

Seasonal Metabolic Acclimatization Varies in Direction and Magnitude among Years in Two Arid-Zone Passerines

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ABSTRACT

Adaptive plasticity in avian thermal physiology is increasingly apparent, with a well-studied example being metabolic upregulation during cold winters in small birds inhabiting temperate and boreal latitudes. Recent studies have revealed greater variation in the direction and magnitude of seasonal metabolic adjustments among subtropical/tropical birds experiencing milder winters compared with higher-latitude counterparts, suggesting that patterns could vary among years within populations. We quantified seasonal metabolic variation (summer vs. winter) in Kalahari Desert populations of two Afrotropical passerines, the white-browed sparrow-weaver (WBSW; *Plocepasser mahali*; ~40 g) and the scaly-feathered weaver (SFW; *Sporopipes squamifrons*; ~10 g) over subsequent years (2014–2017). We used flow-through respirometry to measure basal metabolic rate (BMR) and summit metabolism (M_{sum} ; maximum cold-induced resting metabolic rate) and quantified seasonal fluctuations in air temperature (T_a) and food abundance (arthropod and grass seed abundance) at the study site. Our data reveal that the direction and magnitude of seasonal metabolic acclimatization vary among years in both species, with the winter BMR of WBSWs ranging from ~20% lower to 68% higher compared with the summer BMR. In contrast to higher-latitude species, M_{sum} was not related to the cold-limit temperature of birds or to winter minimum T_a at the study site, but interannual variation in BMR and M_{sum} was significantly lower in seasons with lower food abundance in both WBSWs and SFWs. Our data support the idea that patterns of seasonal acclimatization are more variable in birds from lower latitudes and that there is considerable phenotypic flexibility in avian thermal physiology.

Keywords: acclimatization, phenotypic flexibility, adaptive plasticity, hypothermia, summit metabolism, basal metabolic rate, subtropical birds.

Introduction

Endothermic thermal physiology is variable, with such traits as metabolic rates correlated with climate at both inter- and intra-specific levels (e.g., Weathers 1979; MacMillen and Hinds 1998; Sabat et al. 2006; Londoño et al. 2015). Differences among species or populations of a species can confer adaptive value, although it is often unclear whether these differences result from adaptation via natural selection or adaptive plasticity (Gotthard and Nylon 1995; Angilletta et al. 2010). Adaptive plasticity occurs within individuals via adjustments in the phenotype expressed by a genotype in response to environmental conditions (i.e., phenotypic plasticity) and includes both developmental plasticity (ontogenic variation that becomes fixed on reaching maturity) and phenotypic flexibility (reversible changes within individuals; Via et al. 1995; Piersma and van Gils 2010; Kelly et al. 2012). The beneficial acclimation hypothesis (BAH) posits that acclimation to an environment enhances the performance or fitness of an individual within that particular environment (Leroi et al. 1994). Testing the BAH in the context of thermal physiology has almost entirely been restricted to ectotherms (Huey et al. 1999; Wilson and Franklin 2002; Marais and Chown 2008), primarily on account of the difficulty of quantifying fitness-related performance metrics over a range of body temperatures (T_b) in endotherms.

Phenotypic flexibility is receiving increasing attention as a source of intraspecific variation in the metabolic rates of endotherms and can occur via acclimatization or acclimation to environmental conditions in the field or laboratory, respectively (Piersma and Drent 2003). A frequently cited example of phenotypic flexibility is seasonal acclimatization both in basal metabolic rate (BMR; minimum resting metabolic rate measured in postabsorptive, nonreproductive individuals during their rest phase) and in summit metabolism (M_{sum} ; maximum resting metabolic rate measured during cold exposure; reviewed for birds by McKechnie et al. 2015). Seasonal metabolic acclimatization has been well studied in small north-temperate birds, with the typical pattern involving upregulation of BMR and M_{sum} in winter compared with summer, presumably to enhance cold tolerance during cold winters (reviewed by Swanson 2010; McKechnie et al. 2015).

Seasonal adjustments of BMR are primarily driven by changes in organ masses and/or tissue metabolic intensities (Chappell et al. 1999; Petit et al. 2014; Vézina et al. 2017), whereas M_{sum} is adjusted

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primarily through changes in the size of skeletal muscles (particularly pectoral muscles), cellular metabolic intensities, and/or the transport capacities of O₂ and metabolic substrates (Petit and Vézina 2014a; Zhang et al. 2015; Barceló et al. 2017). Recent studies suggest an uncoupling of adjustments in BMR and M_{sum} (Swanson et al. 2012; Petit et al. 2013; Dubois et al. 2016; Barceló et al. 2017), and several authors have reported differing patterns of seasonal variation for these two variables (Ambrose and Bradshaw 1988; O'Connor 1996; van de Ven et al. 2013; Noakes et al. 2017). The uncoupling of BMR and M_{sum} questions the relevance of using metabolic expansibility (ME; i.e., metabolic scope, calculated as the ratio of M_{sum} to BMR) as a measure of thermogenic capacity (Petit et al. 2013).

Only relatively recently have workers investigated avian seasonal metabolic acclimatization in subtropical and tropical regions with generally milder winters and hotter summers (e.g., Maddocks and Geiser 2000; Smit and McKechnie 2010; van de Ven et al. 2013), and consequently, patterns of metabolic variation remain less well understood among birds from lower latitudes. Smit and McKechnie (2010) analyzed global variation in seasonal changes of avian BMR and proposed the existence of a continuum between enhanced cold tolerance via upregulated BMR in higher-latitude regions with long, cold winters and winter energy conservation via reductions in BMR at lower latitudes with milder, dry winters. However, recent studies have reported winter increases in BMR and M_{sum} in subtropical birds, with these increases similar in magnitude to those typical of north-temperate species (e.g., Lindsay et al. 2009a, 2009b; Wilson et al. 2011). There thus appears to be greater variability in the patterns of seasonal metabolic adjustments in tropical and subtropical species, with BMR ranging from ~35% lower to 60% higher during winter compared with BMR in summer (McKechnie et al. 2015; Pollock et al. 2019). Variation in seasonal metabolic adjustments has also been reported among populations of subtropical species; for example, patterns of seasonal acclimatization in BMR and M_{sum} vary from no seasonal change to winter upregulation among populations of southern red bishops (*Euplectes orix*; van de Ven et al. 2013) and white-browed sparrow-weavers (WBSW; *Plocepasser mahali*; Smit and McKechnie 2010; Noakes et al. 2017).

