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REVIEW

Global patterns of seasonal acclimatization in avian resting metabolic rates

Andrew E. McKechnie · Matthew J. Noakes ·
Ben Smit

Abstract The adjustment of resting metabolic rates represents an important component of avian seasonal acclimatization, with recent studies revealing substantial differences between summer and winter in birds from a wide range of latitudes. We compared seasonal variation in basal metabolic rate (BMR) and summit metabolism (M_{sum}) between temperate and tropical/subtropical latitudes, and examined correlations with latitude and temperature. The direction and magnitude of seasonal adjustments in BMR are broadly related to temperature and latitude, but are significantly more variable among tropical and subtropical species compared to those inhabiting temperate zones. Winter adjustments in BMR among subtropical species, when expressed relative to summer values, range from decreases of approximately 35 % to increases of more than 60 %, whereas the majority of temperate-zone species show increases in BMR during winter. Relatively few seasonal M_{sum} data exist for tropical/subtropical species, but those that are available involve responses ranging from winter decreases to increases of similar magnitude to those characteristic of many temperate-zone species. Recent studies also highlight the substantial variation in seasonal adjustments that may occur within species, and reiterate the need for further investigations of the relative roles of environmental variables such as temperature and food availability as determinants of seasonal metabolic variation.

Keywords Acclimatization · Basal metabolic rate · Latitude · Subtropics · Summit metabolism

A. E. McKechnie (✉) · M. J. Noakes
DST-NRF Centre of Excellence at the Percy FitzPatrick
Institute, Department of Zoology and Entomology, University of
Pretoria, Private Bag X20, Hatfield 0028, South Africa
e-mail: aemckechnie@zoology.up.ac.za

B. Smit
Centre for African Conservation Ecology, Department of
Zoology, Nelson Mandela Metropolitan University,
Port Elizabeth 6031, South Africa

Introduction

Long-distance migration is perhaps the most obvious and spectacular example of habitat seasonality driving the evolution of avian behavior and life history, but a range of seasonal phenotypic adjustments also occur in non-migratory species. These adjustments may include winter plumages of different colouration and thermal properties (Montgomerie et al. 2001), behavioral responses such as food caching (Smith and Reichman 1984), and/or physiological changes. One major category of physiological response to seasonal climates among non-migratory species involves the adjustment of metabolic machinery (reviewed by Swanson 2010; McKechnie 2008).

Historically, most research in this field has focused on north-temperate species, which generally increase resting metabolic rates during winter (Pohl 1971; Pohl and West 1973; Rising and Hudson 1974; Swanson 1990; O'Connor 1996). More recently, data on seasonal metabolic adjustments have also become available for a number of subtropical and tropical species (Maddocks and Geiser 2000; Zheng et al. 2008a; Maldonado et al. 2009; Smit and McKechnie 2010; Wells and Schaeffer 2012). Unlike their temperate-zone counterparts, many of these species decrease basal metabolic rate (BMR) in winter. An analysis of global variation in the magnitude and direction of

seasonal changes in BMR suggested that winter up-regulation is typical of species inhabiting regions characterized by long, cold winters, whereas species from warmer, subtropical regions generally reduce BMR in winter (Smit and McKechnie 2010). These authors proposed that this variation represents a continuum from selection for enhanced cold tolerance in seasonally cold environments to selection for winter energy conservation in subtropical habitats characterized by cool, dry winters.

Several studies also suggest, however, that seasonal metabolic adjustments can vary considerably within species. House Finch (Carpodacus mexicanus) populations from different parts of North America vary in the extent to which summit metabolism (M_{sum}) is increased in winter (O'Connor 1996). More recently, van de Ven et al. (2013) examined seasonal changes in BMR and M_{sum} in a southern African euplectid passerine, the Southern Red Bishop (Euplectes orix), and found that two populations differ in the magnitude and direction of seasonal changes in these resting metabolic rates. A population from a warmer coastal site reduced both BMR and M_{sum} in winter, whereas conspecifics from a cooler inland site showed a winter increase in BMR and no seasonal change in M_{sum} (van de Ven et al. 2013). Even greater intraspecific variation exists in another southern African passerine: Smit and McKechnie (2010) recorded reduced winter BMR in White-browed Sparrow-Weavers (Plocepasser mahali) in the Kalahari Desert, but more recent data for other populations of this species reveal winter BMR up-regulation of similar magnitude as seen in north-temperate species (Noakes and McKechnie, unpublished data).

