Avian seasonal metabolic variation in a subtropical desert: basal metabolic rates are lower in winter than in summer

Ben Smit[1,2]

Andrew E. McKechnie[1,3]

[1]DST/NRF Centre of Excellence at the Percy FitzPatrick Institute

[2]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

[3]Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa

Correspondence:

Ben Smit

Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

E-mail: bsmit@zoology.up.ac.za

Running head: Winter decreases in avian basal metabolism

Summary

1. Most small birds inhabiting temperate latitudes in the Holarctic increase basal metabolic rate (BMR) in winter, a pattern thought to reflect the up-regulation of metabolic machinery required for enhanced winter cold tolerance. In contrast, patterns of seasonal BMR variation in birds inhabiting subtropical latitudes are largely unknown. In this study, we investigate seasonal BMR changes in species from subtropical latitudes, and analyse global variation in the direction and magnitude of these responses.

2. We estimated winter and summer BMR in five species resident in the Kalahari Desert, using flow-through respirometry to measure O_2 consumption and CO_2 production in birds held overnight in a field laboratory.

3. In all five species, mass-specific BMR was significantly lower in winter than in summer, with mean reductions of 23% in African scops-owls (*Otus senegalensis*), 30% in pearl-spotted owlets (*Glaucidium perlatum*), 35% on fork-tailed drongos (*Dicrurus adsimilis*), 29% in crimson-breasted shrikes (*Laniarius atrococcinneus*), and 17% in white-browed sparrow-weavers (*Plocepasser mahali*).

4. An analysis of global variation in seasonal BMR changes reveals that their magnitude and direction vary with latitude, ranging from pronounced winter increases at high latitudes where winters are extremely cold, to the opposite pattern in warmer, subtropical environments.

5. Our empirical results for five species, taken together with the analysis of global variation, are consistent with the hypothesis that winter metabolism in subtropical

environments is driven primarily by the need for energy and/or water conservation rather than cold tolerance.

Key-words: acclimatization, cold tolerance, energetics, latitude, phenotypic flexibility

Introduction

Phenotypic flexibility in traits that determine maintenance energy requirements has been predicted to be important in temporally heterogeneous environments where ecological conditions vary cyclically and/or unpredictably within an organism's life span (Pigliucci, 2001, Piersma & Drent, 2003, Tieleman, Williams, Buschur *et al.* 2003). In birds, seasonal variation in basal metabolic rate (BMR), summit metabolism (M_{sum}) and other thermoregulatory parameters is well documented (Swanson & Liknes, 2006, Liknes, Scott & Swanson, 2002, Cooper & Swanson, 1994, Maddocks & Geiser, 2000, Dawson, 2003, Dawson & Marsh, 1988). However, our current understanding of the functional significance of these changes in free-living birds is based primarily on data from small species inhabiting high northern latitudes, typically above 40°N (West, 1972, Cooper & Swanson, 1994, Liknes *et al.*, 2002, Swanson, 1990, Swanson, 1991, Swanson & Weinacht, 1997; reviewed by Swanson (in press) and McKechnie 2008).

In high-latitude Holarctic environments, where seasonal weather changes are pronounced and winters are often extremely cold, many birds respond to elevated thermoregulatory demands during winter by becoming more cold tolerant, a process often involving substantial increases in M_{sum} (the maximum resting thermogenic metabolic rate) (Dawson & Marsh, 1988, Liknes & Swanson, 1996, Swanson & Liknes, 2006). In

most cases, seasonal metabolic changes also involve elevated winter BMR (i.e., the minimum metabolic rate of a resting, normothermic endotherm at thermoneutrality) (Liknes *et al.*, 2002, Swanson & Olmstead, 1999). Winter BMR elevations have been shown in ~ 80% of acclimatization studies, and increases in BMR have been observed in nearly all studies involving short-term acclimation to low temperatures under laboratory conditions (McKechnie, Chetty & Lovegrove, 2007, Vezina, Jalvingh, Dekinga *et al.*, 2006, Tieleman *et al.*, 2003b, Williams & Tieleman, 2000, Klaassen, Oltrogge & Trost, 2004). In this study, we use the terms "acclimation" and 'acclimatization" to refer to responses to artificial and natural environments, respectively (Piersma & Drent, 2003).

However, avian BMR is not always elevated during winter and a number of species exhibit seasonally stable BMR. A lack of significant seasonal BMR variation has been observed in some north-temperate species, such as house finches (*Carpodacus mexicanus*) and black-capped chickadees (*Parus atricapillus*) (Dawson, Marsh, Buttemer *et al.*, 1983, Rising & Hudson, 1974, O'Connor, 1996), as well as species from the southern subtropics, such as rufous-collared sparrows (*Zonotrichia capensis*) and white-browed scrubwrens (*Sericornis frontalis*) (Ambrose & Bradshaw, 1988, Maldonado, Cavieres, Veloso *et al.*, 2009). Moreover, a reduced BMR during winter has been observed in Australian silver-eyes (*Zosterops lateralis*) and rock kestrels (*Falco rupicolis*) (Maddocks & Geiser, 2000, Bush, Brown & Downs, 2008). However, with the exception of these few studies, patterns of seasonal metabolic variation in species from sub-tropical and tropical latitudes remain largely unknown.

Global variation in the magnitude and direction of seasonal metabolic changes has received little attention, and the factors responsible for the variation highlighted above

remain unclear. Interspecific variation in BMR is correlated with precipitation and temperature (Tieleman & Williams, 2000, White, Blackburn, Martin *et al.*, 2007, Jetz, Freckleton & McKechnie, 2008), raising the possibility that such climatic and environmental variables also influence seasonal patterns of phenotypic flexibility in BMR (Swanson, 1991, Maddocks & Geiser, 2000). In tropical and subtropical latitudes, for instance, the need for enhanced cold tolerance during winter is presumably less than at higher latitudes, and the direction and magnitude of seasonal BMR variation may therefore be expected to be different to the patterns observed in high-latitude Holarctic residents (Swanson, 1991, Maddocks & Geiser, 2000). Another factor potentially influencing seasonal patterns of BMR, and possibly responsible for the summer increases in BMR observed in some species, is changes in body composition associated with reproductive cycles and the metabolic costs of maintaining reproductive organs (Vézina & Williams, 2003, 2005).

If the costs associated with a high BMR (e.g., increased food requirements) exceed the benefits, we might expect BMR to be reduced to the lowest feasible level (i.e., adaptive modulation *sensu* Karasov, 1992). The low overall BMR of desert birds, for instance, is thought to reflect the scarcity and unpredictability of food and water resources in xeric habitats (Tieleman & Williams, 2000, Williams & Tieleman, 2005). In environments where winter is associated with pronounced decreases in food availability, but not significant increases in thermoregulatory demands, one might expect seasonal BMR patterns to differ from those observed at higher latitudes, where prolonged periods of very cold weather demand elevated thermogenic capacity.

In this study, we investigated the magnitude and direction of seasonal BMR changes in five bird species that are resident year-round in the subtropical Kalahari Desert of southern Africa. The climate of the Kalahari region varies seasonally between cool and very dry winters, and summers with high daytime maxima temperatures and unpredictable rainfall (Lovegrove, 1993). We conducted the study in a desert habitat since birds are likely to experience substantial fluctuations in food availability, as well as seasonal variation in environmental temperatures. We also present an analysis of global variation in the magnitude and direction of avian seasonal BMR changes. Within-individual BMR variation has important implications for comparisons between observed and allometrically-predicted values (McKechnie, 2008), and we evaluate our results in the context of recent studies that analysed patterns of avian metabolic scaling.

