compensating physiological mechanisms. The allometric cascade model of Darveau *et al.* (2002) also predicts variation in scaling exponents, but on the basis of differences in the respective contributions and coefficients of multiple rate-limiting steps in energy demand and supply pathways. In an expansion of the original formulation of the allometric cascade model, Hochachka *et al.* (2003) identified numerous potential intrinsic and extrinsic contributors to overall metabolic scaling. Although not specifically predicted by Darveau *et al.* (2002) or Hochachka *et al.* (2003), many of the factors that contribute to metabolic scaling can *a priori* be expected to differ between natural environments and captive conditions. Factors characteristic of captive conditions, such as increased food intake, reduced exercise, and different patterns of time and energy allocation, likely affect several of the contributors to overall control of metabolic scaling (see fig. 1 of Hochachka *et al.* 2003). Our finding that scaling exponents for avian BMR are not fixed, but determined in part by environmental factors, argues against the existence of a universal exponent of 0.75 and lends further support to allometric scaling models that explicitly predict variation in scaling exponents.

In summary, we have identified a signal of phenotypic plasticity in avian metabolic scaling, manifested as different scaling coefficients for BMR in captive-raised and wild-caught birds. The environmental factors and physiological mechanisms underlying these differences remain to be identified, and the relative contributions of developmental plasticity and phenotypic flexibility are unclear. Phenotypic plasticity in traits such as BMR significantly complicates the process of identifying physiological adaptation. Increasingly sophisticated approaches to correcting for the phylogenetic non-independence of comparative data (Felsenstein 1985; Garland *et al.* 1992, 1993; Pagel 1999; Garland & Ives 2000; Martins 2000; Freckleton *et al.* 2002; Martins *et al.* 2002) have yielded new answers to long-standing questions in ecological and evolutionary physiology. Our results highlight a major new challenge: the partitioning of variation in physiological traits into genetic adaptation and phenotypic plasticity. Our results also call into question whether phylogenetically independent interspecific variation in metabolic traits represents true adaptation arising from genetic divergence through natural selection, or environment-mediated phenotypic adjustments.

REFERENCES

Ambrose, S. J. & Bradshaw, S. D. 1988 Seasonal changes in standard metabolic rates in the white-browed scrubwren *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. *Comp. Biochem. Physiol. A* **89**, 79–83. (doi:10.1016/0300-9629(88)91142-5)

Anderson, K. J. & Jetz, W. 2005 The broad-scale ecology of energy expenditure of endotherms. *Ecol. Lett.* **8**, 310–318. (doi:10.1111/j.1461-0248.2005.00723.x)

Banavar, J. R., Damuth, J., Maritan, A. & Rinaldo, A. 2002 Supply–demand balance and metabolic scaling. *Proc. Natl Acad. Sci. USA* **99**, 1056–1059. (doi:10.1073/pnas.162216899)

Bartholomew, G. A. & Trost, C. H. 1970 Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* **72**, 141–146.

Battley, P. F., Dekinga, A., Dietz, M. W., Piersma, T., Tang, S. & Hulsman, K. 2001 Basal metabolic rate declines during long-distance migratory flight in great knots. *Condor* **103**, 838–845.

Broggi, J., Hohtola, E., Orell, M. & Nilsson, J.-Å. 2005 Local adaptation to winter conditions in a passerine spreading north: a common-garden approach. *Evolution* **59**, 1600–1603.

Daan, S., Masman, D. & Groenewold, A. 1990 Avian basal metabolic rates: their association with body compostition and energy expenditure in nature. *Am. J. Physiol.* **R333**, R340.

Darveau, C.-A., Suarez, R. K., Andrews, R. D. & Hochachka, P. W. 2002 Allometric cascade as a unifying principle of body mass effects on metabolism. *Nature* **417**, 166–170. (doi:10.1038/417166a)

Dawson, W. R. & O'Conner, T. P. 1996 Energetic features of avian thermoregulatory responses. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 85–124. New York: Chapman & Hall.

Dekinga, A., Dietz, M. W., Koolhaas, A. & Piersma, T. 2001 Time course and reversability of changes in the gizzards of red knots alternately eating hard and soft food. *J. Exp. Biol.* **204**, 2167–2173.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15. (doi:10.1086/284325)

Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)

Garland, T. & Ives, A. R. 2000 Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am. Nat.* **155**, 346–364. (doi:10.1086/303327)

Garland, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.

Garland, T., Dickerman, A. W., Janis, C. M. & Jones, J. A. 1993 Phylogenetic analysis of covariance by computer simulation. *Syst. Biol.* **42**, 265–292.

Hochachka, P. W., Darveau, C.-A., Andrews, R. D. & Suarez, R. K. 2003 Allometric cascade: a model for resolving body mass effects on metabolism. *Comp. Biochem. Physiol. A* **134**, 675–691. (doi:10.1016/S1095-6433(02)00364-1)

Karasov, W. H. 1996 Digestive plasticity in avian energetics and feeding ecology. In *Avian energetics and nutritional ecology* (ed. C. Carey), pp. 61–84. New York, NY: Chapman & Hall.