Globally, seasonal adjustments in avian BMR and M_{sum} have been examined in 31 and 26 species, respectively (Tables 1, 2). However, the latitudinal distributions of these data are highly uneven and biased towards north-temperate regions, particularly in the case of M_{sum} (Fig. 1). Very few data exist for tropical regions, where the majority of avian biodiversity is found (Wells and Schaeffer 2012). Our goal in the present analysis was to provide an up-to-date analysis of global patterns of variation in avian seasonal metabolic acclimatization in terms of both the lower and upper limits of normothermic resting metabolic rate. Because of the patchy latitudinal distribution of the data that are currently available, we focus the analysis in part on whether broad differences in seasonal metabolic variation exist between birds from temperate and tropical/subtropical latitudes, respectively.

Methods

We compiled data on seasonal adjustments in BMR (Table 1) and M_{sum} (Table 2) from the literature. In all cases, summer and winter data were collected in the same location. We included species irrespective of whether they are resident, nomadic, or partial migrants. Consequently, we cannot control for the possibility of factors such as differences in body mass (M_b) between resident and migratory individuals influencing data for species such as Junco hyemalis, which is a partial migrant (Rising 2011). All reported rates of oxygen consumption were converted to metabolic rate (Watts) assuming a respiratory exchange ratio of 0.75 (i.e., a metabolic substrate consisting primarily of lipids) and the applicable joule equivalence value from Table 4.2 of Withers (1992).

For analyses of BMR, we included data from free-ranging as well as captive-bred populations (e.g., Wilson et al. 2011; Lovegrove et al. 2011) if birds experienced climatic conditions similar to those they experience naturally. However, we opted to exclude data for Monk Parakeets (Myiopsitta monachus; Weathers and Caccamise 1978) and House Sparrows (Passer domesticus; Nzama et al. 2010), as both these data are from feral populations well outside their respective native latitudinal ranges. Although including these two datasets did not appreciably change the outcome of our results, models from which they were excluded showed improved fit and higher r^2 values. We also excluded the datum for the Northern Bobwhite (Colinus virginianus) from M_{sum} analyses, as this species' M_b is more than double that of the next-largest species in the dataset (Table 2). All measurements obtained between 38°N and 38°S were categorized as tropical/subtropical species, and those from higher latitudes as temperate species.

Statistical analyses

For all analyses, BMR, M_{sum} and M_b were $\log_{10}$-transformed. To calculate residual BMR and M_{sum}, we averaged M_b, BMR and/or M_{sum} across seasons for each population or species, fitted a linear regression to average BMR or M_{sum} as a function of average M_b, and then calculated a residual for each original summer or winter datum. We tested for differences in residual BMR and M_{sum} between tropical/subtropical and temperate species. We also determined the magnitude and direction of seasonal BMR and M_{sum} responses by calculating mass-specific winter/summer ratios (W/S; see McKechnie 2008; Smit and McKechnie 2010).

We used conventional analyses of variance (ANOVA), general least squares regression analyses, and phylogenetic generalized least squares (PGLS) in R (R Development Core Team 2011), using the ape (Paradis et al. 2013) and caper (Orme et al. 2013) packages to determine the scaling of BMR and M_{sum} with M_b, and differences in BMR and M_{sum} adjustments (residuals and W/S ratios) between