Materials and methods

Study site and animal capture

The study took place in Molopo Nature Reserve (MNR; 25° 47' S, 22° 56' E, ~ 1000 m a.s.l.) in the Northwest Province of South Africa, during June - August 2007 (austral winter) and January - March 2008 (austral summer). The mean ± SD annual rainfall recorded at Molopo Nature Reserve over a 50-year period was 332 ± 105 mm, falling mainly between December and April (Meyer, Steinhauser, Jeltsch *et al.*, 2007). Air temperature (T_a) was measured in the study area using two temperature-sensitive data loggers (iButton Thermochron, Dallas Semiconductor, Dallas, U.S.A.), housed in ventilated polystyrene cups suspended in the shade ~ 2 m above the ground at two sites ~ 6 km apart. The mean daily minimum T_a measured

during the winter study period was 3.2°C (lowest T_a = -7.6°C), compared to 18.6°C in summer (lowest T_a = 15.6°C). The mean daily maximum T_a in winter was 27.6°C (highest T_a = 36.1°C), compared to 32.5°C in summer (highest T_a = 40.5°C). Mean daily temperatures were 14°C and 25°C during winter and summer, respectively. From November 2007 to March 2008 (summer) more than 500 mm of rain was recorded at MNR, whereas in winter (2007) only 15 mm of rain was recorded, on 4 June 2007.

Metabolic rates were measured in summer and winter in wild-caught nocturnal African scops-owls (*Otus senegalensis*, Swainson), crepuscular pearl-spotted owlets (*Glaucidium perlatum*, Vieillot), and diurnal fork-tailed drongos (*Dicrurus adsimilis*, Bechstein), crimson-breasted shrikes (*Laniarius atrococcineus*, Burchell) and white-browed sparrow-weaver (*Plocepasser mahali*, Smith). In the Kalahari Desert a large proportion of the diets of the five study species consists of terrestrial arthropods (Hockey, Dean & Ryan, 2005). The major egg-laying periods for all five species fall between August and January, when breeding activity is likely to coincide with significant rainfall events, although white-browed sparrow-weavers may lay opportunistically throughout the year (Hockey *et al.*, 2005). All birds were captured during the active phase of their circadian cycle using mist nets or spring traps baited with mealworms. Owls were usually lured into nets using vocalization playback. After capture, birds were weighed using a Pesola® scale (accurate to 0.5 g), and age (juvenile/adult) and moult status were determined from plumage examination (de Beer, Lockwood, Raijmakers, *et al.*, 2001). All individuals used in the study exhibited adult plumage, although the possibility does exist that some could have been immature birds (Hockey *et al.*, 2005). The study species could not be reliably sexed, with the exception of the two owls, where sexes could be

distinguished on the basis of their vocal response to call playback (Hockey, *et al.*, 2005) during trapping. We excluded any individuals that showed signs of breeding activity (e.g., abdominal brood patch or smear marks around beak from feeding chicks), in an effort to avoid obtaining data from reproductively active individuals. Each bird was ringed with an aluminium band for identification and kept individually in an indoor cage (0.125 m^3) constructed from shade cloth for a maximum of two days before experiments. During this time they were fed mealworms *ad libitum*, but food was withheld for at least five hours prior to commencement of metabolic measurements to ensure postabsorptive conditions. All birds were released within 1-2 days of capture. With the exception of two African scops-owls that were trapped during both seasons, all the seasonal metabolic measurements represent different individuals.

Gas exchange measurements

Metabolic rate was estimated from measurements of oxygen consumption ($\dot{V}_{O_2}$) and carbon dioxide production ($\dot{V}_{CO_2}$), obtained using a portable respirometry system in a field laboratory set up at the main camp in MNR. Birds were placed in suitably-sized 1.7 – 1.9 L plastic chambers of various heights within an insulated environmental chamber, constructed by lining the interior of a 66.2 L cooler box with copper tubing, through which temperature-controlled water was pumped (model ME circulator, Julabo Labortechnik, Seelbach, Germany). Air in the environmental chamber was mixed using a small electric fan. A perch was provided in each respirometry chamber, to permit normal sleeping postures above a stainless wire mesh screen, through which faeces dropped into a layer of mineral oil. Up to two respirometry chambers were placed in the environmental

chamber at a time. Air temperature within each respirometry chamber was measured using a 21-gauge Cu-Cn thermocouple (IT-18, Physitemp, Clifton NJ) and a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV, USA).

Atmospheric air from outside the building was drawn through a filter (model F3000-8G, CKD Corporation, China) using an air pump (D7 SE, Charles Austen Pumps, Surrey, UK) and supplied to the respirometry chambers through Bev-A-Line tubing (Thermoplastic Processes Inc., Warren, NJ). The flow rate through each respirometry chamber was regulated using an FMA-series mass flow controller (Omega, Bridgeport, NJ, USA), calibrated using a 1 L soap bubble flow meter (Baker & Pouchot, 1983). Flow rates of $1 - 2$ L min^{-1} were used throughout measurements, resulting in 99% equilibration times of 4 - 9 min, calculated using the equation of Lasiewski, Acosta and Bernstein (1966). We verified that these flow rates maintained the dewpoints of excurrent air well below the air temperatures in the field laboratory. Excurrent air from each respirometry chamber and a reference air supply (atmospheric air subsampled downstream of the filter and pump) was sequentially subsampled using a TR-RM8 Respirometry Multiplexer (Sable Systems). The CO_2 concentration of excurrent air was then measured using a LI-7000 CO_2/H_2O analyzer (Li-Cor, Lincoln, NE, USA). This analyser was regularly zeroed using nitrogen and spanned using a certified gas containing 1513 ppm CO_2. (AFROX, South Africa). The air samples then left the CO_2/H_2O analyzer, and water vapour and CO_2 were scrubbed using a silica gel/soda lime/silica gel column before passing through a FC-10a oxygen analyzer (Sable Systems) to measure fractional O_2 concentration. Baseline O_2 and CO_2 concentrations were obtained from the reference air for 15 minutes every hour. Outputs from these two gas analyzers and the thermocouple meter were

digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using Expedata data acquisition software (Sable Systems), with a sampling interval of 15 s.

Body temperature measurements

To verify that birds remained normothermic during metabolic measurements, and to investigate the possibility of seasonal variation in thermoregulatory variables, body temperature (T_b) was measured during metabolic measurements using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-18, Physitemp, Clifton NJ). This was inserted cloacally to a depth at which a slight withdrawal did not result in a change in the reading (1- 2 cm). The thermocouple was secured by attaching the wire to the feathers immediately behind the cloaca, using adhesive tape and a small wire paperclip. Thermocouple outputs were digitized using a TC-1000 thermocouple meter (Sable Systems).

Experimental protocol

All measurements of gas exchange were obtained during the rest-phase of birds' circadian cycles in darkened chambers, and from individuals that could reasonably be expected to be postabsorptive, based on the time elapsed ($\geq$ 5 hr) since capture or, in the case birds held in captivity the previous night, the removal of food from the holding cages. Measurements for the two owl species were carried out during the day, since both are mainly nocturnal, although Pearl-spotted owlets are sometimes active during the day in winter. Measurements for the three diurnal passerines were obtained at night. Each bird was placed in a respirometry chamber

within the environmental chamber approximately one hour before sunrise (nocturnal species)
or sunset (diurnal species), at which time a cloacal thermocouple was inserted and secured. We
ensured that the birds were perching calmly in the chambers, and then started recording
$\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ data at least one hour after sunset or sunrise. Measurements continued until
approximately one hour before the next sunset or sunrise. Corrections for drift in the O_2 and
CO_2 measurements were made using the appropriate regression analyses in Expedata (Sable
Systems). Resting metabolic rate was calculated from steady state traces of $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ in
Expedata, with the lowest 10 min mean $\dot{V}_{O_2}$ over the test period considered to be indicative of
resting values, following Liknes $et\ al.$ (2002). All $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ values were corrected to
STPD.

