Seasonal Metabolic Variation in Two Populations of an Afrotropical Euplectid Bird

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ABSTRACT

Many birds exhibit seasonal phenotypic flexibility in basal metabolic rate (BMR) and summit metabolism (M_{sum}), but very little information is available for species from subtropical latitudes or for conspecific populations from sites that vary in climate. We measured body mass (M_b), BMR, and M_{sum} in summer and winter in two populations of the southern red bishop *Euplectes orix*, a passerine that is widespread in southern Africa. One population occurs at a comparatively warmer coastal site (mean daily minimum air temperature [T_a] in midwinter, 8.3°C) and the other at a colder inland site (mean daily minimum T_a in midwinter, −2.8°C). Bishops from both populations significantly increased M_b in winter. However, seasonal metabolic adjustments differed considerably between the populations. The inland population significantly increased BMR by approximately 58%, mass-specific BMR by approximately 31%, and M_{sum} by approximately 15% in winter, although mass-specific M_{sum} did not change significantly. In contrast, the coastal population showed no significant seasonal change in BMR and significant winter reductions in mass-specific BMR (~15%), M_{sum} (~8%), and mass-specific M_{sum} (~15%). The interpopulation differences in the magnitude and direction of seasonal mass-specific BMR changes are qualitatively consistent with global patterns, although the increase shown by the inland population is larger than expected. Our data reveal that avian seasonal metabolic adjustments can vary greatly within subtropical species depending on the climatic conditions experienced by the birds, and our findings reiterate the need to better understand metabolic flexibility in species that inhabit lower latitudes.

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Introduction

Birds, like other animals, exhibit considerable metabolic diversity, with rates of energy turnover varying widely among and within species. This variation is evident in minimum and maximum resting metabolic rates measured under standardized conditions (basal metabolic rate [BMR] and summit metabolism [M_{sum}], respectively) as well as in overall daily energy turnover (e.g., Anderson and Jetz 2005). The major sources of avian metabolic diversity include allometric scaling with body mass (M_b; Brody and Proctor 1932; Lasiewski and Dawson 1967; White et al. 2007*b*), phylogenetic inertia (Lasiewski and Dawson 1967; Bennett and Harvey 1987; Reynolds and Lee 1996), adaptation (Tieleman and Williams 2000; Wiersma et al. 2007*b*; McNab 2009), and phenotypic plasticity (Tieleman et al. 2003; McKechnie 2008; Swanson 2010). These sources of metabolic variation have profound implications for how birds interact with physical environments and allocate energy during annual cycles, and an understanding of these sources of variation is crucial for elucidating the selective pressures acting on avian metabolic machinery.

The contribution of phenotypic flexibility, a subcategory of phenotypic plasticity involving short-term, reversible phenotypic adjustments (Piersma and Drent 2003), to overall avian metabolic diversity has been highlighted in recent decades. In addition to metabolic flexibility associated with migration (Battley et al. 2001; Kvist and Lindström 2001) and thermal acclimation under laboratory conditions (Tieleman et al. 2003; Klaassen et al. 2004; McKechnie et al. 2007), one major source of metabolic variation is seasonal acclimatization (Weathers and Caccamise 1978; McKechnie and Swanson 2010; Swanson 2010). Although it has long been known that many species that inhabit temperate latitudes increase BMR and M_{sum} during winter, presumably in response to the need for seasonally enhanced cold tolerance (Weathers and Caccamise 1978; Swanson 2010), it now appears that seasonal variation, at least in BMR, is also widespread in species that inhabit subtropical latitudes (Ambrose and Bradshaw 1988; Maddocks and Geiser 2000; Maldonado et al. 2009; Smit and McKechnie 2010). However, the magnitude and direction of seasonal changes in BMR vary with latitude and temperature: species that inhabit temperate regions typically increase BMR in winter, whereas species that inhabit subtropical regions typically decrease BMR in winter (Smit and

Table 1: Seasonal air temperature variation at two sites in the Eastern Cape province of South Africa where body mass and metabolic variation were investigated in southern red bishops *Euplectes orix*

Site	Summer temperature (°C)		Winter temperature (°C)	
	Minimum	Maximum	Minimum	Maximum
Port Elizabeth (175 m asl)	17.4 ± .2	25.5 ± .8	8.3 ± .6	20.5 ± 1.1
Aliwal North (1,300 m asl)	14.5 ± .8	30.4 ± 1.4	−2.8 ± 1.1	18.0 ± 1.3

Note. Data are mean monthly temperatures (±SD) for the period 2005–2011, which were obtained from the South African Weather Service.