Table 1 Seasonal changes in body mass and basal metabolic rate (BMR) in birds

Species	Body mass (g)		Basal metabolic rate (W)		W/S	Latitude	References	Comments
	Summer	Winter	Summer	Winter		(degrees N/S)		
Colinus virginianus	210.0	228.0	1.154	1.257	1.004	43	1	
Aegotheles cristatus	45.6	45.7	0.352	0.285	0.807	31	2	
Tauraco corythaix	308.9	286.5	1.041	1.175	1.218	29	3	
Otus senegalensis	62.2	55.4	0.411	0.280	0.765	26	4	
Asio otus	246.4	244.4	1.313	1.407	1.080	53	5	
Glaucidium perlatum	66.4	70.3	0.526	0.383	0.688	26	4	
Picoides pubescens	23.3	24.8	0.330	0.491	1.398	43	6	
Todus mexicanus	6.5	6.5	0.136	0.117	0.860	18	7	
Falco tinnunculus	214.0[a]		1.646	1.443	0.877	29	8	
Coracopsis vasa	456.2	454.3	4.372	2.905	0.667	30	9	
Myiopsitta monachus	83.1	80.4	0.681	0.515	0.782	40	10	
Malurus cyaneus	9.5	9.2	0.141	0.152	1.114	38	11	
Laniarius atrococcineus	43.0	41.0	0.398	0.267	0.704	26	4	
Dicrurus adsimilis	44.8	42.6	0.424	0.266	0.660	26	4	
Zosterops lateralis	10.9	11.2	0.175	0.144	0.799	31	12	
Poecile atricapillus	13.1	13.0	0.244	0.288	1.187	43	13	South Dakota
Poecile atricapillus	11.4	12.4	0.301	0.264	0.807	65	14	Alaska
Poecile atricapillus	10.3[a]		0.253	0.253	1.000	42	15	New York
Poecile gambeli	11.1	11.1	0.231	0.271	1.174	42	16	
Baeolophus ridgwayi	16.1	17.2	0.271	0.331	1.144	29	16	
Pycnonotus sinensis	25.6	33.2	0.408	0.622	1.175	27	17	
Onychognathus morio	128.0	137.0	1.293	1.776	1.284	30	18	
Sitta carolinensis	18.3	20.4	0.288	0.428	1.333	47	6	
Chalcomitra amethystina	16.0	14.8	0.309	0.202	0.709	30	19	Howick
Chalcomitra amethystina	15.5	14.5	0.284	0.282	1.061	31	19	Oribi Gorge
Chalcomitra amethystina	14.5	14.5	0.283	0.461	1.631	30	19	Underberg
Euplectes orix	21.0	23.8	0.312	0.301	0.852	31	20	Port Elizabeth
Euplectes orix	19.9	24.1	0.265	0.417	1.303	34	20	Aliwal North
Carduelis tristis	12.8	14.5	0.302	0.376	1.097	42	21	Michigan
Carduelis tristis	12.3	13.9	0.237	0.348	1.296	43	22	South Dakota
Carpodacus mexicanus	22.5	23.5	0.408	0.408	0.957	42	23	Michigan
Carpodacus mexicanus	20.7	20.5	0.331	0.332	1.014	31	24	California
Carpodacus mexicanus	19.8	20.6	0.345	0.364	1.013	34	24	Colorado
Carduelis flammea	12.8	15.6	0.267	0.410	1.259	65	25	
Plocepasser mahali	46.3	46.4	0.493	0.522	1.057	27	26	Frankfort
Plocepasser mahali	41.5	42.4	0.326	0.497	1.490	24	26	Polokwane
Plocepasser mahali	40.6	40.6	0.346	0.290	0.838	26	4	
Plocepasser mahali	39.0	41.0	0.366	0.557	1.450	27	26	Askham
Passer domesticus	25.4	26.0	0.328	0.538	1.605	44	27	Wisconsin
Passer domesticus	24.0	24.0	0.270	0.594	2.198	30	28	Pietermaritzburg
Passer montanus	18.2	18.9	0.408	0.577	1.363	45	29	
Zonotrichia capensis	19.1	19.8	0.383	0.381	0.958	43	30	
Zonotrichia leucophrys	26.3	28.3	0.396	0.465	1.091	47	31	
Fringilla montifringilla	22.5	25.8	0.485	0.546	0.982	48	32	

Table 1 continued

Species	Body mass (g)		Basal metabolic rate (W)		W/S	Latitude	References	Comments
	Summer	Winter	Summer	Winter		(degrees N/S)		
Junco hyemalis	17.8	19.4	0.291	0.341	1.076	42	33	