To obtain a reliable estimate of BMR requires that metabolic rate is measured within the
thermoneutral zone (TNZ). Thus, during each season the first two or three individuals of each
species caught were subjected to a ramped T_a profile during each test. An individual bird
experienced at least three T_a values, between 5° and 35°C, during a single measurement
session, lasting no longer than 10 h. Least-squares linear regression models were fitted to
metabolic rate and T_a data, and the lower critical limit of thermoneutrality (T_{lc}) was estimated
for each bird from the intercept of the regression line and the lowest observed metabolic rate.
Because of the small sample sizes for our T_{lc} estimates, which were between 26° and 29°C for
all five species, we conservatively measured BMR at a T_a equivalent to 1- 2°C higher than the
estimated T_{lc} of each species, in order to ensure that all measurements took place within the
TNZ.

Data analyses

$\dot{V}_{O_2}$ was calculated using the relevant equation in Withers (1977) and $\dot{V}_{CO_2}$ using

equation 3 in Walsberg and Wolf (1995). Respiratory exchange ratios (RER) were

determined as $\dot{V}_{CO_2} / \dot{V}_{O_2}$ and averaged 0.88 ± 0.06 (mean $\pm$ SD, data pooled for all

species) during the study. Although RER = 0.71 is generally considered indicative of

lipid metabolism, and thus a postabsorptive state, fasting birds may exhibit RER values

considerably higher (Walsberg & Wolf, 1995). Gas exchange measurements were

converted to metabolic rate (W) using the thermal equivalence data in table 4-2 in

Withers (1992). This approach assumes that only carbohydrates and lipids are

metabolized, and a maximum error of 6% is associated with protein metabolism

(Walsberg & Wolf, 1995).

Seasonal data were analyzed separately for each species. We used analyses of variance

(ANOVA) to test for seasonal changes in body mass (M_b) and T_b and BMR. In the one species

showing significant seasonal variation in M_b, we also performed analyses of covariance

(ANCOVA) on whole-animal BMR, with M_b as a covariate. In this manner we could

distinguish seasonal changes in BMR reflecting M_b changes from increases or decreases in

mass-specific BMR. In all species, a small number of individuals were undergoing light

primary moult during summer (moult scores of zero or ≥ 43 in 9-primaried species or ≥ 47 in

10-primaried species, de Beer *et al.*, 2001), but we found no statistical difference (or visual

difference when n < 3) between mass-specific BMR of moulting and non-moulting birds, and

summer BMR data were thus pooled for comparison with winter BMR. To compare our

observed BMR values to those predicted on the basis of M_b, we obtained predicted values from

McKechnie, Jetz & Freckleton's (2006) analysis of BMR in wild-caught birds and Tieleman &

William's (2000) phylogenetically-corrected equation for BMR in desert birds.

We examined global variation in the magnitude and direction of avian seasonal

BMR variation using winter/summer BMR ratios (ΔBMR) from the five species in this

study and an additional 21 species from the literature (obtained from review by

McKechnie 2008 and several more recent studies) using only data that represented mass-

specific BMR after acclimatization (Table 1). To test the hypothesis that climate (in

particular cold winter conditions) is a determinant of seasonal BMR variation, we

investigated possible relationships between ΔBMR and latitude, temperature and

hemisphere. To account for the possible effects of phylogenetic inertia (i.e., the tendency

for closely related species to resemble each other), we first tested for phylogenetic signal

in M_b and ΔBMR, using randomization tests for the mean-squared error, and by

calculating the K-statistic, as described by Blomberg, Garland and Ives (2003, Matlab

program PHYSIG_LL.m). We constructed a phylogeny based on that of Hackett,

Kimball, Reddy *et al.*, (2008), with relationships within the passerines based on Sibley

and Ahlquist's (1990) phylogeny, using PDTREE (Garland, Dickerman, Janis *et al.*,

1993) (Fig. 1). Two populations of *Poecile atricapillus* (Kansas and New York, USA)

were assumed to have a nucleotide distance between them of 0.56% (Gill, Mostrom &

Mack, 1993). All ΔBMR values were arcsine-transformed before analyses, whereas M_b

data were $\log_{10}$-transformed. For each species, latitude and climate data (Table 1) were

obtained from either the original papers or from http://www.worldclimate.com using the

data from the weather station nearest to the site of capture. We tested for effects of

latitude, mean T_a during the coldest month, mean daily minimum T_a during the coldest

month, and annual variation in T_a (i.e., the difference between mean T_a during the warmest and coldest months) on ΔBMR and M_b using both conventional and phylogenetically independent multiple regressions, following Lovegrove (2003). Since latitude and climate variables are intercorrelated, we used a correlation matrix to identify multicollinearity between these factors. All the climatic variables were significantly correlated with each other, as well as with latitude, and we subsequently included only a single environmental parameter in any one multiple regression model for ΔBMR ratios and M_b.

Independent contrasts for ΔBMR and M_b were calculated using PDTREE (Garland, Harvey & Ives, 1992). Transformation of branch lengths was performed using Grafen's transformation (rho = 0.25), confirming homogeneity of variances among contrasts (Garland *et al.*, 1992). We verified that passerines and non-passerines showed no obvious trends between independent contrasts and the square root of the sum of their branch lengths, which may indicate heterogeneous rates of character evolution between these clades. Regressions of independent contrasts for ΔBMR and M_b were then performed on independent contrasts of latitude and climate data, calculated using a star phylogeny (i.e., all tips radiating from a common ancestor using equal branch lengths), which produces estimates of correlations identical to conventional species data (Lovegrove, 2003, Wolf, Garland & Griffith, 2001, Purvis & Garland, 1993).

Results

Body mass

Significant changes in seasonal M_b were observed only in African scops-owls (Table 2),

with the mean M_b of the winter sample 12% lower than in summer.

Body temperature

All birds remained normothermic during metabolic measurements and none of the study

species showed any seasonal changes in T_b (Table 2), although we did not obtain

sufficient T_b data from the two owl species during metabolic measurements to perform

statistical analysis.

Basal metabolic rate

Whole-animal BMR was significantly lower in winter than in summer in all species

expect pearl-spotted owlets (Table 2). Mass-specific BMR was significantly lower in

winter than in summer in all five species, with mean reductions of 23% in African scops-

owls, 30% in pearl-spotted owlets, 35% on fork-tailed drongos, 29% in crimson-breasted

shrikes, and 17% in white-browed sparrow-weavers (Table 2, Fig. 2). The magnitude of

seasonal variation in whole-animal BMR was generally consistent with mass-specific

BMR changes (Table 2). In the African scops-owls, however, the winter BMR reductions

were largely explained by the 12% reduction in M_b that occurred during winter (Fig. 2),

and whole-animal BMR did not differ significantly between seasons after correcting for

M_b (ANCOVA, $F_{1,11} = 2.100$, $P = 0.175$). In all five species, both summer and winter

BMR were lower than the values predicted for wild-caught birds, but consistent with predictions for desert birds (Table 3)

Global variation in seasonal BMR changes

A significant phylogenetic signal was found for M_b, but not for ΔBMR (Table 4). In both conventional and PI multiple-regression analyses, M_b was not significantly related to ΔBMR, whereas ΔBMR was significantly related to all temperature variables and latitude in both conventional and PI regression analyses (Table 5, Fig. 3). Species inhabiting subtropical regions where mean daily temperatures during the coldest month of the year are above 0°C tended to have lower winter than summer BMR, whereas the opposite was true for species inhabiting colder, high-latitude regions (Fig. 3). There was no significant difference in ΔBMR between hemispheres after accounting for M_b and latitudinal variation (ANCOVA, $F_{1,27} = 2.240$, $P = 0.148$).