McKechnie 2010). This latitudinal gradient in seasonal metabolic responses is thought to reflect broad variation in the relative importance of cold tolerance during severe temperate-zone winters versus energy conservation during winter at subtropical latitudes (Smit and McKechnie 2010).

Our knowledge of seasonal metabolic adjustments in birds from tropical and subtropical latitudes remains rudimentary, and there are a number of questions that have yet to be addressed. First, no data are available on seasonal variation in M_{sum} in subtropical species, which makes it difficult to evaluate the functional significance of BMR adjustments. Second, how do seasonal metabolic changes vary among habitats that differ in factors such as temperature, primary productivity, and precipitation seasonality? Relationships between BMR and climatic variables such as temperature, aridity, and primary productivity have been explored at an interspecific level, with a single BMR value per species (Tieleman and Williams 2000; White et al. 2007*a*; Jetz et al. 2008), but the influence of these variables on seasonal adjustments in metabolic rates remains unclear. Third, intraspecific variation remains largely unexplored; does the direction and/or magnitude of seasonal metabolic changes vary among populations of subtropical species that inhabit different environments? Although we are not aware of any such data for seasonal acclimatization in free-living subtropical birds, rufous-collared sparrows *Zonotrichia capensis* from habitats with more pronounced climatic seasonality showed greater changes in BMR in response to thermal acclimation than did populations from more seasonally stable environments (Cavieres and Sabat 2008). Finally, it is also unclear to what extent seasonal metabolic changes differ between captive and free-ranging populations; captive populations of some species, such as the greater vasa parrot *Coracopsis vasa* (Lovegrove et al. 2011), appear to fit the general pattern of winter BMR downregulation in subtropical latitudes identified by Smit and McKechnie (2010), whereas other species, such as the red-winged starling *Onychognathus morio* (Chamane and Downs 2009) and house sparrow *Passer domesticus* (Nzama et al. 2010), do not.

In this study, we addressed a subset of the questions outlined above by quantifying seasonal variation in both BMR and M_{sum} in two wild populations of a widespread southern African passerine, the southern red bishop *Euplectes orix*. This nonmigratory species occurs throughout the more mesic eastern regions of southern Africa and inhabits grasslands, marshes, and cultivated areas (Craig 2005). We predicted that (1) seasonal patterns of metabolic adjustments should vary with temperature,

with a population from a warmer environment exhibiting more pronounced winter downregulation of BMR than the population from a colder environment and that (2) M_{sum} adjustments should mirror those of BMR. The latter prediction arises from the observation that small, temperate-zone species tend to increase both BMR and M_{sum} in winter (reviewed in McKechnie and Swanson 2010; Swanson 2010) as well as the qualitatively similar relationships between mean winter temperature and both BMR and M_{sum} (Swanson and Olmstead 1999).

Material and Methods

Study Sites and Bird Capture

During summer (January and February 2011) and winter (June and July 2011), we measured BMR and M_{sum} in southern red bishop populations at two sites in the Eastern Cape province of South Africa, namely, Aliwal North (30°42′S, 26°43′E; 1,300 m asl) and Port Elizabeth (33°59′S, 25°30′E; 175 m asl). At Aliwal North, birds were caught in reed beds adjacent to a 0.9-km² dam, whereas at Port Elizabeth they were trapped in reed beds at a small catchment characterized by shallow water levels. These two sites vary considerably in terms of seasonal patterns of air temperature, particularly with regard to minimum temperatures in winter and seasonal temperature range (table 1). Bishops at both sites have access to artificial food resources: the Port Elizabeth birds occur in proximity to a large number of suburban gardens, whereas the Aliwal North birds have access to at least one grain silo. At both sites, birds were captured with mist nets and were marked with individual identification rings. We used only adult female birds for the study to avoid the potentially confounding effects of breeding season ornamentation in males. In this region, most egg laying takes place between November and January (Craig 2005), so it is possible that some of the individuals that we used were reproductive at the time of measurement, although we minimized this possibility by excluding birds with obvious brood patches. Immediately after capture, birds were transported to a field laboratory near each capture site. BMR and M_{sum} data were obtained from the same individuals within seasons (but with sample sizes varying slightly) and from different individuals across seasons. Typically, birds were captured on day 1 and BMR measurements were obtained that night; birds were then held in captivity for 24–48 h in cages (45 cm × 30 cm × 40 cm) with water and food available ad lib., after which time M_{sum} was measured.