W/S the ratio of winter to summer mass-specific BMR

[a] Single mean body mass reported

References: 1. Swanson and Weinacht (1997), 2. Doucette and Geiser (2008), 3. Wilson et al. (2011), 4. Smit and McKechnie (2010), 5. Wijnandts (1984), 6. Liknes and Swanson (1996), 7. Merola-Zwartjes and Ligon (2000), 8. Bush et al. (2008), 9. Lovegrove et al. (1999), 10. Weathers and Caccamise (1978), 11. Lill et al. (2006), 12. Maddocks and Geiser (2000), 13. Cooper and Swanson (1994), 14. Sharbaugh (2001), 15. Rising and Hudson (1974), 16. Cooper (2000), 17. Zheng et al. (2008a), 18. Chamane and Downs (2009), 19. Lindsay et al. (2009a, b), 20. van de Ven et al. (2013), 21. Dawson and Carey (1976), 22. Liknes et al. (2002), 23. O'Connor (1995), 24. Dawson et al. (1985), 25. Pohl and West (1973), 26. Noakes and McKechnie, unpublished data, 27. Arens and Cooper (2005), 28. Nzama et al. (2010), 29. Zheng et al. (2008b), 30. Maldonado et al. (2009), 31. Southwick (1980), 32. Pohl (1971), 33. Swanson (1991)

temperate and tropical/subtropical species. We also tested whether BMR and M_{sum} vary as a function of winter temperature and latitude of the site of acclimatization; we obtained mean daily and mean minimum temperatures for the coldest month of the year for the nearest weather station to each study site from http://www.worldclimate.com or http://www.wundergound.com. We obtained the maximum consensus tree in Mesquite (Maddison and Maddison 2011) from 100 hypothetical trees sampled from http://www.birdtree.org (Jetz et al. 2012) using the Hackett et al. (2008) phylogeny as a backbone. For each species with multiple data points, we created a polytomy for the species, with each population representing a tip and branch lengths of zero between the populations. Significant phylogenetic signal (Blomberg et al. 2003) was detected in mean M_b ($K = 1.96$, $p < 0.001$), mean BMR ($K = 1.33$, $p < 0.001$), and mean M_{sum} ($K = 1.12$, $p < 0.001$), but not in W/S ratio of BMR ($K = 0.05$, $p = 0.747$).

Results

Basal metabolic rate

BMR scaled positively with M_b during both winter ($r^2 = 0.75$, $F_{1,40} = 122$, $p < 0.001$) and summer ($r^2 = 0.88$, $F_{1,40} = 297$, $p < 0.001$) in conventional analyses (Fig. 2). In both the above models, there was a significant effect of climate zone (i.e., temperate vs. tropical/subtropical) on the scaling of BMR (winter $F_{1,40} = 9.30$, $p < 0.01$; summer $F_{1,40} = 5.37$, $p < 0.05$). Temperate species showed a higher intercept, but the slopes were not significantly different; the interaction between M_b and climate zone was not significant in either season (winter $p = 0.20$; summer $p = 0.07$). In the PGLS analyses, BMR scaled positively with M_b both during winter ($r^2 = 0.78$,

$F_{2,42} = 149$, $p < 0.001$) and summer ($r^2 = 0.90$, $F_{2,42} = 384$, $p < 0.001$). There was no significant effect of climate zone on the scaling in the PGLS analysis (all $p > 0.3$). BMR during winter was significantly negatively related to mean winter temperatures (minimum: $r^2 = 0.77$, $F_{2,40} = 73.4$, $p < 0.001$; mean: $r^2 = 0.79$, $F_{2,40} = 79.8$, $p < 0.001$), and significantly positively related to latitude ($r^2 = 0.77$, $F_{2,40} = 71.5$, $p < 0.01$) (all models include winter M_b). Similarly, in PGLS analyses, BMR remained significantly negatively related to winter temperatures (minimum: $r^2 = 0.81$, $F_{3,40} = 89.9$, $p < 0.001$; mean: $r^2 = 0.84$, $F_{3,40} = 108.6$, $p < 0.001$) and positively related to latitude ($r^2 = 0.83$, $F_{3,40} = 102.2$, $p < 0.001$).