Discussion

We have shown that BMR is lower in winter than during summer in free-living birds from two orders and four families in the Kalahari Desert, suggesting that such a pattern may be widespread in birds inhabiting sub-tropical regions. The pattern we observed contrasts with the increased winter BMR typically observed in northern hemisphere species. Although winter BMR reductions have previously been reported in a small number of species, these studies involved individuals that were acclimatized under captive conditions (Weathers & Caccamise 1978, Maddocks & Geiser 2000, Bush *et al*. 2008).

The functional significance of BMR changes following winter acclimatization remains unclear (Liknes *et al.*, 2002). Thus far, seasonal BMR variation has been explained using the "energy demand hypothesis" (Williams & Tieleman, 2000, Tieleman *et al.*, 2003b), based on the notion that seasonal variation in support costs are needed to sustain the higher energy demand of nutritional organs and thermogenically active tissues during colder winter periods (Liknes *et al.*, 2002). In the present study, however, the coldest period of the year did not elicit higher maintenance energy demands. The processes responsible for the absence of winter BMR increases remain unclear, but one possibility is that the need for large winter metabolic changes, such as the elevations in M_{sum} associated with enhanced cold tolerance (Liknes *et al.*, 2002), are unnecessary for species resident in the Kalahari. The coldest T_a that our study species experienced (~ $-7°C$) is considerably higher than the winter temperatures birds typically experience at high latitudes in the Holarctic (frequently $T_a < -30°C$). For instance, the metabolic rates we observed in African scops-owls below their TNZ (B. Smit & A.E. McKechnie, unpublished data) suggest that their metabolic rate at the minimum T_a recorded during the study would be 2.5 – 3 X BMR, compared to 3 – 8 X BMR recorded for north-temperate birds under more severe cold exposure (Dutenhoffer & Swanson, 1996, Saarela, Klapper & Heldmaier, 1995, Marsh & Dawson, 1989). Moreover, our study species at MNR only experienced sub-zero T_a for a few hours each night, with daytime T_a typically above 20°C. The comparatively mild winter temperatures, together with reduced food availability and the general absence of breeding activity (Hockey *et al.*, 2005), may combine to make reductions in BMR more feasible than in very cold environments at higher latitudes. Whereas the prolonged periods of extremely cold weather experienced

by north-temperate species place increased thermogenic demands on organs and tissues responsible for nutrient uptake, processing and delivery, these seasonal elevations in demand for metabolic heat production are in all likelihood reduced or absent entirely in species at lower latitudes.

In small mammals, seasonal changes in BMR are often attributable to seasonal variation in M_b (Lovegrove, 2005). In the present study, neither the three passerine species nor Pearl-spotted owlets exhibited any significant seasonal changes in M_b, suggesting that their mass-specific BMR changes were largely the result of changes in body composition and/or the metabolic intensity of specific organs. On the other hand, the seasonal patterns of M_b in African scops-owls were consistent with the Dehnel effect observed in many small mammals, where winter M_b reductions are thought to be related to reduced metabolic costs (Lovegrove, 2005, Mezhzherin, 1964).

Our summer metabolic measurements took place outside of the peak egg-laying periods for the five study species, and we avoided, as far as possible, measuring BMR in individuals that were reproductively active. We are thus confident that the elevated summer BMRs we observed did not represent direct metabolic costs of reproduction, such as egg synthesis. However, factors such as an overall increase in thyroid activity, stress hormone levels and/or changes in organ masses during the breeding season can result in increased metabolic rate (Siegel, 1980, Wingfield & Farner, 1993, Vézina & Williams, 2003, 2005). Factors related to reproduction, which in desert birds is often directly related to rainfall (Maclean 1996), may well have influenced the seasonal patterns of BMR we observed, since unusually wet conditions occurred at MNR during our summer study period.

Desert birds generally have lower BMR than species from more mesic habitats (Tieleman & Williams 2000, Tieleman, Williams & Bloomer, 2003), and our observation that in all five species, both summer and winter BMR were similar to values predicted for desert birds, but 28 – 60% lower than values predicted for wild-caught birds (i.e., desert and non-desert species combined) is consistent with this idea. The reduced maintenance metabolic rates of desert birds and mammals are thought to facilitate reduced energy requirements in resource-poor environments, although a reduced metabolic rate would also facilitate water savings by reducing water flux and respiratory evaporative water loss (Williams & Tieleman, 2005, Tieleman & Williams, 2000, Lovegrove, 2000). The winter BMR reductions in our study corresponded with drier conditions and an 85% reduction in the abundance of terrestrial arthropods compared with summer (B. Smit & A.E. McKechnie, unpublished data), which comprise a major dietary component in all five species (Hockey *et al.*, 2005). A possible link between greater food availability and increased BMR involves larger sizes of digestive organs and/or increased metabolic intensity of maintenance organs (Williams & Tieleman, 2000), although a number of species held under captive conditions also showed winter reductions in BMR even when food was provided *ad libitum* (Weathers & Caccamise, 1978, Maddocks & Geiser, 2000, Bush *et al.*, 2008). In the latter studies, the weather conditions experienced by captive individuals were similar to those that would have been experienced by free-ranging individuals in natural habitats, although the monk parakeets in Weathers and Caccamise's (1978) study originated from a feral and not a natural population.

Our analysis of environmental correlates of the magnitude and direction of avian seasonal BMR variation reveals strong correlations with latitude and winter climate

variables. Mid-winter temperatures, in particular, explained most of the variation (60%) in the conventional analysis of seasonal BMR changes (Table 5). At lower latitudes, where winters are milder and seasonal changes in temperature are less pronounced, birds tend to have a seasonally stable or reduced winter BMR (Fig. 3A,B). The global pattern of a negative relationship between winter BMR and winter temperatures implies that birds requiring seasonal enhancements in thermogenic capacity experience concomitant increases in maintenance costs. However, the current lack of data from lower latitudes in the northern Hemisphere and higher latitudes in the southern Hemisphere means that any conclusions regarding correlations with latitude and/or temperature, or the existence of hemispheric differences, must remain tentative. Further limitations on our current understanding of global variation in avian seasonal metabolic variation include very limited data from the true tropics ($< 20°$ N or S), with one of the few exceptions being a study on the Puerto Rican Tody (*Todus mexicanus,* Merola-Zwartjes & Ligon, 2000). Moreover, we know very little about how seasonal BMR changes are influenced by interactions between energy and/or water availability and climatic variables, or how responses vary between free-ranging and captive populations. Future studies examining seasonal measurements of M_b, BMR, M_{sum} and field metabolic rate are necessary to elucidate the influence of BMR variation on energy and water balance.

In summary, the seasonal BMR changes exhibited by five species resident in a arid environment in the Kalahari Desert raise the possibility that these adjustments are related to energy and/or water savings, rather than increased thermoregulatory capacity or cold tolerance. On a global scale, the direction and magnitude of seasonal BMR variation are correlated with winter climate and latitude. It is possible that the dichotomy

observed in the global patterns of BMR variation represents an energy-saving/cold-tolerance trade-off, where extremely cold winter conditions result in up-regulated metabolic machinery associated with thermogenesis, but which incurs the cost of higher maintenance energy requirements. Future studies should examine more closely the functional roles of specific environmental variables (e.g. food and water availability, temperature and photoperiod) on seasonal metabolic variation, particularly in sub-tropical and tropical species.

Acknowledgements

Literature cited

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. *Comparative Biochemistry and Physiology* **89A**, 79-83.

Baker, W.C. & Pouchot, J.F. (1983) The measurement of gas flow. Part II. *Journal of the Air Pollution Control Association* **33**, 156-162.

Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 717-745.

Bush, N.G., Brown, M. & Downs, C.T. (2008) Seasonal effects on thermoregulatory responses of the Rock Kestrel, *Falco rupicolis*. *Journal of Thermal Biology* **33**, 404-412.

Cooper, S.J. (2000) Seasonal energetics of mountain chickadees and juniper titmice. *Condor* **102**, 635-644.

Cooper, S.J. & Swanson, D.L. (1994) Seasonal acclimatization of thermoregulation in the black-capped chickadee. *Condor* **96**, 638-646.

Dawson, W.R. (2003) Plasticity in avian responses to thermal challenges - an essay in honor of Jacob Marder. *Israeli Journal of Zoology* **49**, 95-109.

Dawson, W.R. & Carey, C. (1976) Seasonal acclimation to temperature in Cardueline finches. *Journal of Comparative Physiology* **112**, 317-333.

Dawson, W.R. & Marsh, R.L. (1988) Metabolic acclimatization to cold and season in birds. *Physiology of cold adaptation in birds.* (eds C. Bech & R.E. Reinertsen), pp. 83-94. Plenum Press, New York.

Dawson, W.R., Marsh, R.L., Buttemer, W.A. & Carey, C. (1983) Seasonal and geographic variation of cold resistance in house finches. *Physiological Zoology* **56**, 353-369.

de Beer, S.J., Lockwood, G.M., Raijmakers, J.H.F.A., Raijmakers, J.M.H., Scott, W.A., Oschadleus, H.D. & Underhill, L.G. (2001) *SAFRING bird ringing manual. ADU Guide 5.* Avian Demography Unit, University of Cape Town, Cape Town.

Doucette, L.I. & Geiser, F. (2008) Seasonal variation in thermal energetics of the Australian owlet-nightjar (*Aegotheles cristatus*). *Comparative Biochemistry and Physiology A* **151**, 615-620.

Dutenhoffer, M.S. & Swanson, D.L. (1996) Relationship of basal to summit metabolic rate in passerine birds and the aerobic capacity model for the evolution of endothermy. *Physiological Zoology* **69**, 1232-1254.

Garland, T., Dickerman, A.W., Janis, C.M. & Jones, J.A. (1993) Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**, 265-292.

Garland, T., Harvey, P.H. & Ives, A.R. (1992) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* **41**, 18-32.

Gill, F.B., Mostrom, A.M. & Mack, A.L. (1993) Speciation in North American chickadees: I. patterns of mtDNA genetic divergence. *Evolution* **47**, 195-212.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia,

K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A phylogenetic study of birds reveals their evolutionary history. *Science* **320**, 1763-1768.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (2005) *Roberts birds of southern Africa.*7ᵗʰ Ed. John Voelcker Bird Book Fund, Cape Town.

Jetz, W., Freckleton, R.P. & McKechnie, A.E. (2008) Environment, migratory tendency, phylogeny and basal metabolic rate in birds. *PLoS One* **3**, e3261.

Karasov, W.H. (1992) Tests of adaptive modulation hypothesis for diet control of intestinal nutrient transport. *American Journal of Physiology* **263**, R496-R502.

Klaassen, M., Oltrogge, M. & Trost, L. (2004) Basal metabolic rate, food intake, and body mass in cold- and warm-acclimated garden warblers. *Comparative Biochemistry and Physiology A* **137**, 639-647.

Lasiewski, R.C., Acosta, A.L. & Bernstein, M.H. (1966) Evaporative water loss in birds - I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comparative Biochemistry and Physiology* **19**, 445-457.

Liknes, E.T., Scott, S.M. & Swanson, D.L. (2002) Seasonal acclimatization in the American Goldfinch revisited: to what extent do metabolic rates vary seasonally? *Condor* **104**, 548-557.

Liknes, E.T. & Swanson, D.L. (1996) Seasonal variation in cold tolerance, basal metabolic rate, and maximal capacity for thermogenesis in white-breasted nuthatches *Sitta carolinensis* and downy woodpeckers *Picoides pubescens*, two unrelated arboreal temperate residents. *Journal of Avian Biology* **27**, 279-288.

Lill, A., Box, J. & Baldwin, J. (2006) Do metabolism and contour plumage insulation vary in response to seasonal energy bottlenecks in superb fairy-wrens? *Australian Journal of Zoology* **54**, 23-30.

Lovegrove, B.G. (1993) *The living deserts of southern Africa.* Fernwood Press, Vlaeberg.

Lovegrove, B.G. (2000) The zoogeography of mammalian basal metabolic rate. *American Naturalist* **156**, 201-219.

Lovegrove, B.G. (2003) The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B* **173**, 87-112.

Lovegrove, B.G. (2005) Seasonal thermoregulatory responses in mammals. *Journal of Comparative Physiology B* **175**, 231-247.

Maclean, G.L. (1996) Ecophysiology of desert birds. Springer-Verlag, Berlin.

Maddocks, T.A. & Geiser, F. (2000) Seasonal variations in thermal energetics of Australian silvereyes (*Zosterops lateralis*). *Journal of Zoology, London* **252**, 327-333.

Maldonado, K.E., Cavieres, G., Veloso, C., Canals, M. & Sabat, P. (2009) Physiological responses in rufous-collared sparrows to thermal acclimation and seasonal acclimatization. *Journal of Comparative Physiology B* **179**, 335-343**.**

Marsh, R.L. & Dawson, W.R. (1989) Avian adjustments to cold. *Advances in Comparative and Environmental Physiology 4: Animal Adaptation to the Cold* (ed L.C.H. Wang), pp. 206-253. Springer-Verlag, Berlin.

McKechnie, A.E. (2008) Phenotypic flexibility in basal metabolic rate and the changing view of avian physiological diversity: a review. *Journal of Comparative Physiology B* **173**, 235-247.

McKechnie, A.E., Chetty, K. & Lovegrove, B.G. (2007) Phenotypic flexibility in basal metabolic rate in Laughing Doves: responses to short-term thermal acclimation. *Journal of Experimental Biology* **210**, 97-106.

McKechnie, A.E., Freckleton, R.P. & Jetz, W. (2006) Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society B* **273**, 931-937.

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

Meyer, J., Steinhauser, J., Jeltsch, F. & Brandl, R. (2007) Large trees, acacia shrubs, and the density of *Thallomys nigricauda* in the thornveld savannah of South Africa. *Journal of Arid Environments* **68**, 363-370.

Mezhzherin, V.A. (1964) Dehnel's phenomenon and its possible explanation. *Acta Theriologica* **8**, 95-114.

O'Conner, T.P. (1995) Metabolic characteristics and body composition in house finches: effects of seasonal acclimatization. *Journal of Comparative Physiology B* **165**, 298-305.

O'Connor, T.P. (1996) Geographic variation in metabolic seasonal acclimatization in house finches. *Condor* **98**, 371-381.

Piersma, T. & Drent, J. (2003) Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology and Evolution* **18**, 228-233.

Pigliucci, M. (2001) *Phenotypic plasticity: beyond nature and nurture.* Johns Hopkins University Press, Balfimore.

Pohl, H. (1971) Seasonal variation in metabolic functions of bramblings. *Ibis* **113**, 185-193.

Pohl, H. & West, G.C. (1973) Daily and seasonal variation in metabolic response to cold during rest and exercise in the common redpoll. *Comparative Biochemistry and Physiology* **45A**, 851-867.

Purvis, A. & Garland, T. (1993) Polytomies in comparative analyses of continuous characters. *Systematic Biology* **42**, 569-575.

Rising, J.D. & Hudson, J.W. (1974) Seasonal variation in the metabolism and thyroid activity of the black-capped chickadee (*Parus atricapillus*). *Condor* **76**, 198-203.