The relative roles of proximate cues (less predictable, short-term trends; e.g., variation in daily temperatures and food abundance) versus ultimate cues (predictable, long-term trends; e.g., seasonal variation in climate and photoperiod) as determinants of seasonal acclimatization in avian metabolic rates remain unclear (Swanson and Vézina 2015). There is, however, evidence that avian metabolic rates are adjusted over shorter time scales, and seasonal variation may reflect physiological responses to conditions over days to weeks (Swanson and Olmstead 1999; Broggi et al. 2007; Petit and Vézina 2014b; Dubois et al. 2016). For example, data for several north-temperate birds reveal that BMR and M_{sum} are more closely related to short-term (0–5 d; *Spizella arborea*) and medium-term (14–30 d; *Poecile atricapillus* and *Junco hyemalis*) fluctuations in winter minimum temperatures than to long-term trends (Swanson and Olmstead 1999). Moreover, two arid-zone WBSW populations in the Kalahari Desert of southern Africa (Molopo and Askham) had contrasting patterns of seasonal BMR variation (no seasonal change and ~52% higher BMR in winter compared with BMR in summer, respectively; Smit and McKechnie 2010; Noakes

et al. 2017), suggesting that the direction of seasonal metabolic adjustments may not be fixed in populations.

In light of (a) the variability in observed seasonal metabolic adjustments in subtropical species and (b) the evidence for a proximate effect of temperature on intrawinter metabolic rates in north-temperate passerines, we hypothesized that variation in patterns of seasonal metabolic acclimatization in subtropical species is modulated along a cold tolerance/energy conservation continuum in response to environmental conditions. Specifically, we predicted that patterns of seasonal variation in BMR and M_{sum} in two passerines would vary over the study period, with an upregulation in metabolic rates during colder winters with high food abundance and downregulation during milder winters with low food abundance. During seasons with contrasting environmental selection pressures (e.g., a cold winter with low food abundance), we expected to find either no seasonal metabolic change or seasonal patterns prioritizing the more pressing environmental factor.

To investigate flexibility in the magnitude and direction of seasonal metabolic variation in Afrotropical passerine birds, we measured seasonal variation in BMR and M_{sum} over a 3-yr period in Kalahari Desert populations of two ploceid passerine species with a fourfold variation in body mass (M_b): the WBSW (~40 g) and the scaly-feathered weaver (SFW; *Sporopipes squamifrons*; ~10 g). We simultaneously quantified variation in potential ecological correlates of metabolic acclimatization: daily minimum and maximum T_a ($T_{a,\text{min}}$ and $T_{a,\text{max}}$), rainfall, and food abundance (arthropod and grass seed abundance). For WBSWs, we included metabolic data collected during 2014 by Noakes et al. (2017), providing a 4-yr data set on seasonal variation in BMR and M_{sum} in this species.

Methods

Study Site

We examined thermoregulation in WBSWs and SFWs during winter (July–August) and summer (January–February) over a 3-yr period (2015–2017) at Murray Guest Farm near Askham in the Kalahari Desert (Northern Cape Province, South Africa; 26° 59'S, 20° 51'E). For WBSWs, we included data from a previous study that recorded seasonal metabolic variation at the same study site during 2014 (Noakes et al. 2017). We caught, housed, and maintained WBSWs following Noakes et al. (2017). We caught SFWs using mist nets, except for five individuals we found roosting in a WBSW nest, and maintained SFWs in the same manner as WBSWs. Individual WBSWs were sexed according to the color of their beaks (du Plessis 2005); however, we did not sex SFWs, as they are not sexually dimorphic (Dean 2005). Physiological data were collected using a field respirometry system within 60 h of capture, after which all birds were released at the site of capture. The natural diet of WBSWs includes arthropods and grass seeds (~30% arthropods; Ferguson 1988; du Plessis 2005) and that of adult SFWs consists of grass seeds (juveniles supplemented with arthropods; Herremans 1997; Dean 2005).

Seasonal Variation in Temperature and Food Abundance

To investigate whether patterns of seasonal metabolic acclimatization in WBSWs and SFWs vary with environmental factors,

we quantified seasonal fluctuations in T_a extremes and food abundance (arthropod and grass seed abundance) during each year we collected gas exchange data. Daily $T_{a,\min}$ and $T_{a,\max}$ and rainfall data were obtained from the South African Weather Service, using the weather stations closest to Askham (T_a : Twee Rivieren; ~62 km northwest; 27°28'S, 20°36'E; rainfall: Witdraai police station; ~9 km west; 26°57'S, 20°42'E). We calculated mean daily $T_{a,\min}$ and $T_{a,\max}$ as well as total rainfall, over the hottest summer months (December–January) and coldest winter months (June–July) of each year, which also included the month directly before gas exchange data were collected.

At our study site, five locations where we frequently observed WBSWs and SFWs foraging were chosen to serve as replicates for food abundance measurements (conducted concurrently with metabolic measurements), with replicates being >300 m apart and <120 m from trees with active WBSW colonies (WBSWs typically forage 60–120 m from their colony; Lewis 1982). Arthropod abundance was estimated using pitfall traps, which are likely to provide reliable estimates of availability for WBSWs, as they are ground-foraging birds (Collias and Collias 1978; Lewis 1982; Ferguson 1988). Each replicate consisted of two grids of traps (<100 m apart), one in the dune valley and another about halfway up the dune slope. Each grid consisted of 10 traps arranged in two rows of five traps spaced 10 m apart (thus, 20 traps per replicate, 100 traps in total per season). We used plastic cups (200 mL) as pitfall traps. The cups were buried in the ground and filled up to one-third with a liquid soap (Body Wash, Clicks, Cape Town, South Africa) and water mixture (ratio: ~1 part soap to 100 parts water) to impede the evaporation of liquid. Traps were collected and replaced every second or third day, with a total sampling period of 7 d per season. After collection, the soap-water mixture was drained from traps, and arthropod samples were stored in resealable plastic bags containing 70% ethanol to preserve specimens. Arthropods were classified to order level, and the data for orders that are part of the WBSW's diet (du Plessis 2005) were pooled for each season to provide an estimate of arthropod abundance in the summer and winter of each year (see appendix for the respective abundances of each order).

Percentage grass cover was used as an estimate of seasonal variation in grass seed abundance over the study period. We did step counts at the same five replicates used for pitfall trapping in the dune valley and on the slope. Each step count involved walking 50 steps (thus, 100 steps per replicate, 500 steps in total per season) and recording whether live grass or dead grass/bare ground was stepped on to provide an estimate of live grass density per area. The grass species most commonly identified were *Stipagrostis* spp. (positively identified: *S. ciliata* and *S. amabilis*) and *Schmidtia kalahariensis*, which flower throughout most of the year (*S. kalahariensis*: January–December; *S. amabilis*: August–May; *S. ciliata*: August–October and February–June; Fish et al. 2015).

Gas Exchange and Temperature Measurements

We measured O_2 consumption (\dot{V}_{O_2}) and CO_2 production (\dot{V}_{CO_2}) using open flow-through respirometry. We used the same experimental setup and calibration procedures described by Minnaar

et al. (2014) and Noakes et al. (2017). We used 4-L and 1.2-L clear plastic containers (Lock and Lock, Seoul, South Korea) as metabolic chambers for WBSWs and SFWs, respectively. We maintained flow rates of ~2 L min⁻¹ for WBSWs and ~1.4 L min⁻¹ for SFWs during M_{sum} measurements and ~1 L min⁻¹ for WBSWs and ~0.5 L min⁻¹ for SFWs during BMR measurements. For BMR measurements, we placed metabolic chambers in a modified ice chest (~75 L) and regulated T_a using a Peltier device (AC-162, TE Technology, Traverse City, MI) and custom-built digital controller. For M_{sum} measurements, we placed metabolic chambers in a modified fridge-freezer (40 L; ARB, Kilsyth, Victoria, Australia).