In the conventional models, temperate birds showed higher winter residual BMR compared to tropical/subtropical birds ($F_{1,42} = 11.7$, $p < 0.01$). However, significant heteroscedasticity was detected in this model (Levene's test, $F_{1,42} = 13.1$, $p < 0.001$; tropical/subtropical birds showed higher variance in winter residual BMR. In PGLS analyses, in contrast, there was no significant difference in winter residual BMR between temperate and subtropical species ($F_{2,42} = 2.50$, $p = 0.09$), with qualitatively similar differences in variance with latitude suggestive of significant heteroscedasticity. In both conventional ($F_{1,42} = 0.064$, $p = 0.8$) and PGLS ($F_{1,42} = 1.78$, $p = 0.2$) models, temperate species showed significantly higher summer residual BMR compared to tropical/subtropical species. Summer residual BMR also showed significant heteroscedasticity (Levene's test, $F_{1,42} = 4.59$, $p < 0.05$). In both conventional and PGLS analyses, winter residual BMR was significantly negatively related to winter temperatures (PGLS, minimum winter, $r^2 = 0.12$, $F_{2,41} = 6.87$, $p < 0.05$; mean winter, $r^2 = 0.15$, $F_{2,41} = 8.56$, $p < 0.01$). In conventional analyses, winter BMR residual showed a significant positive relationship with latitude ($r^2 = 0.22$, $F_{1,41} = 12.4$, $p < 0.01$). In PGLS

Table 2 Seasonal changes in body mass and summit metabolism (M_{sum}) in birds

| Species	Body mass (g)		Summit metabolism (W)		W/S	Latitude	References	Comments
	Summer	Winter	Summer	Winter		(degrees N/S)		
Colinus virginianus	220.0	230.0	6.752	7.363	1.043	43	1	
Picoides pubescens	25.0	26.6	2.214	3.357	1.425	43	2	
Amazilia tzacatl	5.5	5.6	1.177	0.803	0.682	9	3	
Picoides pubescens	25.8	26.0	2.585	2.404	0.923	43	4	
Cercomacra tyrannina	16.1	16.8	1.311	1.013	0.773	9	3	
Myrmeciza exsul	26.2	27.0	2.140	1.679	0.784	9	3	
Thamnophilus atrinucha	24.0	24.4	2.070	1.341	0.648	9	3	
Poecile gambeli	11.2	10.8	1.425	1.796	1.307	42	5	
Poecile atricapillus	13.1	13.0	1.598	2.170	1.368	43	6	
Baeolophus ridgwayi	16.9	16.8	1.612	1.873	1.169	42	5	
Baeolophus bicolor	20.4	22.4	1.722	2.495	1.449	39	3	
Sturnus vulgaris	79.6	89.8	5.795	6.297	0.963	45	7	
Sitta carolinensis	19.8	21.3	1.732	2.689	1.443	43	3	
Sitta carolinensis	19.6	21.8	1.629	2.077	1.146	43	4	
Euplectes orix	21.0	23.8	2.248	2.070	0.813	34	8	Port Elizabeth
Euplectes orix	19.9	24.1	2.126	2.451	0.953	31	8	Aliwal North
Carduelis tristis	12.5	13.7	1.428	1.876	1.199	43	9	South Dakota
Carduelis tristis	12.8	14.5	1.411	1.859	1.163	43	10	Michigan
Carpodacus mexicanus	21.3	21.0	2.020	2.190	1.100	43	4	
Plocepasser mahali	41.5	42.4	2.400	3.144	1.280	24	11	Polokwane
Plocepasser mahali	46.3	46.4	3.852	3.856	0.999	27	11	Frankfort
Plocepasser mahali	39.0	41.0	3.132	3.927	1.194	27	11	Askham
Passer domesticus	26.8	27.1	2.820	3.130	1.098	43	4	South Dakota
Passer domesticus	27.9	27.9	2.792	3.648	1.307	44	12	Wisconsin
Passer domesticus	27.1	29.4	2.341	3.344	1.317	45	7	
Carduelis spinus	12.8	13.2	1.398	1.515	1.051	51	13	
Carduelis chloris	27.1	26.6	2.070	1.736	0.854	51	13	
Coccothraustes vespertinus	58.0	62.1	4.123	4.849	1.098	45	7	
Thraupis episcopus	30.5	31.4	2.719	2.374	0.873	9	3	
Cardinalis cardinalis	41.4	48.3	2.710	3.650	1.154	43	4	South Dakota
Cardinalis cardinalis	41.5	47.2	2.023	2.451	1.212	39	14	Ohio
Sporophila corvine	11.3	11.3	1.237	0.903	0.730	9	3	
Coereba flaveola	9.7	9.6	1.110	0.953	0.858	9	3	
Junco hyemalis	16.9	18.2	1.933	2.471	1.187	44	15	