Food was withheld for 2–3 h before all metabolic measurements.

Metabolic Rate Measurements

Metabolic rates were measured indirectly as oxygen consumption ($\dot{V}_{O_2}$) using a portable open-flow respirometry system at each field site, with an air atmosphere for BMR measurements and helox (21% O_2, 79% He) for M_{sum}. Birds were placed individually in 1.9-L chambers constructed from airtight plastic containers, each fitted with wooden perches to ensure normal perching postures. Chambers containing birds were placed in a darkened environmental chamber constructed from a 70-L cooler box with its interior lined with copper tubing through which temperature-controlled water was pumped by a circulating water bath (model FRB22D, Lasec, Cape Town, South Africa). A small fan was used to ensure air circulation within the cooler box. Air temperatures within the respirometry chambers were measured with temperature-sensitive data loggers (iButton Thermochron DS1922L, Maxim, Sunnyvale, CA). The iButtons were calibrated in a temperature-controlled water bath against a digital thermometer with accuracy traceable to the National Institute of Standards and Technology.

For resting metabolic rate and BMR measurements, atmospheric air was pulled through each chamber by a pump (MFS-2, Sable Systems, Las Vegas, NV), with a silica gel column upstream of the pump. Flow rates of approximately 450 mL min^{-1}, selected to ensure that chamber O_2 remained within 0.5% of incurrent O_2, were used for all measurements. Excurrent air from each chamber (up to two birds were measured simultaneously) and a reference channel consisting of an empty chamber through which air was drawn at similar flow rates were sequentially subsampled by manually switching the airstreams. Subsampled air was pulled through soda lime and silica gel columns to remove CO_2 and water vapor, respectively, before passing through an oxygen analyzer to measure fractional O_2 concentration (Foxbox-C Field Gas Analysis System, Sable Systems). The latter system includes a subsampling pump, and digital outputs were recorded using Expedata data acquisition software (Sable Systems) on a personal computer, with a sampling interval of 1 s. The oxygen analyzer was spanned using dried atmospheric air before each set of measurements.

For M_{sum} measurement, helox gas (Afrox, Johannesburg, South Africa) was pushed through the chamber at flow rates of 1.4 L min^{-1} using an FMA-series mass flow controller (Omega, Bridgeport, NJ), which was calibrated using a 1-L soap bubble flow meter (Baker and Pouchot 1983). Baseline chamber [O_2] was measured at the start of each run using an empty chamber with helox flowing through for 10 min, after which time a bird was placed in the chamber. An additional 10-min baseline measurement was performed at the end of each run.

Experimental Protocol

Before metabolic rate measurement, the body mass of each bird was recorded to 0.5 g with a 50-g spring balance (Pesola, Baar,

Switzerland). For each population (Port Elizabeth and Aliwal North) in each season (summer and winter), the thermoneutral zone (TNZ) was determined by measuring $\dot{V}_{O_2}$ in four postabsorptive individuals during the rest phase at a series of air temperatures (10°, 15°, 20°, 25°, 28°, 30°, 32°, 35°, and 38°C) in random order. For each individual, the lower critical limit of thermoneutrality (T_{lc}) was calculated as the intercept of a regression model fitted to $\dot{V}_{O_2}$ at mean air temperature (T_a) values that were clearly below the TNZ, and the mean BMR was calculated from the lowest $\dot{V}_{O_2}$ values. For BMR measurements, birds were placed in the chambers at night, at least 30 min before the start of measurements, at an air temperature 1°–2°C above the mean T_{lc} for that season and population combination. Each measurement cycle consisted of fractional O_2 in each chamber being measured for 10 min, followed by a 10-min measurement for the reference channel. Each bird spent 2.2–2.7 h in the chamber, with BMR being determined from measurements taken toward the end of this period, when $\dot{V}_{O_2}$ appeared to reach minimum values. The BMR was measured in 14–18 birds per site and season and was taken as the lowest mean $\dot{V}_{O_2}$ over a period of 6.7 min. The BMRs were always measured at least 1.5 h after the birds were placed in the chambers, so we are confident that all measurements represent data from postabsorptive individuals.