We measured T_a in the metabolic chambers using thermistor probes (TC-100, Sable Systems, Las Vegas, NV) during BMR measurements and a Cu-Cn thermocouple and thermocouple reader (RDXL12SD, OMEGA Engineering, Norwalk, CT) during M_{sum} measurements, which were inserted into the chambers through a small hole sealed with a rubber grommet. We measured core T_b in WBSWs using temperature-sensitive passive integrated transponder tags (Destron Fearing, St. Paul, MN), and the tags were implanted and calibrated and the T_b monitored as described by Noakes et al. (2017). We did not implant tags in SFWs, as they are substantially smaller than WBSWs, and thus measured cloacal T_b directly after M_{sum} measurements using a Cu-Cn thermocouple and thermocouple reader.

Experimental Protocol

To measure BMR of WBSWs and SFWs, we exposed birds to $T_a \approx 30^\circ\text{C}$ (actual $T_a = 30.0^\circ \pm 0.4^\circ\text{C}$) for the entire night and used the same protocol as Noakes et al. (2017; $n = 10$ for each species per season per year, except $n = 14$ for WBSWs in winter 2016 and $n = 11$ for SFWs in winter 2017). A T_a of 30°C was chosen because this T_a is within the thermoneutral zone of WBSWs (Smit and McKechnie 2010; Noakes et al. 2017) and SFWs (Whitfield et al. 2015), although metabolic measurements for SFWs were recorded from birds at rest during the daytime (active phase; current study was during the rest phase). We also conducted overnight resting metabolic rate (RMR) measurements at $5^\circ \leq T_a \leq 35^\circ\text{C}$ (at 5°C increments, two to three T_a per night) to confirm that $T_a = 30^\circ\text{C}$ represented thermoneutrality for WBSWs and SFWs during every season of data collection ($n \approx 6$ individuals per species per T_a).

To quantify M_{sum} in WBSWs and SFWs, we used the sliding cold exposure method in a helox environment (Swanson et al. 1996) and protocol described by Minnaar et al. (2014) and Noakes et al. (2017; $n = 10$ for each species per season per year, except $n = 11$ and 13 for WBSWs in the winters of 2016 and 2017, respectively, and $n = 11$ for SFWs in winter 2017). To habituate birds to the experimental setup, we initially provided atmospheric air and regulated chamber T_a at $\sim 10^\circ\text{C}$ and 20°C for ~10 min for WBSWs and SFWs, respectively—a higher initial T_a was used for SFWs to avoid individuals becoming hypothermic too early during measurements. After the habituation period, we switched to providing helox in the system and set the fridge-freezer to -15°C to allow a constant decrease in T_a . We visually monitored O_2 and CO_2 traces during measurements for a plateau in increasing metabolic rate

indicating that maximum thermogenic capacity (i.e., M_{sum}) had been elicited. We terminated measurements when O_2 and CO_2 traces indicated a distinct decrease in metabolic rate from this plateau, indicative of M_{sum} , and measured T_b of birds upon removal from chambers to confirm hypothermia. Hypothermia was assumed in WBSWs if T_b decreased by $\geq 5.0^\circ\text{C}$ from initial values upon entering the chamber (mean decrease in T_b : $9.4^\circ \pm 2.3^\circ\text{C}$). We did not have initial T_b values for SFWs but assumed hypothermia if $T_b \leq 36.0^\circ\text{C}$ after removal from the chamber (mean T_b after measurements: $33.0^\circ \pm 1.7^\circ\text{C}$). All individuals met these criteria for hypothermia, and thus, all data were included in analyses.

Data Analysis

We calculated whole-animal metabolic rates (BMR and M_{sum}) and ME values as described by Noakes et al. (2017), with BMR representing the lowest 5-min metabolic rate measured overnight for each individual and M_{sum} representing the highest 5-min metabolic rate obtained during sliding cold exposure measurements. The average respiratory exchange ratio (RER; $\dot{V}_{\text{CO}_2}/\dot{V}_{\text{O}_2}$) during measurements was 0.60 ± 0.13 , which is below the expected range of 0.71 to 1.00 (Withers 1992). As thermal equivalence data are not available for $\text{RER} < 0.71$, we assumed an RER of 0.71 to calculate metabolic rates in watts for measurements below this value and repeated statistical analyses with \dot{V}_{O_2} and \dot{V}_{CO_2} as the response variable to confirm this was not a source of error in our results. We used the helox temperature at which M_{sum} was reached as an estimate of the cold-limit temperature for each bird (T_{CL}). All values are presented as mean \pm standard deviation.

We used R version 3.5.1 (R Core Team 2018) to fit linear models to our data, and assumptions of all models were checked by inspecting model residual plots (residuals vs. fitted, normal Q-Q, scale-location, and residuals vs. leverage plots). We used the “lm” base function to investigate how BMR, M_{sum} , ME, and T_{CL} varied among years and seasons and how M_b varied among years and seasons in each species. Sex was initially included as a predictor variable in models for WBSWs, but as it was never included in the top models explaining variation in response variables and Noakes et al. (2017) also reported no sex differences in this species, we excluded sex from further analyses. We used the “dredge” function from the MuMIn package (Bartoń 2018) to determine the combination of predictor variables that produced linear models that best explained variation in our response variables. Post hoc tests of multiple comparisons of means (Tukey contrasts for linear models; multcomp package; Hothorn et al. 2008) were used to investigate variation among year \times season groups for each response variable.

We also fitted linear models to investigate interannual variation in BMR, M_{sum} , and M_b in summer and winter respectively in relation to environmental variables: T_a extremes (mean $T_{a,\text{max}}$ for summer and $T_{a,\text{min}}$ for winter) and food abundance. We used percentage grass cover as an estimate of grass seed abundance for the food abundance of SFWs (Herremans 1997), and for WBSWs, we calculated standardized residuals for arthropod and grass abundance and combined these values into one metric for food

abundance using diet proportions reported by Ferguson (1988; 30% arthropods and 70% seed). Rainfall was correlated with percentage grass cover and thus was excluded from these models.

Results

Interannual Variation in Temperature and Food Abundance

There was consistent seasonal variation in rainfall, $T_{a,\text{min}}$, and $T_{a,\text{max}}$ at the study site over the study period, with summers being considerably hotter and wetter compared with winters (fig. 1C). There was no rain during any of the winters (June–July) over the study period, and the summer of 2015 (December 2014–January 2015) had substantially lower total rainfall (15.0 mm) compared with the summers of other years (70.0 mm for both summers 2014 and 2016, 42.5 mm for summer 2017). The winter $T_{a,\text{min}}$ was similar across years of the study period (1.4°C range in mean values), but there was greater variation in the summer $T_{a,\text{max}}$ (range of 2.5°C in mean values), with the summer of 2016 being hotter than the other years (fig. 1C). The coldest $T_{a,\text{min}}$ recorded was -9.4°C (winter 2014), and the hottest $T_{a,\text{max}}$ was 45.4°C (summer 2016).