W/S is the ratio of winter to summer mass-specific M_{sum}

References: 1. Swanson and Weinacht (1997), 2. Liknes and Swanson (1996), 3. Wells and Schaeffer (2012) 4. Swanson and Liknes (2006), 5. Cooper (2002), 6. Cooper and Swanson (1994), 7. Hart (1962), 8. van de Ven et al. (2013), 9. Liknes et al. (2002), 10. Dawson and Carey (1976), 11. Noakes and McKechnie, unpublished data, 12. Arens and Cooper (2005), 13. Saarela et al. (1995), 14. Sgueo et al. (2012), 15. Swanson (1990)

analyses, in contrast, there was no significant relationship between winter residual BMR and latitude ($p = 0.66$).

In both conventional and PGLS analyses there was no effect of M_b on W/S ratios of BMR (all $p > 0.5$). In conventional analyses, temperate-zone birds showed significantly higher W/S ratios of BMR compared to tropical/subtropical birds ($F_{1,41} = 6.10$, $p < 0.05$), but in

PGLS analyses there was no difference in W/S between climate zones ($p > 0.5$). In both conventional and PGLS analyses W/S ratios showed significant negative relationships with winter temperatures (PGLS, minimum, $r^2 = 0.14$, $F_{2,42} = 7.88$, $p < 0.01$; mean, $r^2 = 0.13$, $F_{2,42} = 7.52$, $p < 0.01$); W/S ratios of BMR were higher (>1) in regions with cold winter temperatures. In contrast,
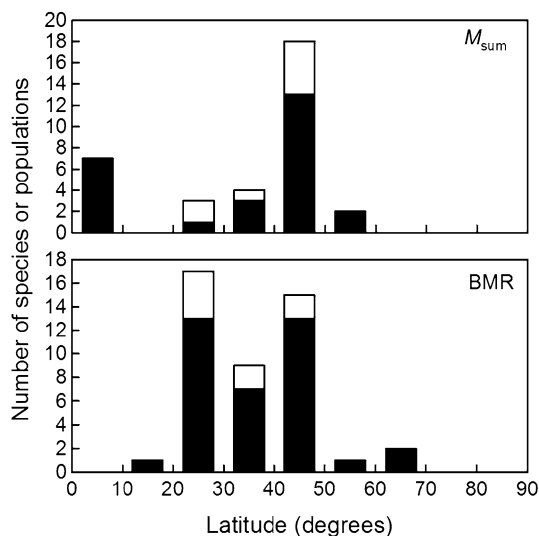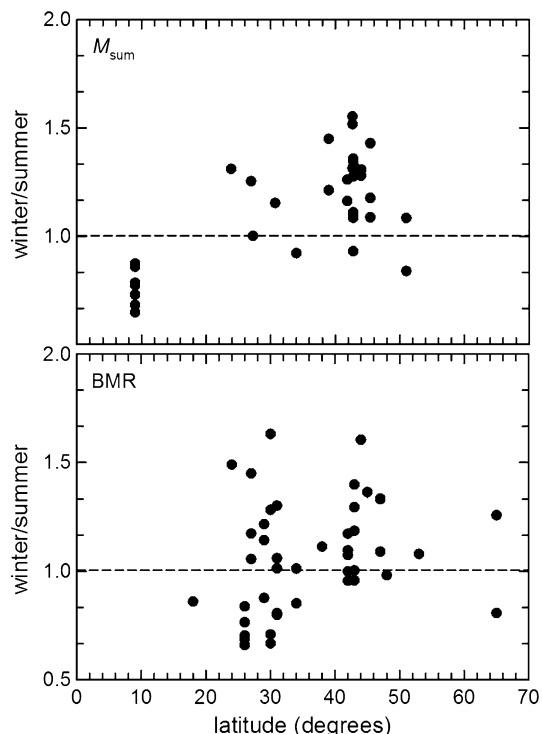
Fig. 1 Latitudinal distribution of data on seasonal adjustments of avian basal metabolic rate (BMR) and summit metabolism (M_{sum}). The *solid bars* indicate species, and the *white stacked bars* the number of additional data points for populations
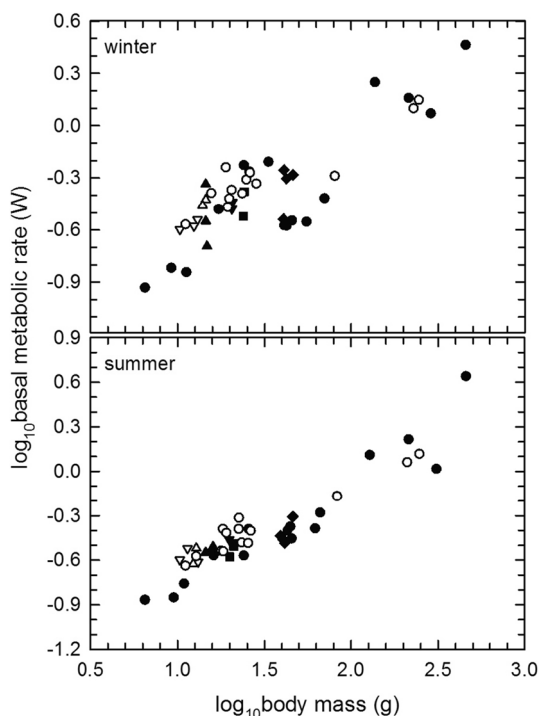
Fig. 2 Scaling of basal metabolic rate during winter (*upper*) and summer (*lower*) in the species for which seasonal data are available. Species from tropical and sub-tropical latitudes (<38°N/S) are indicated with *filled symbols*, and species from temperate regions with *open symbols*. *Circles* indicate species with data for a single population, whereas other *shapes* indicate multiple populations for a given species