Klaassen, M., Oltrogge, M. & Trost, L. 2004 Basal metabolic rate, food intake, and body mass in cold- and warm-acclimated Garden Warblers. *Comp. Biochem. Physiol. A* **137**, 639–647. (doi:10.1016/j.cbpb.2003.12.004)

Kvist, A. & Lindström, Å. 2001 Basal metabolic rate in migratory waders: intra-individual, intraspecific, inter-specific and seasonal variation. *Funct. Ecol.* **15**, 465–473. (doi:10.1046/j.0269-8463.2001.00549.x)

Lasiewski, R. C. & Dawson, W. R. 1967 A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* **69**, 13–23.

Levey, D. J., Place, A. R., Rey, P. J. & Martinez del Rio, C. 1999 An experimental test of dietary enzyme modulation in pine warblers *Dendroica pinus*. *Physiol. Biochem. Zool.* **72**, 576–587. (doi:10.1086/316689)

Lindström, Å. 1997 Basal metabolic rates of migrating waders in the Eurasian Arctic. *J. Avian Biol.* **28**, 87–92.

Lindström, Å. & Klaassen, M. 2003 High basal metabolic rates of shorebirds while in the Arctic: a circumpolar view. *Condor* **105**, 420–427.

Lovegrove, B. G. 2000 The zoogeography of mammalian basal metabolic rate. *Am. Nat.* **156**, 201–219. (doi:10.1086/303383)

Lovegrove, B. G. 2003 The influence of climate on the basal metabolic rate of small mammals: a slow–fast metabolic continuum. *J. Comp. Physiol. B* **173**, 87–112.

Lovegrove, B. G. 2005 Seasonal thermoregulatory responses in mammals. *J. Comp. Physiol. B* **175**, 231–247. (doi:10.1007/s00360-005-0477-1)

Martinez del Rio, C., Brugger, K. W., Rios, J. L., Vergara, M. E. & Witmer, M. C. 1995 An experimental and comparative study of dietary modulation of intestinal enzymes in the European starling. *Physiol. Zool.* **68**, 490–511.

Martins, E. P. 2000 Adaptation and the comparative method. *Trends Ecol. Evol.* **15**, 296–299. (doi:10.1016/S0169-5347(00)01880-2)

Martins, E. P. & Hansen, T. F. 1997 Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am. Nat.* **149**, 646–667. (doi:10.1086/286013)

Martins, E. P., Diniz-Filho, J. A. F. & Housworth, E. A. 2002 Adaptive constraints and the phylogenetic comparative method: a computer simulation test. *Evolution* **56**, 1–13.

McKechnie, A. E. 2001 Patterns, mechanisms and evolution of avian facultative hypothermic responses: a southern African perspective. Ph.D. thesis, University of Natal, Pietermaritzburg.

McKechnie, A. E. & Lovegrove, B. G. 2001a Heterothermic responses in the speckled mousebird (*Colius striatus*). *J. Comp. Physiol. B* **171**, 507–518. (doi:10.1007/s003600100201)

McKechnie, A. E. & Lovegrove, B. G. 2001b Thermoregulation and the energetic significance of clustering behavior in the white-backed mousebird (*Colius colius*). *Physiol. Biochem. Zool.* **74**, 238–249. (doi:10.1086/319669)

McKechnie, A. E. & Lovegrove, B. G. 2003 Facultative hypothermic responses in an Afrotropical arid-zone

passerine, the red-headed finch (*Amadina erythrocephala*). *J. Comp. Physiol. B* **173**, 339–346. (doi:10.1007/s00360-003-0341-0)

McKechnie, A. E. & Wolf, B. O. 2004a The allometry of avian basal metabolic rate: good predictions need good data. *Physiol. Biochem. Zool.* **77**, 502–521. (doi:10.1086/383511)

McKechnie, A. E. & Wolf, B. O. 2004b Partitioning of evaporative water loss in white-winged doves: plasticity in response to short-term thermal acclimation. *J. Exp. Biol.* **207**, 203–210. (doi:10.1242/jeb.00757)

McNab, B. K. 1986 The influence of food habits on the energetics of eutherian mammals. *Ecol. Monogr.* **56**, 1–19.

McNab, B. K. 1988 Complications inherent in scaling the basal rate of metabolism in mammals. *Q. Rev. Biol.* **63**, 25–54. (doi:10.1086/415715)

McNab, B. K. 1997 On the utility of uniformity in the definition of basal rates of metabolism. *Physiol. Zool.* **70**, 718–720.

McNab, B. K. 2001 Energetics of toucans, barbets and a hornbill: implications for avian frugivory. *Auk* **118**, 916–933.

McNab, B. K. 2003 Ecology shapes bird bioenergetics. *Nature* **426**, 620–621. (doi:10.1038/426620b)

Merola-Zwartjes, M. & Ligon, J. D. 2000 Ecological energetics of the Puerto Rican tody: heterothermy, torpor and intra-island variation. *Ecology* **81**, 990–1002.

Moss, R. 1972 Effects of captivity on gut lengths in red grouse. *J. Wildl. Manage.* **36**, 99–104.