There was considerable variation in food abundance (arthropod and grass seed abundance) from 2015 to 2017 but no consistent pattern of seasonal differences (fig. 1D). There was a 10-fold range in the total number of arthropods caught in our traps during respective seasons, with the highest abundance occurring in winter 2016 and summer 2017 and the lowest abundance in winter 2015 (fig. 1D). Variation in the percentage of grass cover (an estimate of grass seed abundance) reflected variation in summer rainfall, ranging from a minimum of 22% cover in summer 2015 to a maximum of 90% cover in summer 2016 (fig. 1D).

White-Browed Sparrow-Weavers

The M_b of WBSWs varied among individuals during the study period from a minimum of 33.2 g to a maximum of 46.4 g (both values from summer 2015). The top model explaining variation in the M_b of WBSWs included only season (table 1), with birds being ~ 1.5 g heavier in winter compared with summer (table 2). The top model explaining interannual variation in M_b in relation to fluctuations in environmental variables was the model supporting the null hypothesis (i.e., no environmental variables included as predictors). BMR and M_{sum} increased significantly with increasing M_b , and T_{CL} decreased significantly with increasing M_b (table 1). There was also significant variation in BMR, M_{sum} , and T_{CL} with the year \times season interaction (table 1), but no interactions between M_b and the other predictor variables were included in the top models for any response variables of WBSWs, suggesting that variation among years and seasons does not solely reflect M_b differences.

The BMR of individual WBSWs varied from a minimum of 0.3 W (summer 2015) to a maximum of 1.0 W (summer 2017). The direction and magnitude of seasonal acclimatization in BMR differed among years, including significantly higher BMR in winter compared with summer ($\sim 52\%$ and 68% higher in winter 2014 vs. summers 2014 and 2015, respectively), no significant seasonal variation in 2015 and 2016, and significantly lower BMR

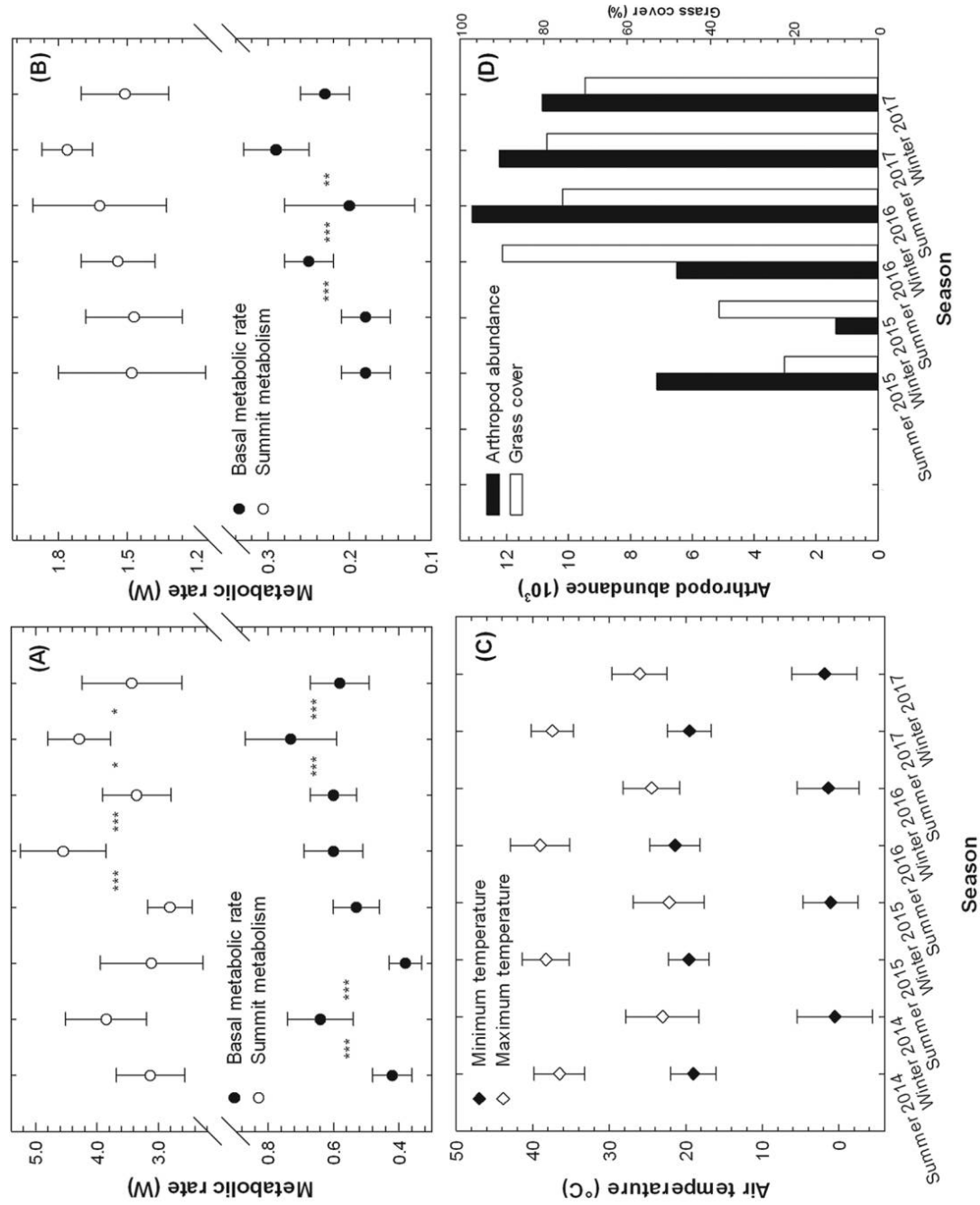


Figure 1. Basal metabolic rate and summit metabolism of two arid-zone passerine birds, white-browed sparrow-weavers (*Plocepasser mahali*; A) and scaly-feathered weavers (*Sporopipes squamifrons*; B), were measured during summers and winters over a 3-yr period (2015–2017; $n \approx 10$ for each species per season per year; mean \pm SD values are presented). Data were also included from a previous study for *P. mahali* in 2014 (Noakes et al. 2017). Significant differences between adjacent summers and winters are denoted by asterisks (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$); values obtained from linear models and post hoc tests of multiple comparisons of means; Tukey contrasts). Interannual variation is also presented for seasonal temperature extremes (C) and food abundance (arthropod and grass seed abundance; D). Mean \pm SD values of daily minimum and maximum air temperatures are presented for the hottest summer months (December–January) and the coldest winter months (June–July) using data obtained from the South African Weather Service. Arthropod abundance was estimated using pitfall trapping, and values represent the total number of arthropods caught per season for all orders that are part of the diet of *P. mahali* (diet: 30% arthropods, 70% seed). Grass cover (%) was used as an estimate of grass seed abundance and was measured using grass step counts during each season (diet of *S. squamifrons* consists of grass seeds). There were no estimates of food abundance during the summer and winter of 2014.