Fig. 3 Winter/summer ratios of avian mass-specific basal metabolic rate (*BMR, lower*) and summit metabolism (M_{sum}, *upper*)
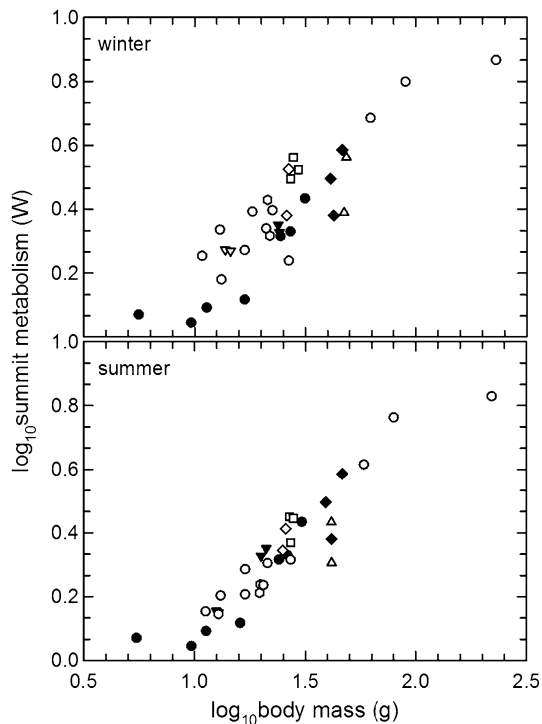
Summit metabolism

Summit metabolism scaled significantly with M_b during winter and summer (winter: $r^2 = 0.69$, $F_{1,31} = 72.6$, $p < 0.001$; summer: $r^2 = 0.73$, $F_{1,31} = 86.8$, $p < 0.001$) (Fig. 4). There was no effect of climate zone on the scaling of M_{sum} in either season (although this approached significance, $p = 0.06$). The relationship between M_{sum} and M_b was similarly significant in PGLS, but there was a significant interaction between M_b and climate zone for both seasons (temperate birds had higher slopes); although the intercept was significantly different only for summer data (overall model in winter: $r^2 = 0.72$, $F_{4,29} = 28.5$, $p < 0.001$; summer: $r^2 = 0.75$, $F_{4,29} = p < 0.001$).

In conventional analyses, winter M_{sum} was significantly negatively related to winter temperatures (minimum: $r^2 = 0.78$, $F_{2,30} = 56.7$, $p < 0.01$; mean: $r^2 = 0.77$, $F_{2,30} = 55.9$, $p < 0.01$) and positively related to latitude ($r^2 = 0.75$, $F_{2,30} = 46.7$, $p < 0.05$) (all models include M_b as a significant covariate). Similarly, in PGLS winter M_{sum} was significantly negatively related to winter temperature (minimum: $r^2 = 0.66$, $F_{3,30} = 32.1$, $p < 0.05$; mean: $r^2 = 0.66$, $F_{3,30} = 32.3$, $p < 0.05$), although latitude had no significant effect ($p > 0.3$).