The M_{sum} was measured as the maximum cold-induced $\dot{V}_{O_2}$ in a helox atmosphere using the static cold exposure method (Swanson et al. 1996). Helox increases heat-loss rates in small birds approximately threefold compared with those experienced in air, which allows measurements of M_{sum} to take place at moderate air temperatures (Rosenmann and Morrison 1974; Swanson 1993). The $\dot{V}_{O_2}$ was measured in postabsorptive birds during the active phase at four helox temperatures (approximately 5°, 8°, 10°, and 15°C) in random order to determine the cold limit (T_{cl}). The cold limit was established as the helox temperature at which $\dot{V}_{O_2}$ was maximum. When M_{sum} values were not significantly different (t-test) between two helox temperatures, the higher of the two was considered the T_{cl}. Once the T_{cl} was established for each site and season (mean values for Aliwal North, 6.7°C in winter and 8.6°C in summer; mean values for Port Elizabeth, 7.5°C in winter and 6.9°C in summer), M_{sum} was measured in 11–18 individuals per site and season at the T_{cl}. During M_{sum} measurements, body temperatures (T_b) were measured with the use of a fine-gauge Cu-Cn thermocouple (TopTronic T235H) inserted approximately 5 mm into the cloaca until a slight withdrawal did not result in a change in the measured value. T_b measurements were obtained before and less than 20 s after each M_{sum} measurement. Hypothermia in birds during measurements was detected either by a steady decrease in oxygen consumption or by $T_b < 37$°C (Swanson et al. 1996). Hypothermic birds were immediately removed from the chamber. Individuals were measured for a maximum period of 40 min, because the absolute maximum $\dot{V}_{O_2}$ was always detected within this time. The M_{sum} was taken as the highest mean $\dot{V}_{O_2}$ over a period of 13.3 min. Reanalysis of most of the data with a shorter sampling period (5 min) made very small (1.5%–3.7%) differences to measured mean

M_{sum} values, and we are thus satisfied that our data provide an accurate reflection of maximum resting metabolic rate in this species.

Data Analysis

The $\dot{V}_{O_2}$ was calculated using the relevant equations provided by Lighton (2008). Body mass, BMR, mass-specific BMR (MS-BMR), M_{sum}, and mass-specific M_{sum} (MS-M_{sum}) data were tested for normality using the Shapiro-Wilk test and homoscedasticity using Levene's test. Relationships between metabolic rates and M_b were investigated using linear regressions. We analyzed variation in M_b, BMR, and MS-BMR using two-way ANOVA with site and season as categorical predictor variables and Holm-Sidak posthoc tests. The complete M_{sum} and MS-M_{sum} data sets were significantly heteroscedastic (Levene's test, $P < 0.05$), which precluded analysis with two-way ANOVA. Instead, we used unequal variance t-tests (Ruxton 2006) to compare M_{sum} and MS-M_{sum} among seasons within sites. Statistical analyses were conducted using SigmaPlot 12 and Statistica 10 software.

Results

Body Mass

Body mass varied significantly with season ($F_{1,63} = 36.492$, $P < 0.001$) but not with site ($F_{1,63} = 0.549$, $P = 0.461$) or season × site ($F_{1,63} = 1.396$, $P = 0.242$). Posthoc tests indicated that both populations significantly increased M_b during winter (table 2).

BMR

BMR was not significantly related to M_b in any of the four combinations of season and site, and we therefore compared both BMR and MS-BMR directly among sites and seasons. BMR varied significantly with season ($F_{1,63} = 29.673$, $P < 0.001$) and site ($F_{1,63} = 7.285$, $P = 0.009$), and there was a significant season × site interaction ($F_{1,63} = 39.152$, $P < 0.001$). Posthoc tests indicated that the BMR of the inland population was significantly higher in winter than in summer, but that of the coastal population did not differ between seasons (table 2).

MS-BMR did not vary significantly with season ($F_{1,63} = 2.646$, $P = 0.109$) but did vary with site ($F_{1,63} = 7.295$, $P = 0.009$). However, the season × site interaction was significant ($F_{1,63} = 31.063$, $P < 0.001$), and posthoc tests revealed that, within each site, MS-BMR differed significantly between seasons (table 2). Bishops from the coastal population exhibited lower MS-BMR in winter than in summer, equivalent to a 15.0% decrease below summer values (table 2). In contrast, bishops from the inland population increased MS-BMR by 30.7% in winter (table 2). The MS-BMR of inland birds was significantly higher than that of coastal birds during winter (Holm-Sidak test, $t = 6.098$, $P < 0.001$).