Table 1: Statistical results from models fitted to data from two arid-zone passerine birds, white-browed sparrow-weavers (*Plocepasser mahali*, WBSW) and scaly-feathered weavers (*Sporopipes squamifrons*, SFW)

Species, variable	Body mass			Year			Season			Year × season		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
WBSW:												
M_b	65.601	1, 86	.006
BMR	16.467	1, 75	<.001	21.764	3, 75	<.001	8.589	1, 75	.004	16.195	3, 75	<.001
M_{sum}	7.261	1, 75	.009	10.120	3, 75	<.001	10.346	1, 75	.002	9.374	3, 75	<.001
ME	17.265	1, 77	<.001
T_{CL}	5.541	1, 75	.021	8.742	3, 75	<.001	.514	1, 75	.476	12.714	3, 75	<.001
SFW:												
M_b	2.146	2, 56	.127	.007	1, 56	.980	10.154	2, 56	<.001
BMR	37.500	1, 54	<.001	28.720	2, 54	<.001	18.823	1, 54	<.001	2.753	2, 54	.073
M_{sum}	49.849	1, 56	<.001	4.173	2, 56	.020	2.054	1, 56	.157
ME	.005	1, 51	.942	10.830	2, 51	<.001	9.060	1, 51	.004	4.419	2, 51	.017
T_{CL}	32.871	1, 59	<.001

Note. Predictor variables were included in the final models for each response variable only if the model selection indicated that they improved model fit. Response variables for each species include body mass (M_b), basal metabolic rate (BMR), summit metabolism (M_{sum}), metabolic expansibility (ME), and helox temperature at cold limit (T_{CL} ; i.e., temperature at which M_{sum} was reached). Statistical results (*F* values, *P* values, and degrees of freedom [df]) are from the top linear models fitted to data. *P* values in bold indicate significance. Data were collected in the summer and winter of each year over the time period 2014–2017, and predictor variables included body mass (except when body mass was the response variable), year, season, and the year × season interaction.

in winter compared with summer (~20% lower in winters 2016 and 2017 vs. summer 2017; fig. 1A; table 2). Food abundance (estimated assuming WBSW's diet: 30% arthropods and 70% seeds; Ferguson 1988) was the only predictor variable included in the top models investigating interannual variation in BMR, and BMR significantly decreased with decreasing food abundance among summers ($F_{1,28} = 43.913$, $P < 0.001$) and winters ($F_{1,32} = 5.817$, $P = 0.022$; fig. 1).

The M_{sum} of individual WBSWs varied from a minimum of 2.3 W (winter 2015) to a maximum of 5.4 W (summer 2016). Patterns of seasonal acclimatization in M_{sum} differed among years, ranging from no significant seasonal variation in 2014 and 2015 to significantly lower M_{sum} in winter compared with summer (~20%–38% lower in winters 2015, 2016, and 2017 vs. summers 2016 and 2017; fig. 1A; table 2). M_{sum} significantly decreased with decreasing food abundance during summers ($F_{1,28} = 23.004$, $P < 0.001$) and winters ($F_{1,32} = 6.427$, $P = 0.016$; fig. 1). Patterns of seasonal variation in T_{CL} also differed among years but were not related to variation in M_{sum} , including significantly lower T_{CL} in winter compared with summer (reaching $T_a \sim 7.3^\circ\text{C}$ lower in winter 2015 vs. summers 2015 and 2016), no significant seasonal variation, and significantly higher T_{CL} in winter compared with summer (~8.5°C higher in winter vs. summer 2017; table 2). In contrast, the top model for variation in ME (i.e., the ratio of BMR to M_{sum}) of WBSWs only included season (table 1), with ME being ~1.3 lower in winter compared with summer (table 2).

In summary, patterns of seasonal acclimatization in the BMR, M_{sum} , and T_{CL} of WBSWs varied among years, but variation in patterns was not consistent among variables (table 2). BMR and M_{sum} significantly decreased with decreasing food abundance among summers and winters over the study period (fig. 1; table 2).

Repeating analyses using \dot{V}_{O_2} and \dot{V}_{CO_2} instead of metabolic rate (W) as the response variable revealed the same patterns of variation for BMR and M_{sum} of WBSWs.

Scaly-Feathered Weavers

The M_b of individual SFWs varied from a minimum of 8.4 g during the summer of 2015 to a maximum of 12.0 g during the summer of 2017. M_b varied significantly with the year × season interaction (table 1) and was significantly higher in the summer of 2017 compared with the winter of 2017, as well as compared with all other summers (table 2). Interannual variation in M_b in each season respectively was significantly related to variation in T_a extremes, decreasing with increasing $T_{a,max}$ among summers ($F_{1,28} = 20.323$, $P = 0.035$) and increasing with decreasing $T_{a,min}$ among winters ($F_{1,30} = 4.855$, $P < 0.001$). BMR and M_{sum} increased significantly with increasing M_b , and T_{CL} decreased significantly with increasing M_b (table 1). ME significantly varied with the year × season interaction, and the effect of year × season on BMR was marginally not significant, whereas year but not season was a significant predictor of M_{sum} (table 1). Interaction terms between M_b and the other predictor variables were not included in the top models for any response variables of SFWs, suggesting that variation among years and seasons does not reflect M_b differences.

The BMR of individual SFWs varied from a minimum of 0.1 W during the winter of 2016 to a maximum of 0.4 W during the summer of 2017. Patterns of seasonal acclimatization in BMR differed among years, from no seasonal variation to lower BMR in winter compared with summer (~20%–31% lower in winter 2015 vs. summer 2016 and in winter 2016 vs. summers 2016 and 2017; fig. 1B; table 2). The top models explaining interannual variation

Table 2: Data for two arid-zone passerine birds, white-browed sparrow-weavers (*Plocepasser mahali*, WBSW) and scaly-feathered weavers (*Sporopipes squamifrons*, SFW), during summer and winter over a 4-yr period