Saarela, S., Klapper, B. & Heldmaier, G. (1995) Daily rhythm of oxygen consumption and thermoregulatory responses in some European winter- or summer-acclimatized finches at different ambient temperatures. *Journal of Comparative Physiology B* **165**, 366-376.

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

Siegel, H.S. (1980) Physiological stress in birds. *BioScience* **30**, 529-534.

Southwick, E.E. (1980) Seasonal thermoregulatory adjustments in white-crowned sparrows. *Auk* **97**, 76-85.

Swanson, D.L. (1990) Seasonal variation in cold hardiness and peak rates of cold-induced thermogenesis in the dark-eyed junco (*Junco hyemalis*). *Auk* **107**, 561-566.

Swanson, D.L. (1991) Seasonal adjustments in metabolism and insulation in the Dark-eyed Junco. *Condor* **93**, 538-545.

Swanson, D.L. (in press) Seasonal metabolic variation in birds: functional and mechanistic correlates. *Current Ornithology*.

Swanson, D.L. & Liknes, E.T. (2006) A comparative analysis of thermogenic capacity and cold tolerance in small birds. *Journal of Experimental Biology* **209**, 466-474.

Swanson, D.L. & Olmstead, K.L. (1999) Evidence for a proximate influence of winter temperatures on metabolism in passerine birds. *Physiological and Biochemical Zoology* **72**, 566-575.

Swanson, D.L. & Weinacht, D.P. (1997) Seasonal effects on metabolism and thermoregulation in northern bobwhite. *Condor* **99**, 478-489.

Tieleman, B.I. & Williams, J.B. (2000) The adjustment of avian metabolic rates and water fluxes to desert environments. *Physiological and Biochemical Zoology* **73**, 461-479.

Tieleman, B.I., Williams, J.B. & Bloomer, P. (2003a) Adaptation of metabolic rate and evaporative water loss along an aridity gradient. *Proceedings of the Royal Society B* **270**, 207-214.

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

Vezina, F., Jalvingh, K., Dekinga, A. & Piersma, T. (2006) Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. *Journal of Experimental Biology* **209**, 3141-3154.

Vézina, F. & Williams, T.D. (2003) Plasticity in body composition in breeding birds: what drives the metabolic costs of egg production? *Physiological and Biochemical Zoology*, **76**(5), 716-30.

Vézina, F. & Williams, T.D. (2005) The metabolic cost of egg production is repeatable. *Journal of Experimental Biology*, **208**, 2533-38.

Walsberg, G.E. & Wolf, B.O. (1995) Variation in the respirometry quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. *Journal of Experimental Biology* **198**, 213-219.

Weathers, W.W. & Caccamise, D.F. (1978) Seasonal acclimatization to temperature in monk parakeets. *Oecologia* **35**, 173-183.

West, G.C. (1972) The effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. *Comparative Biochemistry and Physiology* **43A**, 293-310.

White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) The basal metabolic rate of birds is associated with habitat temperature and precipitation, not productivity. *Proceedings of the Royal Society B* **274**, 287-293.

Wijnandts, H. (1984) Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* **72**, 1-92.

Williams, J.B. & Tieleman, B.I. (2000) Flexibility in basal metabolic rate and evaporative water loss among hoopoe larks exposed to different environmental temperatures. *Journal of Experimental Biology* **203**, 3153-3159.

Williams, J.B. & Tieleman, B.I. (2005) Physiological adaptation in desert birds. *BioScience* **55**, 416-425.

Wingfield, J.C. & Farner, D.S. (1993) Endocrinology of reproduction in wild species. *Avian Biology, Volume IX* (eds D.S. Farner, J.R. King & K.C. Parkes), pp. 163-327. Academic Press, San Diego, Caifornia, USA.

Withers, P.C. (1977) Measurement of VO_2, VCO_2, and evaporative water loss with a flow- through mask. *Journal of Applied Physiology* **42**, 120-123.

Withers, P.C. (1992) *Comparative animal physiology.* Saunders College Publishing, Fort Worth.

Wolf, C.M., Garland, T. & Griffith, B. (2001) Predictors of avian and mammalian translocation success: reanalysis with phylogenetically independent contrasts. *Biological Conservation* **86**, 243-255.

Zheng, W.-H., Li, M., Liu, J.-S. & Shao, S.-L. (2008a) Seasonal acclimatization of metabolism in Eurasian tree sparrows (*Passer montanus*). *Comparative Biochemistry and Physiology A* **151**, 519-525.

Zheng, W.-H., Liu, J.-S., Jiang, X.-H., Fang, Y.-Y. & Zhang, G.-K. (2008b) Seasonal variation on metabolism and thermoregulation in Chinese bulbul. *Journal of Thermal Biology* **33**, 315-319.

Table 1: Avian species in which seasonal adjustments in mass-specific BMR have been investigated. For each species, body mass (M_b), winter BMR/summer BMR (W/S) and hemisphere (H; N = northern, S = southern) are provided.

Species	H	M_b (g)	W/S	Reference
Northern Bobwhite (*Colinius virginianus*)	N	218	1.063	1
Australian Owlet-nightjar (*Aegotheles cristatus*)	S	45.6	0.961	2
Long-eared Owl (*Asio otus*)	N	244	1.072	3
Downy Woodpecker (*Picoides pubescens*)	N	24.1*	1.398	4
Rock Kestrel (*Falco rupicolis*)	S	214	0.877	5
Monk Parakeet (*Myiopsitta monachus*)	N	83.1	0.756	6
Superb Fairy-wren (*Malurus cyaneus*)	S	9.05*	1.117	7
White-breasted Nuthatch (*Sitta carolinensis*)	N	19.4*	1.333	4
Juniper Titmouse (*Baeolophus ridgwayi*)	N	16.6	1.144	8
Black-capped Chickadee (*Poecile atricapillus*)	N	11.9	1.000	9
Black-capped Chickadee (*Poecile atricapillus*)	N	13.1	1.144	10
Mountain Chickadee (*Poecile gambeli*)	N	11.1	1.174	8
Chinese Bulbul (*Pycnonotus sinensis*)	N	29.4*	1.174	11
Australian Silver-eye (*Zosterops lateralis*)	S	11.1	0.799	12
Eurasian Tree-sparrow (*Passer montanus*)	N	18.6*	1.350	13
Brambling (*Fringilla montifringilla*)	N	24.1*	0.982	14
Common Redpoll (*Acanthis flammea*)	N	14.6*	1.308	15
American Goldfinch (*Carduelis tristis*)	N	13.7*	1.097	16
House Finch (*Carpodacus mexicanus*)	N	20.1*	0.957	17
White-crowned Sparrow (*Zonotrichia leucophrys*)	N	26.3	1.326	18
Rufous-crowned Sparrow (*Zonotrichia capensis*)	S	19.5	1.000	19
Dark-eyed Junco (*Junco hyemalis*)	N	18.6*	1.092	20

* = significant variation in body mass between winter and summer.

References: 1. Swanson and Weinacht (1997), 2. Doucette and Geiser (2008), 3. Wijnandts (1984), 4. Liknes and Swanson (1996), 5. Bush et al. (2008). 6. Weathers and Caccamise (1978), 7. Lill, Box and Baldwin (2006), 8. Cooper (2000), 9. Cooper and Swanson (1994), 10. Rising and Hudson (1974), 11. Zheng, Liu, Jiang *et al.* (2008b), 12. Maddocks and Geiser (2000), 13. Zheng Li, Liu *et al*. (2008a), 14. Pohl (1971), 15. Pohl and West (1973), 16. Dawson and Carey (1976), 17. O'Connor (1995), 18. Southwick (1980), 19. Maldonado *et al.* (2009), 20. Swanson (1991).