Summit Metabolism

Like BMR and MS-BMR, M_{sum} and MS-M_{sum} were not significantly related to M_b in either population during either season. In the coastal population, M_{sum} decreased slightly but significantly during winter (table 2). M_{sum} in the inland bishops, in contrast, increased significantly during winter (table 2).

The MS-M_{sum} of bishops from the coastal site was significantly lower in winter than in summer (table 2), equivalent to 7.4 × MS-BMR values in summer and 7.5 × MS-BMR in win-

Table 2: Seasonal body mass, whole-animal and mass-specific (MS) basal metabolic rate (BMR), and summit metabolism (M_{sum}) of southern red bishops *Euplectes orix* from Port Elizabeth and Aliwal North, South Africa

Site, characteristic	Summer	Winter	t	P
Port Elizabeth (coastal):				
Body mass[a] (g)	21.03 ± 2.16 (17)	23.84 ± 3.15 (18)	**3.529**	**<.001**
BMR (mL O_2 h^{-1})	55.9 ± 9.1 (17)	54.0 ± 9.2 (18)	.588	.558
MS-BMR (mL O_2 g^{-1} h^{-1})	2.68 ± .47 (17)	2.28 ± .34 (18)	**2.867**	**.006**
M_{sum} (mL O_2 h^{-1})	403.3 ± 33.3 (17)	371.5 ± 53.5 (18)	**2.124**[uv]	**.042**[uv]
MS-M_{sum} (mL O_2 g^{-1} h^{-1})	19.86 ± 2.01 (17)	16.98 ± 3.39 (18)	**3.076**[uv]	**.005**[uv]
Aliwal North (inland):				
Body mass[a] (g)	19.92 ± 1.87 (14)	24.10 ± 1.88 (18)	**4.979**	**<.001**
BMR (mL O_2 h^{-1})	47.5 ± 10.0 (14)	74.9 ± 9.9 (18)	**8.068**	**<.001**
MS-BMR (mL O_2 g^{-1} h^{-1})	2.38 ± .45 (14)	3.12 ± .40 (18)	**4.963**	**<.001**
M_{sum} (mL O_2 h^{-1})	381.5 ± 78.0 (11)	439.8 ± 36.6 (18)	**−2.325**[uv]	**.037**[uv]
MS-M_{sum} (mL O_2 g^{-1} h^{-1})	19.32 ± 4.23 (11)	18.17 ± 2.12 (18)	.841[uv]	.415[uv]

Note. Data are mean ± SD (with sample size given in parentheses) unless otherwise indicated. The t value and probability are estimated from a Holm-Sidak posthoc test or an unequal variance t-test (indicated by superscript uv). Significant results are presented in bold font.

[a]Taken as first measurement after capture, before BMR measurement.

ter. However, no significant seasonal change in MS-M_{sum} occurred in the inland population (table 2). In the latter population, MS-M_{sum} values during winter were equivalent to 5.8 × winter MS-BMR, and summer values were equivalent to 8.1 × summer MS-BMR.

Discussion

Patterns of seasonal metabolic variation differed considerably between two populations of southern red bishops at sites that were located 380 km apart but which differed in altitude by approximately 1,100 m. In bishops from the warmer, coastal site, BMR did not differ significantly between summer and winter, a pattern resulting from a combination of significant winter increases in M_b but significant decreases in MS-BMR. However, M_{sum} in this population decreased slightly (∼8%) but significantly during winter, reflecting a reduction of approximately 15% in MS-M_{sum}. In contrast, bishops from a colder, inland site significantly increased BMR by approximately 58% in winter, reflecting increases in both M_b (∼22%) and MS-BMR (∼31%). The M_{sum} of the inland population also increased during winter, by approximately 15%, with this increase driven by changes in M_b but not MS-M_{sum}. These data reveal that considerable variation in seasonal metabolic and M_b adjustments can occur within species inhabiting subtropical latitudes. The fact that M_{sum} in the bishops ranged from 5.9 times the BMR (Aliwal North, winter) to 8.0 times the BMR (Aliwal North, summer) is quantitatively consistent with typical avian values (Swanson 2010).