Species, variable	2014		2015		2016		2017	
	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter
WBSW:								
M_b (g)	38.51 ± 2.54	40.30 ± 2.87	36.85 ± 4.07	40.28 ± 2.28	38.66 ± 2.95	40.03 ± 3.14	39.57 ± 2.67	39.99 ± 2.59
BMR (W)	.42 ± .06 ^{A,*}	.64 ± .10 ^{B,*}	.38 ± .05 ^A	.53 ± .07 ^B	.60 ± .09 ^B	.60 ± .07 ^{ab,*}	.73 ± .14 ^{C,*}	.58 ± .09 ^{ab}
M_{sum} (W)	3.13 ± .56 ^A	3.85 ± .66 ^A	3.11 ± .84 ^A	2.81 ± .36 ^{b,*}	4.55 ± .70 ^{B,*}	3.35 ± .56 ^{ab,*}	4.29 ± .51 ^{B,*}	3.43 ± .81 ^{ab}
ME	7.44 ± 1.14	6.12 ± 1.56	8.25 ± 2.71	5.47 ± 1.11	7.79 ± 1.55	5.48 ± 1.25	6.17 ± 1.68	6.18 ± 1.64
T_{CL} (°C)	-2.26 ± 2.85 ^A	-5.96 ± 3.95 ^{ab}	-2.39 ± 3.25 ^{A,*}	-9.72 ± 4.07 ^{a,*}	-2.52 ± 3.82 ^A	-3.74 ± 5.21 ^b	-4.45 ± 5.10 ^{A,*}	4.00 ± 4.54 ^c
SFW:								
M_b (g)	10.05 ± .67 ^A	10.66 ± .51 ^a	9.83 ± .47 ^A	10.29 ± .83 ^a	10.99 ± .56 ^{B,*}	10.00 ± .70 ^a
BMR (W)18 ± .03 ^{AB}	.18 ± .03 ^{ab,*}	.25 ± .03 ^{A,*}	.20 ± .08 ^{ab,*}	.29 ± .04 ^B	.23 ± .03 ^b
M_{sum} (W)	1.48 ± .32 ^A	1.47 ± .21 ^A	1.54 ± .16 ^B	1.62 ± .29 ^B	1.76 ± .11 ^{AB}	1.51 ± .19 ^{AB}
ME	8.29 ± 1.59 ^A	8.44 ± 1.87 ^{a,*}	6.16 ± .65 ^{B,*}	8.63 ± 1.76 ^{ab,*}	6.10 ± .71 ^B	6.62 ± .63 ^b
T_{CL} (°C)	12.37 ± 2.37	10.45 ± 3.7	12.36 ± 3.17	12.55 ± 3.71	8.84 ± 3.24	9.71 ± 4.74

Note. Body mass (M_b), basal metabolic rate (BMR), summit metabolism (M_{sum}), metabolic expansibility (ME), and helox temperature at cold limit (T_{CL}) were measured during summer and winter over a 3-yr period (2015–2017; $n \approx 10$ for each species per season per year; mean ± SD presented). Data were also included from a previous study of WBSW's in 2014 at the same study site in the Kalahari Desert (Noakes et al. 2017). Statistical results are from linear models and post hoc tests of multiple comparisons of means (Tukey contrasts). If the year × season interaction was a significant predictor of response variables (WBSW: BMR, M_{sum} and T_{CL} ; SFW: M_b , BMR, and ME), we conducted post hoc tests to investigate variation between pairs of different seasons. Asterisks denote significant seasonal variation between adjacent summers and winters (placed after the mean value of the earlier season of each pair), and superscript letters denote patterns of significant variation among the summers (uppercase) and winters (lowercase), respectively (all $P < 0.05$). Year but not year × season was a significant predictor of the M_{sum} of SFW, and thus, patterns of significant variation among years are denoted by uppercase superscript letters regardless of season.

in BMR among summers and winters, respectively, revealed that summer BMR significantly decreased with increasing $T_{a,max}$ ($F_{1,27} = 7.817$, $P = 0.009$) and decreasing food abundance (i.e., grass seed abundance; $F_{1,27} = 48.086$, $P < 0.001$) and that winter BMR significantly increased with increasing $T_{a,min}$ ($F_{1,27} = 48.086$, $P < 0.001$; fig. 1).

The M_{sum} of individual SFWs varied from a minimum of 0.8 W during the summer of 2015 to a maximum of 2.1 W during the winter of 2016. There was no seasonal variation in M_{sum} , but there was variation among years (table 1), with significantly higher M_{sum} in 2015 compared with M_{sum} in 2016 (~7% higher), and M_{sum} in 2017 did not significantly differ from 2015 or 2016 (fig. 1B; table 2). The top model explaining interannual variation in summer M_{sum} revealed a significant decrease with increasing $T_{a,max}$ ($F_{1,27} = 5.293$, $P = 0.029$) and a decrease with decreasing food abundance, although this effect was marginally not significant ($F_{1,27} = 3.897$, $P = 0.059$; fig. 1). In contrast, the model supporting the null hypothesis (i.e., including no environmental variables) was the top model for interannual variation in winter M_{sum} (fig. 1). There was no variation in T_{CL} with year or season (table 1). Seasonal variation of ME of SFWs followed the same patterns of seasonal acclimatization of BMR over the study period, ranging from no seasonal variation to lower ME in winter compared with summer (~2.3–2.5 lower in winters; table 2).

In summary, patterns of seasonal acclimatization in the BMR and ME of SFWs varied among years, with the same patterns of seasonal variation for BMR and ME (table 2). Summer BMR and M_{sum} decreased with increasing $T_{a,max}$ and decreasing food abundance over the study period (fig. 1). Repeating analyses using \dot{V}_{O_2} and \dot{V}_{CO_2} instead of metabolic rate (W) as the response variable revealed the same patterns of variation for BMR and M_{sum} of SFWs.

Discussion

Our data reveal considerable flexibility in the thermal physiology of two species of subtropical passerines, highlighting the importance of phenotypic plasticity as a source of intraspecific variation in endotherm thermal physiology. We found significant variation in the magnitude and direction of seasonal acclimatization of BMR and M_{sum} , supporting the idea that patterns of seasonal metabolic variation are more variable among subtropical and tropical birds compared with north-temperate counterparts (McKechnie et al. 2015). Seasonal metabolic changes ranged from winter downregulation in some years to winter upregulation in others, with magnitudes similar to those observed in species from cold, higher-latitude regions (McKechnie et al. 2015). Our results partly support our prediction that patterns of seasonal acclimatization vary among years in a manner reflecting a trade-off between energy conservation and cold tolerance during winter (Smit and McKechnie 2010). Food abundance appears to be an important proximate factor determining interannual variation in metabolic rates of WBSWs and SFWs, as both BMR and M_{sum} decreased with decreasing food abundance, and metabolic rates were never related to winter $T_{a,min}$ in a manner associated with enhancing cold tolerance. Our results suggest that food abundance is

an important driver of metabolic adjustments in these two subtropical species, but unlike their temperate-zone counterparts, enhancing cold tolerance by metabolic increases is less important during milder subtropical winters.

White-Browed Sparrow-Weavers

Metabolic rates of WBSWs in the current study were generally higher than values predicted using allometric equations for tropical and passerine birds (table 3), which is unexpected because lower-latitude species are generally considered to have a “slower pace of life” than their temperate counterparts (Weathers 1979; Hail 1983; Londño et al. 2015). Mean BMR values for each season were higher than values predicted for tropical (37%–90% higher) and passerine (16%–40% higher) birds, except during the summers of 2014 and 2015 when BMR was similar to predicted values (table 3; Londño et al. 2015) and significantly lower than the other summers during the study period (fig. 1A; table 2). Mean M_{sum} values were higher than values predicted for tropical birds (31%–119% higher; Wiersma et al. 2007) and for oscine passerines (24%–80% higher), except during the winter of 2015 when M_{sum} was downregulated by the greatest magnitude and thus was similar to the value predicted for oscine passerines (tables 2, 3; Swanson and Bozinovic 2011).