Table 2. Seasonal changes in body temperature, body mass, whole-animal basal metabolic rate (WA BMR) and mass-specific basal metabolic rate (MS BMR) in African scops-owls (*Otus senegalensis*), pearl-spotted owlets (*Glaucidium perlatum*), fork-tailed drongos (*Dicrurus adsimilis*), crimson-breasted shrikes (*Laniarius atrococcineus*) and white-browed sparrow-weavers (*Plocepasser mahali mahali*) in Molopo Nature Reserve, South Africa. Sample sizes are provided in parentheses. For each parameter, the *F*-ratio and probability estimated from an analysis of variance (ANOVA) comparing values between seasons is provided.

Species	Summer	Winter	*F*	*P*
African scops-owl				
Body temperature (°C)	39.3 (1)	38.7 ± 0.4 (2)	-	
Body mass (g)	62.2 ± 4.1 (7)	55.4 ± 3.7 (7)*	$F_{1,12} = 11.570$	.005
WA BMR (W)	0.411 ± 0.094 (7)	0.280 ± 0.042 (7)*,a	$F_{1,12} = 13.109$	.004
MS BMR (mW g^{-1})	6.584 ± 1.330 (7)	5.045 ± 0.617 (7)*	$F_{1,12} = 8.228$	.014
Pearl-spotted owlet				
Body temperature (°C)	39.3 ± 0.3 (3)	39.6 (1)	-	
Body mass (g)	66.4 ± 4.8 (5)	70.3 ± 5.7 (3)	$F_{1,6} = 1.100$	.335
WA BMR (W)	0.526 ± 0.107 (5)	0.383 ± 0.059 (3)	$F_{1,6} = 5.505$	.057
MS BMR (mW g^{-1})	7.881 ± 1.142 (5)	5.496 ± 1.132 (3)*	$F_{1,6} = 8.940$	.024
Fork-tailed drongo				
Body temperature (°C)	38.6 ± 0.4 (6)	38.6 ± 0.7 (6)	$F_{1,10} = 0.000$	.989
Body mass (g)	44.8 ± 2.6 (8)	42.6 ± 4.0 (7)	$F_{1,13} = 1.670$	.219
WA BMR (W)	0.424 ± 0.107 (8)	0.266 ± 0.072 (7)*	$F_{1,13} = 17.075$	.001
MS BMR (mW g^{-1})	9.425 ± 2.035 (8)	6.164 ± 1.215 (7)*	$F_{1,13} = 13.135$	.003
Crimson-breasted shrike				

Species	Summer	Winter	F	P
Body temperature (°C)	38.6 ± 0.3 (5)	38.0 ± 0.8 (5)	$F_{1,8} = 3.380$	.103
Body mass (g)	43.0 ± 2.8 (6)	41 ± 2.3 (5)	$F_{1,9} = 1.58$	.240
WA BMR (W)	0.398 ± 0.081 (6)	0.267 ± 0.050 (5)*	$F_{1,9} = 11.686$	.008
MS BMR (mW g^{-1})	9.210 ± 1.444 (6)	6.520 ± 1.109 (5)*	$F_{1,9} = 12.793$	.006
White-browed sparrow-weaver				
Body temperature (°C)	38.8 ± 0.5 (4)	39.1 ± 1.2 (4)	$F_{1,6} = 0.310$	.601
Body mass (g)	40.6 ± 2.5 (7)	40.6 ± 3.4 (6)	$F_{1,11} = 0.000$	.950
WA BMR (W)	0.346 ± 0.033 (7)	0.290 ± 0.049 (6)*	$F_{1,11} = 5.857$	.034
MS BMR (mW g^{-1})	8.573 ± 1.347 (7)	7.097 ± 0.636 (6)*	$F_{1,11} = 6.884$	.024

* = significant difference (ANOVA)

[a] = no significant difference after controlling for the effects of body mass using an ANCOVA.

Table 3. Mean (± SD) seasonal basal metabolic rate (BMR) of five species as percentages of the values predicted by allometric equations for wild-caught birds (McKechnie *et al.*, 2006) and desert birds (Tieleman & Williams, 2000) respectively. For all five species, summer and winter BMR was lower than the predicted values for wild-caught birds (McKechnie *et al.*, 2006), but consistent with the predictions for desert birds (Tieleman & Williams, 2000).

Species	McKechnie et al (2006) %		Tieleman & Williams (2000) %	
	summer	winter	summer	winter
African scops-owl	57 ± 12.5	40 ± 5.6	99 ± 5.7	90 ± 3.8
Pearl-spotted owlet	72 ± 13.1	52 ± 8.6	104 ± 4.2	95 ± 5.2
Fork-tailed drongo	66 ± 15.8	42 ± 10.2	106 ± 6.0	93 ± 6.8
Crimson-breasted shrike	63 ± 11.8	43 ± 7.7	104 ± 4.1	95 ± 5.2
White-browed sparrow-weaver	56 ± 6.3	46 ± 6.6	103 ± 4.1	97 ± 3.6

Table 4. Statistics for tests for phylogenetic signal (randomization test) and phylogenetic signal strength (K) (adapted from Blomberg, Garland & Ives 2003), for $\log_{10}$-transformed body mass (M_b) and arcsin-transformed winter BMR/summer BMR ratios (ΔBMR) of 26 bird species.

Trait	n	MSE candidate	MSE star	Expected MSE_o/MSE	Observed MSE_o/MSE	K	P
$\log_{10} M_b$	27	0.070	0.163	2.501	4.345	1.737	<0.001
Arcsin ΔBMR	27	0.193	0.073	2.501	0.385	0.154	0.264

Table 5. Statistics for four conventional and phylogenetically independent (PI) multiple regression models investigating the influence of latitude and temperature variables on arcsin-transformed winter BMR/summer BMR ratios (ΔBMR) of 26 bird species. In the PI models, linear contrasts were calculated from a hierarchical phylogeny for heritable traits [$\log_{10}$body mass (M_b) and arcsin ΔBMR] and from a non-hierarchical star phylogeny for the latitude and temperature variables. *Beta* is the standardized partial regression of each independent variable and is thus a measure of strength of the variable on arcsin ΔBMR.

	Model 1		Model 2		Model 3		Model 4	
	Beta	*P*	*Beta*	*P*	*Beta*	*P*	*Beta*	*P*
Conventional models								
$\log_{10}M_b$	−0.256	0.092^{ns}	−0.127	0.366^{ns}	−0.200	0.203^{ns}	−0.149	0.295^{ns}
Latitude	0.617	<0.001						
Mean T_a (coldest month)			−0.721	<0.001				
Minimum daily T_a (coldest month)					−0.611	0.001		
Mean T_a (warmest month) − mean T_a (coldest month)							0.702	<0.001
Model $F_{(2,26)}$	12.364		17.977		11.260		16.724	
Model r^2	0.507		0.600		0.484		0.582	
Model *P*	<0.001		<0.001		<0.001		<0.001	
Phylogenetically independent models								
$\log_{10}M_b$	−0.185	0.289^{ns}	−0.078	0.640^{ns}	−0.123	0.489^{ns}	−0.056	0.741^{ns}
Latitude	0.553	0.003						
Mean T_a (coldest month)			−0.634	0.001				
Minimum daily T_a (coldest month)					−0.551	0.004		

Mean T_a (warmest month) − mean T_a (coldest month)				0.635 0.001
Model $F_{(2,25)}$	6.979	9.064	6.429	8.766
Model r^2	0.378	0.441	0.359	0.433
Model P	0.004	0.001	0.006	0.001

Figure legends

Fig. 1. Phylogeny of 26 avian species in which seasonal adjustments in mass-specific

basal metabolic rate have been investigated, constructed using the phylogenetic data from

the five species in this study and an additional 21 species from the literature (Table 1).