Seasonal variation in M_b, as observed in both populations in this study, is common in birds, with many north-temperate species increasing M_b in winter (Dawson and Marsh 1986; Rogers et al. 1993; O'Connor 1996; Vézina et al. 2006). Winter increases in M_b often involve fattening (Dawson and Marsh 1986; Rogers et al. 1993) but may also be ascribed to increases in organ mass, such as enlarged pectoral muscles that support shivering thermogenesis (Vézina et al. 2011). However, the lack of body composition data for the bishops makes it impossible to identify the mechanisms driving the winter mass increases. Although the season × site interaction term for M_b was not significant, the observation that the mean fractional winter M_b increase in inland birds was approximately double that of the coastal population suggests that intraspecific variation in seasonal M_b adjustments in the bishops should be further investigated.

Intraspecific variation in the direction of seasonal MS-BMR variation was in broad agreement with the pattern identified by Smit and McKechnie (2010), in that bishops from the warmer site showed winter decreases in MS-BMR, but birds from a colder site increased MS-BMR during winter (fig. 1). However, the position of the Aliwal North *Euplectes orix* datum relative to the linear regression fitted by Smit and McKechnie (2010) and the fact that it falls outside the upper 95% prediction interval suggest that the magnitude of winter fractional MS-BMR increases in this population is greater than expected on the basis of the site's mean winter temperature. Indeed, the
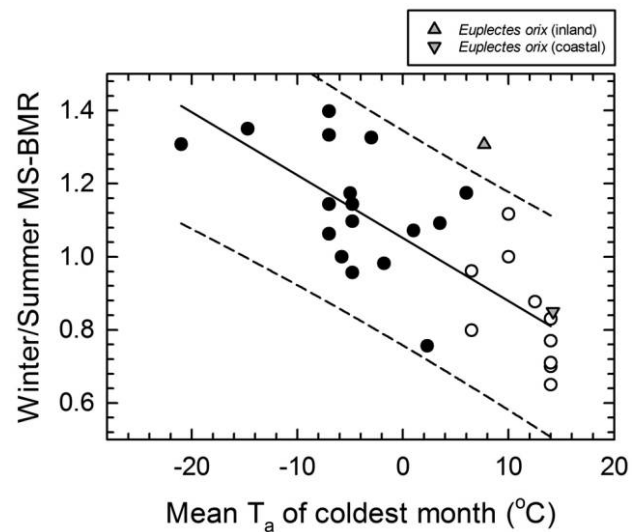

Figure 1. The relationship between the ratio of winter to summer avian mass-specific basal metabolic rate (MS-BMR) as a function of mean air temperature (T_a) during the coldest month of the year in two populations of southern red bishops *Euplectes orix* in comparison with other Northern Hemisphere (filled circles) and Southern Hemisphere (open circles) species; see Smit and McKechnie (2010) for sources. The solid line is a linear regression model fitted to the data used by Smit and McKechnie (2010), which excludes the data for *E. orix*, and the dashed lines are the corresponding 95% prediction intervals.

magnitude of fractional winter MS-BMR increases in this population is quantitatively similar to those observed in some species that inhabit cold, high-latitude temperate habitats (fig. 1). Similar winter increases have also been reported in captive populations of other southern African species, such as red-winged starling *Onychognathus morio* and the introduced house sparrow *Passer domesticus*. In the former species, winter MS-BMR was 28% higher than summer MS-BMR (Chamane and Downs 2009), whereas the corresponding difference in MS-BMR in the latter species was a massive 120% (Nzama et al. 2010). In stark contrast, both the BMR and MS-BMR of greater vasa parrots *Coracopsis vasa*, a species that occurs on the islands of Madagascar and the Cormoros, was approximately 51% higher in summer than in winter (Lovegrove et al. 2011). Collectively, these findings suggest greater diversity in avian seasonal metabolic adjustments than is currently appreciated and, moreover, that future comparative analyses will need to consider more variables than were included in the study by Smit and McKechnie (2010). These authors found that the ratio of winter-to-summer MS-BMR was significantly related to latitude and temperature but not to M_b. In both conventional and phylogenetically independent models, the strongest predictor of winter to summer MS-BMR ratio was the mean T_a during the coldest month of the year (Smit and McKechnie 2010).