Mean BMR values of WBSWs during each season (table 2) were similar to values previously reported among four WBSW populations across a climatic gradient of ~7°C in winter $T_{a,min}$ and ~11°C in summer $T_{a,max}$ (mean BMR range: 0.38–0.64 W; Noakes et al. 2017). The magnitude and direction of seasonal acclimatization of BMR in WBSWs varied substantially among years in the current study (from ~20% lower to 68% higher during winter compared with summer; fig. 1A), surpassing variation among populations in WBSWs (no seasonal change to 52% higher in winter; Noakes et al. 2017), and are also comparable to the range of variability in seasonal patterns across all subtropical species for which data are available (35% lower to 60% higher in winter vs. summer; McKechnie et al. 2015). As far as we are aware, the upregulation of BMR by 68% in winter compared with summer is the largest seasonal metabolic change recorded in a field-acclimatized bird (i.e., measured within 3 d of capture), with the greatest difference previously reported being 64% higher BMR during winter in temperate *Passer domesticus* in Wisconsin (Arens and Cooper 2005).

Mean M_{sum} values of WBSWs during each season (table 2) were similar to values reported for interpopulation variation by Noakes et al. (2017; mean M_{sum} range: 2.40–3.86 W). The ME of WBSWs (table 2) approached the upper end of the typical avian range for ME (~3–8; Swanson 2010; highest reported avian ME = 9, *P. domesticus*; Arens and Cooper 2005). We found variation in the magnitude and direction of seasonal acclimatization of M_{sum} in WBSWs (from no seasonal change to 38% lower in winter compared with summer; fig. 1A), whereas no seasonal variation in M_{sum} was reported in any populations by Noakes et al. (2017). Downregulation in M_{sum} during winter compared with summer has been reported in other birds from lower latitudes (e.g., winter decreases of 12%–35% in seven tropical species; Wells and Schaeffer 2012;

Table 3: Basal metabolic rate (BMR) and summit metabolism (M_{sum}) of white-browed sparrow-weavers (*Plocepasser mahali*, WBSW) and scaly-feathered weavers (*Sporopipes squamifrons*, SFW) during summer and winter over a 4-yr period, expressed as percentages of allometrically predicted metabolic rates

Species, variable, category	2014		2015		2016		2017	
	Summer (%)	Winter (%)	Summer (%)	Winter (%)	Summer (%)	Winter (%)	Summer (%)	Winter (%)
WBSW:								
BMR:								
Tropical	111	165	103	137	158	155	190	150
Passerine	95	140	88	116	135	132	162	128
M_{sum} :								
Tropical	151	179	156	131	219	157	203	161
Oscine	124	149	127	108	180	130	167	133
SFW:								
BMR:								
Tropical	105	102	148	115	161	135
Passerine	94	91	133	103	143	121
M_{sum} :								
Tropical	214	202	226	229	236	219
Oscine	133	128	141	144	150	137

Note. Allometric equations for BMR were obtained from Londño et al. (2015) for tropical and passerine birds, and equations for M_{sum} were obtained from Wiersma et al. (2007) for tropical birds and from Swanson and Bozinovic (2011) for oscine passerines. Predicted values of BMR and M_{sum} for each season were calculated using the mean body mass for that season for each species.

McKechnie et al. 2015). In contrast to north-temperate birds, higher M_{sum} in WBSWs did not appear to be associated with enhancements in cold tolerance (Swanson 2001; Cooper 2002; Swanson and Liknes 2006); for example, during the winter of 2015, we found both the lowest mean T_{CL} and the lowest mean M_{sum} .

We also report interannual metabolic variation in relation to environmental factors, with BMR and M_{sum} of WBSWs decreasing with decreasing food availability among seasons but never influenced by fluctuations in winter $T_{\text{a,min}}$. Moreover, metabolic rates generally mirrored fluctuations in food abundance during the study period regardless of season, being lower and less seasonally variable during years with lower food abundance (fig. 1). These interannual patterns partly support our prediction that a cold tolerance/energy conservation continuum drives patterns of seasonal metabolic variation in subtropical birds, as food abundance is highlighted as an important determinant of metabolic rates, but metabolic variation was never related to winter $T_{\text{a,min}}$. Our results for WBSWs reveal considerable variation in seasonal metabolic responses, adding to the growing evidence of considerable flexibility in the thermal physiology of this species (Smit and McKechnie 2010, 2015; Smit et al. 2013; Noakes et al. 2016, 2017; Noakes and McKechnie 2019).

Scaly-Feathered Weavers

Metabolic rates of SFWs were also generally higher than those predicted using allometric equations for tropical and passerine birds (table 3), suggesting that higher-than-predicted metabolic rates are the norm rather than the exception for both WBSWs and SFWs. Mean BMR values were higher than predicted for tropical birds

(35%–61% higher) and for passerine birds (21%–33% higher) during the summers of 2016 and 2017 and the winter of 2017, but they were similar to predicted values during the summer of 2015 and the winters of 2015 and 2016 (table 3; Londño et al. 2015). Mean M_{sum} values for each season were consistently greater than double the values predicted for tropical birds (102%–136% higher; Wiersma et al. 2007), as well as 28%–50% higher than values predicted for oscine passerines (table 3; Swanson and Bozinovic 2011).

As far as we are aware, no previous studies have measured BMR or M_{sum} of SFWs, although Lubbe et al. (2018) investigated the effect of communal roosting and nest use on RMR at $-5^{\circ} \leq T_{\text{a}} \leq 20^{\circ}\text{C}$ for SFWs caught at the same site in the Kalahari Desert as the current study. These authors reported lower RMR values at $T_{\text{a}} = 20^{\circ}\text{C}$ for individuals roosting in groups of two and four birds within a nest (RMR = 0.16 ± 0.05 W and 0.15 ± 0.07 W, respectively; Lubbe et al. 2018), compared with the BMR values of SFWs during the current study (table 2). This raises the potential importance of huddling in quantifying BMR in species that roost communally, as it is possible that solitary SFWs during our study had elevated metabolic rates due to higher stress levels (sensu Chappell et al. 2016). However, SFWs used by Lubbe et al. (2018) were acclimated to 25°C for ~ 30 d before the onset of metabolic measurements, and previous studies have demonstrated reductions in metabolic rates in wild-caught birds after periods of captivity (Piersma et al. 1996; Al-Mansour 2005; McKechnie et al. 2007; Noakes and McKechnie 2019).

The magnitude and pattern of seasonal acclimatization of BMR in SFWs varied among years (from no seasonal change to $\sim 31\%$ lower during winter) but not as substantially as for WBSWs (fig. 1B). Winter reductions in BMR have been reported for several

other subtropical species (McKechnie et al. 2015); for example, BMRs of *Zosterops lateralis* (Maddocks and Geiser 2000) and *Falco tinnunculus* (Bush et al. 2008) were ~18% and 12% lower in winter compared with summer, respectively. Similar to the ME of WBSWs, the ME of SFWs (table 2) also approached the upper end of the avian range for ME (Swanson 2010). There was no significant seasonal variation in the M_{sum} or T_{Cl} of SFWs over the study period; however, there were the same patterns of seasonal variation in ME as there were for BMR (table 2). This suggests that, unlike the pattern typical for higher-latitude species (Stager et al. 2016), adjustments in the ME of SFWs were driven by changes in BMR rather than M_{sum} , supporting the idea that ME is not necessarily a good indicator of avian thermogenic capacity (Petit et al. 2013).