Mueller, P. & Diamond, J. 2001 Metabolic rate and environmental productivity: well-provisioned animals evolved to run and idle fast. *Proc. Natl Acad. Sci. USA* **98**, 12 550–12 554. (doi:10.1073/pnas.221456698)

Pagel, M. 1994 Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proc. R. Soc. B* **255**, 37–45.

Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)

Piersma, T. & Drent, J. 2003 Phenotypic flexibility and the evolution of organismal design. *Trends Ecol. Evol.* **18**, 228–233. (doi:10.1016/S0169-5347(03)00036-3)

Piersma, T., Cadée, N. & Daan, S. 1995 Seasonality in basal metabolic rate and thermal conductance in a long distance migrant shorebird, the knot (*Calidris canutus*). *J. Comp. Physiol.* **165**, 37–45.

Reynolds, P. S. & Lee, R. M. 1996 Phylogenetic analysis of avian energetics: passerines and non-passerines do not differ. *Am. Nat.* **147**, 735–759. (doi:10.1086/285877)

Rezende, E. L., Swanson, D. L., Novoa, F. F. & Bozinovic, F. 2002 Passerines versus nonpasserines: so far, no statistical differences in the scaling of avian energetics. *J. Exp. Biol.* **205**, 101–107.

Sakamoto, Y., Ishiguro, M. & Kitagawa, G. 1986 *Akaike information criterion statistics*. Dordrecht, The Netherlands: D. Reidel.

Savage, V. M., Gillooly, J. F., Woodruff, W. H., West, G. B., Allen, A. P., Enquist, B. J. & Brown, J. H. 2004 The predominance of quarter-power scaling in biology. *Funct. Ecol.* **18**, 257–282. (doi:10.1111/j.0269-8463.2004.00856.x)

Schleucher, E. 2002 Metabolism, body temperature and thermal conductance of fruit-doves (Aves: Columbidae, Treronidae). *Comp. Biochem. Physiol. A* **131**, 417–428. (doi:10.1016/S1095-6433(01)00499-8)

Schleucher, E. & Withers, P. C. 2002 Metabolic and thermal physiology of doves and pigeons. *Physiol. Biochem. Zool.* **75**, 439–450. (doi:10.1086/342803)

Schlichting, C. D. & Pigliucci, M. 1998 *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA: Sinauer Associates.

Scholander, P. F., Hock, R., Walters, V. & Irving, L. 1950 Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation and basal metabolic rate. *Biol. Bull.* **99**, 259–271.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds*. New Haven, CT: Yale University Press.

Starck, J. M. 1999 Phenotypic flexibility of the avian gizzard: rapid, reversible and repeated changes of organ size in response to changes in dietary fibre content. *J. Exp. Biol.* **202**, 3171–3179.

Swanson, D. L. In press. Seasonal metabolic variation in birds: functional and mechanistic correlates. *Curr. Ornithol.* 17.

Swanson, D. L. & Olmstead, K. L. 1999 Evidence for a proximate influence of winter temperatures on metabolism in passerine birds. *Physiol. Biochem. Zool.* **72**, 566–575. (doi:10.1086/316696)

Tieleman, B. I. & Williams, J. B. 2000 The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiol. Biochem. Zool.* **73**, 461–479. (doi:10.1086/317740)

Tieleman, B. I. & Williams, J. B. 2002 Cutaneous and respiratory water loss in larks from arid and mesic environments. *Physiol. Biochem. Zool.* **75**, 590–599. (doi:10.1086/344491)

Tieleman, B. I., Williams, J. B. & Buschur, M. E. 2002 Physiological adjustments to arid and mesic environments in larks (Alaudidae). *Physiol. Biochem. Zool.* **75**, 305–313. (doi:10.1086/341998)

Tieleman, B. I., Williams, J. B., Buschur, M. E. & Brown, C. R. 2003 Phenotypic variation of larks along an aridity gradient: are desert birds more flexible? *Ecology* **84**, 1800–1815.

Weathers, W. W. 1979 Climatic adaptation in avian standard metabolic rate. *Oecologia* **42**, 81–89.

Weathers, W. W., Weathers, D. L. & van Riper, C. 1983 Basal metabolism of the apapane: comparison of freshly caught birds with long-term captives. *Auk* **100**, 977–978.

West, G. B., Brown, J. H. & Enquist, B. 1997 A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122–126. (doi:10.1126/science.276.5309.122)

West, G. B., Savage, V. M., Gillooly, J. F., Enquist, B., Woodruff, W. H. & Brown, J. H. 2003 Why does metabolic rate scale with body size? *Nature* **421**, 713. (doi:10.1038/421713a)

White, C. R. & Seymour, R. S. 2003 Mammalian basal metabolic rate is proportional to body mass$^{2/3}$. *Proc. Natl Acad. Sci. USA* **100**, 4046–4049. (doi:10.1073/pnas.0436428100)

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E. 2003 Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proc. R. Soc. B.* **270**, 2383–2388. (doi:10.1098/rspb.2003.2500)