The total height of the phylogeny from the base node to the branch tips is 28 $\Delta T_{50}H$ units

(Sibley & Ahlquist, 1990).

Fig. 2. Mean ± SD whole-animal basal metabolic rate [BMR (W)] and body mass (g)

measured in winter and summer in five bird species in Molopo Nature Reserve, South

Africa.

Fig. 3. Relationships between avian winter/summer mass-specific basal metabolic rate

(BMR) ratios and mean temperatures of acclimatization sites during the coldest month

(A), latitude (B), and $\log_{10}$body mass (C). Latitude and temperature values were obtained

from either the original papers or http://www.worldclimate.com. Conventional (i.e., non-

phylogenetically independent) linear regression models with significant fits are indicated

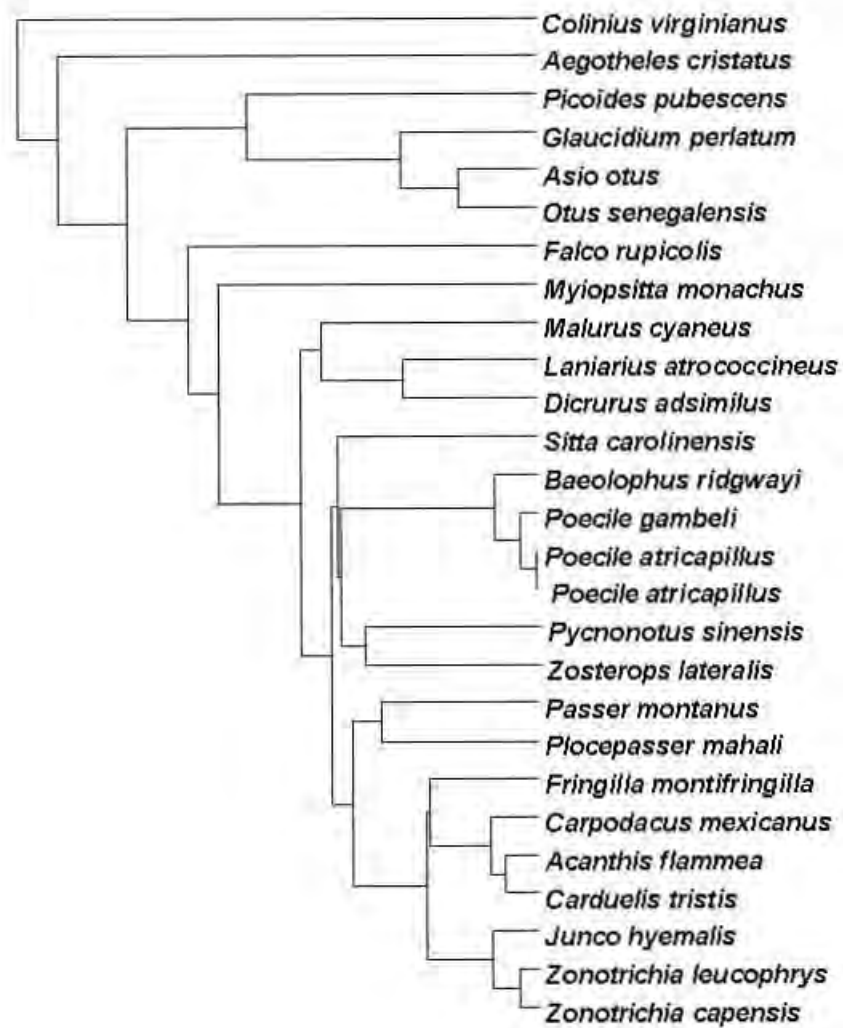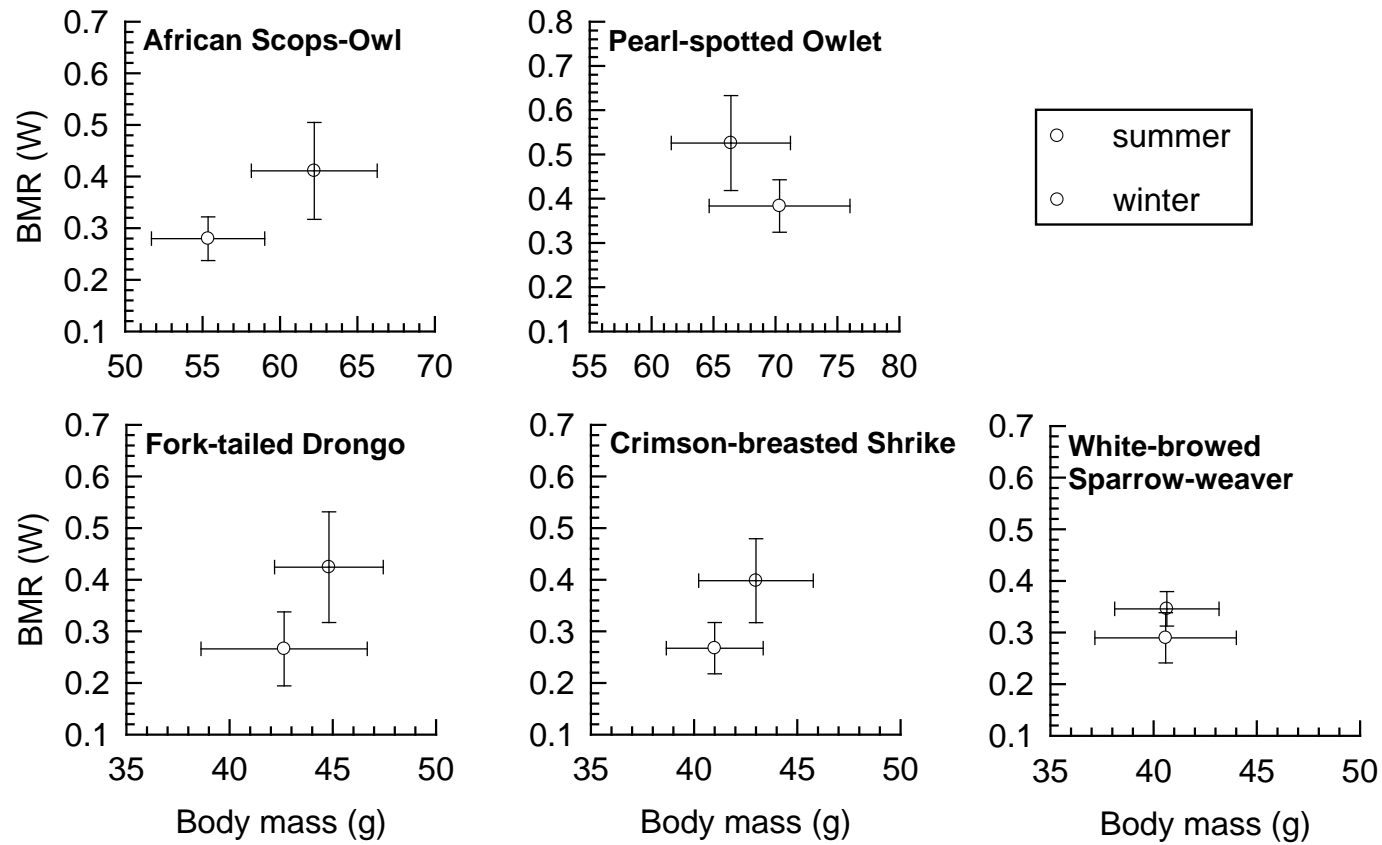by solid lines (see Table 5 for statistics).

Figure 1

Figure 2

Figure 3