Interannual metabolic variation in SFWs was also related to variation in environmental variables, but there were different patterns for BMR and M_{sum} during each season respectively. Among summers, BMR and M_{sum} of SFWs decreased with decreasing food abundance and decreased significantly with increasing $T_{\text{a,max}}$ and downregulating metabolic rates during hotter summers could have an adaptive value by reducing heat production. Among winters, neither BMR nor M_{sum} varied with food abundance, but BMR increased significantly with increasing winter $T_{\text{a,min}}$, which contrasts with the pattern reported in higher-latitude birds that typically increase both BMR and M_{sum} during colder periods (Swanson and Olmstead 1999; Broggi et al. 2007; Petit et al. 2013; Petit and Vézina 2014b). As for WBSWs, metabolic rates of SFW were generally lower and less seasonally variable during years with lower food abundance, with metabolic variation mirroring fluctuations in food abundance regardless of season (fig. 1). Thus, patterns of interannual metabolic variation in SFWs also partly support our enhanced cold tolerance/energy conservation hypothesis, as food availability was identified as an important determinant of BMR and M_{sum} during summer, but metabolic variation was never related to winter $T_{\text{a,min}}$ in a manner reflecting changes in cold tolerance.

Global Variation in Patterns of Seasonal Acclimatization

Studies on small, higher-latitude birds have frequently reported upregulation in BMR and M_{sum} during winter associated with increased cold tolerance, colder climates, and lower intrawinter mortality (Swanson 2010; McKechnie et al. 2015; Petit et al. 2017). At lower latitudes with comparatively milder winters, there appears to be greater variation in the magnitude and direction of seasonal metabolic responses, a pattern reported at both the interspecific and the interpopulation level (McKechnie et al. 2015; Noakes et al. 2017). The present study extends this pattern to the intrapopulation level, as we found considerable interannual variation in the magnitude and direction of seasonal adjustments in BMR and M_{sum} of two subtropical species. This does not necessarily imply that lower-latitude birds possess an inherently greater physiological flexibility compared with higher-latitude counterparts, but rather, it could reflect the extreme winter T_{a} at higher latitudes overwhelming other environmental factors that

could drive patterns of avian seasonal metabolic variation (Noakes et al. 2017).

In contrast to higher-latitude birds, seasonal metabolic variation in WBSWs and SFWs was not related to enhancing winter cold tolerance, and M_{sum} of both species was never significantly higher in winter compared with summer. Moreover, interannual variation in BMR and M_{sum} was never related to winter $T_{\text{a,min}}$ in a manner reflecting changes in cold tolerance. The lowest daily winter T_{a} recorded during our study period was -9.4°C , and extrapolating the relationship between RMR and T_{a} below the thermoneutral zone from previous studies suggests that M_{sum} in both WBSWs and SFWs (table 2) is about three- and twofold higher, respectively, than the RMR required to defend T_{b} at this T_{a} (1.26 W for Askham WBSWs during winter [Noakes et al. 2017]; 0.83 W for solitary SFWs in the absence of a nest [Lubbe et al. 2018]). It is therefore conceivable that metabolic upregulation to enhance cold tolerance is not required during milder winters at lower latitudes (McKechnie et al. 2015).

It has been suggested that ecological factors other than winter $T_{\text{a,min}}$ could also drive patterns of seasonal acclimatization in birds, a potential candidate being food availability, as birds may downregulate metabolism to conserve energy if food is in short supply (Smit and McKechnie 2010). This notion is supported by interannual variation in the BMR and M_{sum} of WBSWs and SFWs, which decreased with decreasing food abundance, suggesting a proximate effect of food availability on metabolic rates in these species. BMR and M_{sum} of WBSWs and SFWs were typically higher than values predicted using allometric equations for tropical and passerine birds (table 3), which could increase the pressure to downregulate metabolic rates during periods of low food abundance. Studies on north-temperate birds have reported a proximate effect of short-term (days to weeks) fluctuations in $T_{\text{a,min}}$ on BMR in *Parus major* (Broggi et al. 2007) and on M_{sum} in *Poecile atricapillus*, *Junco hyemalis*, and *Spizella americana* (Swanson and Olmstead 1999; Petit et al. 2013; Petit and Vézina 2014b). These contrasting patterns of proximate factors driving metabolic variation in birds are reminiscent of the different patterns of mammalian seasonal metabolic changes between small ($M_{\text{b}} < 100$ g, reduced BMR for energy conservation) and intermediate-sized ($0.1 < M_{\text{b}} < 10$ kg, increased thermogenic capacity; Lovegrove 2005) species, although all birds in the above examples are considered small ($M_{\text{b}} < 50$ g). During the current study, there was substantial variation in food abundance among seasons and low variability in mean $T_{\text{a,min}}$ among winters ($\sim 1.4^{\circ}\text{C}$ range; fig. 1C, 1D), and thus, it is possible that patterns of avian seasonal metabolic acclimatization are driven by a cold tolerance/energy conservation continuum but that food abundance was the more limiting factor during the milder winters of the Kalahari Desert.

In conclusion, our data reveal considerable flexibility in the thermal physiology of two Afrotropical passerine species, reiterating the importance of phenotypic plasticity as a source of intraspecific variation in endotherms. The magnitude and direction of seasonal metabolic variation varied among years in both species, supporting the idea that patterns of seasonal acclimatization are more variable in subtropical and tropical birds compared with

their temperate-zone counterparts (McKechnie et al. 2015). In contrast to higher-latitude birds, patterns of BMR and M_{sum} adjustments were not associated with enhancing cold tolerance in either species, but food abundance was a significant proximate factor driving interannual variation in metabolic rates in relation to energy conservation. Further studies are required to compare flexibility in BMR and M_{sum} in birds from higher and lower latitudes and to understand whether subtropical birds possess greater physiological plasticity or whether milder winters simply provide more opportunities for variation in seasonal metabolic responses.

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APPENDIX

Table A1: Interannual and seasonal variation in the abundance (count data) of the arthropod orders that form part of the diet of white-browed sparrow-weavers (*Plocepasser mahali*)

Arthropod	2015		2016		2017	
	Summer	Winter	Summer	Winter	Summer	Winter
Blattodea	75	15	158	356	321	73
Coleoptera	1,068	148	3,663	446	2,764	869
Hemiptera	65	429	24	3,218	3,453	578
Hymenoptera	5,635	773	2,541	9,417	5,539	9,289
Orthoptera	305	7	123	19	155	39
Total	7,148	1,372	6,509	13,101	12,232	10,848

Note. Arthropods were collected using pitfall traps at our study site near Askham in the Kalahari Desert, with equal sampling effort during each season.

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