Our M_{sum} data are, to the best of our knowledge, the first such measurements for an Afrotropical bird species. Compared with the values predicted by Swanson and Bozinovic's (2011) phylogenetically corrected regression for oscine passerines, M_{sum}

in the bishops ranged from 107.0% (Port Elizabeth, winter) to 127.5% (Aliwal North, winter) of expected values. Little is known about intraspecific variation in seasonal M_{sum} adjustments (McKechnie and Swanson 2010; Swanson 2010). House finch (*Carpodacus mexicanus*) populations in Colorado and California exhibited no significant change in M_{sum} or MS-M_{sum} between seasons (Dawson et al. 1983, 1985; Liknes et al. 2002), whereas a population in Michigan increased M_{sum} in winter (O'Connor 1995). The pattern of seasonal acclimatization in inland bishops, in which M_{sum} increased significantly during winter but MS-M_{sum} did not (which suggests that body composition remained approximately constant), is similar to that observed in American goldfinches *Carduelis tristis* from Michigan and South Dakota (Dawson and Carey 1976; Liknes et al. 2002) and northern cardinals *Cardinalis cardinalis* in Ohio (Sgueo et al. 2012). House finches from Michigan exhibited significant winter increases in both M_{sum} and MS-M_{sum} (O'Connor 1995).

Although the patterns of seasonal variation in M_{sum} in bishops from Aliwal North are broadly consistent with those of previous studies, we are not aware of any other published instance of winter decreases in both M_{sum} and MS-M_{sum}, as occurred in bishops from Port Elizabeth. The factors driving this winter decrease in M_{sum} in coastal bishops remain unclear, but one possible explanation is suggested by the combination of M_b increasing by approximately 13%, both MS-BMR and MS-M_{sum} decreasing by approximately 15%, BMR remaining constant, and M_{sum} decreasing by approximately 8% during winter (table 2). The latter pattern could arise if body composition varied seasonally in such a way that tissues that contribute to BMR remained an approximately constant fraction of total M_b (i.e., the 15% winter decrease in MS-BMR was cancelled out by the 13% increase in M_b) but the tissues that contribute to M_{sum} represented a smaller fraction of total M_b during winter. The BMR mainly reflects the metabolic intensity and mass of a bird's major organs, whereas M_{sum} predominantly reflects the properties of skeletal muscles (Hoppeler and Weibel 1998; Swanson 2010). Thus, a pattern whereby the fractional mass of major organs remained constant between seasons but fractional muscle mass decreased during winter (perhaps associated with reduced activity levels in the nonbreeding season) could potentially explain the seasonal metabolic changes observed in the Port Elizabeth bishops. However, an investigation of seasonal changes in body composition is needed to evaluate this possibility.

Our data also reiterate the need to consider both whole-animal and mass-specific metabolic rates when examining the metabolic components of seasonal acclimatization and shed new light on the functional linkages between BMR and M_{sum} (Liknes et al. 2002). Most strikingly, the 31% increase in MS-BMR during winter in the Aliwal North birds was not associated with a corresponding significant increase in MS-M_{sum}. Moreover, when considered on a whole-animal basis, BMR in the latter population increased by approximately 58% in winter, but M_{sum} increased by only approximately 15%. Although there is strong evidence for a correlation between avian MS-BMR

and MS-M_{sum} at an interspecific level among species from temperate latitudes (Dutenhoffer and Swanson 1996; Rezende et al. 2002), such a correlation does not appear to exist among tropical species (Wiersma et al. 2007a). There is far less evidence at an intraspecific level for a functional linkage between avian MS-BMR and MS-M_{sum} in temperate-zone species, but Lewden et al. (2012) recently reported a significant correlation in black-capped chickadees *Poecile atricapillus*. Swanson et al. (2012) found that whole-animal BMR and M_{sum} were correlated in black-capped chickadees and house sparrows *P. domesticus*. Our data for Aliwal North bishops, in which seasonal MS-M_{sum} changes are functionally decoupled from those involving MS-BMR, reiterate that winter increases in MS-BMR do not necessarily reflect concomitant changes in MS-M_{sum} and, moreover, that seasonal fractional changes in whole-animal BMR and M_{sum} are not necessarily quantitatively consistent.

In summary, our results highlight that there is still much to learn regarding seasonal metabolic adjustments in birds inhabiting tropical and subtropical latitudes. The picture emerging from the limited available data is one of tropical and subtropical species exhibiting a degree of phenotypic flexibility in body mass and metabolic rate that is quantitatively comparable to that of species permanently resident in highly seasonal habitats at temperate and boreal latitudes. Our data also argue against the notion that nonmigratory tropical species have less flexible BMRs than do migratory species (Şekercioğlu et al. 2012).

Acknowledgments

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