Significant heteroscedasticity in residual M_{sum} was not detected in winter (Levene's test, $F_{1,31} = 0.685$, $p = 0.40$) nor summer (Levene's test, $F_{1,22} = 0.222$, $p = 0.64$). In

latitude did not show a significant relationship with W/S ratios of BMR in either conventional and PGLS analyses (all $p > 0.05$) (Fig. 3).

Fig. 4 Scaling of summit metabolism during winter (*upper*) and summer (*lower*) in the species for which seasonal data are available. Species from tropical and sub-tropical latitudes (<38°N/S) are indicated with *filled symbols*, and species from temperate regions with *open symbols*. *Circles* indicate species with data for a single population, whereas other *shapes* indicate multiple populations for a given species

conventional analyses, winter residual M_{sum} was significantly higher in temperate compared to tropical/subtropical species ($F_{1,31} = 12.6$, $p = 0.01$). Summer residual M_{sum} did not differ significantly between temperate and tropical/subtropical species ($F_{1,31} = 0.887$, $p = 0.345$). Similarly, in PGLS winter residual M_{sum} was significantly higher in temperate compared to tropical/subtropical species (winter: $F_{2,31} = 6.69$, $p < 0.01$), but summer residual M_{sum} did not differ significantly ($p > 0.43$). In both conventional and PGLS models, winter residual M_{sum} was significantly negatively related to winter temperature (PGLS, minimum winter, $r^2 = 0.26$, $F_{2,31} = 12.3$, $p < 0.01$; mean winter, $r^2 = 0.24$, $F_{2,31} = 11.1$, $p < 0.01$) and significantly positively related to latitude (PGLS, $r^2 = 0.13$, $F_{2,31} = 5.92$, $p < 0.05$).

In conventional analyses, there were significant effects of M_b, climate zone and the interaction between M_b and climate zone on W/S ratios of M_{sum} (whole model: $F_{3,29} = 10.62$, $p < 0.01$); temperate species had a higher intercept and significantly different slope relating M_{sum} with M_b. In contrast, PGLS analyses showed no effect of M_b on W/S ratios ($p > 0.4$), but showed a significant effect of climate zone ($F_{2,31} = 11.15$, $p < 0.01$); temperate zone species had higher W/S ratios of M_{sum}. In both

conventional and PGLS analyses, there was a significant negative effect of winter temperature (PGLS, minimum winter, $r^2 = 0.29$, $F_{2,31} = 14.1$, $p < 0.001$; mean winter, $r^2 = 0.28$, $F_{2,31} = 13.6$, $p < 0.01$) and positive effect of latitude ($r^2 = 0.17$, $F_{2,31} = 7.42$, $p < 0.001$) on W/S ratios of M_{sum}. M_b was not important in the relationships between W/S ratios of M_{sum} and winter temperatures or latitude.

Discussion

The overall picture that emerges from our analysis is that differences in seasonal metabolic adjustments between birds inhabiting temperate and tropical/subtropical latitudes primarily reflect correlations between BMR and M_{sum} and temperature. In the case of BMR, there is significantly more variance in tropical/subtropical latitudes, whereas corresponding heteroscedasticity is not evident for M_{sum}. The magnitude and direction of seasonal adjustments, expressed as W/S ratios, also varies consistently with temperature and latitude.

The present analysis of BMR suggests that global variation is more complex than the linear relationships between winter/summer BMR ratio and latitude and temperature of the coldest month of the year reported by Smit and McKechnie (2010). The differences between our present findings and those of the latter study can primarily be ascribed to recent data revealing substantial intraspecific variation in the magnitude and direction of seasonal BMR adjustments in two Afrotropical passerines (van de Ven et al. 2013; Noakes and McKechnie, unpublished data), and studies such as those of Wilson et al. (2011) and Lindsay et al. (2009a, b), who found winter increases in BMR among subtropical species. Several of these species or populations showed winter increases in BMR of similar fractional magnitude to those typical of high-latitude north-temperate species (Fig. 3).

A key finding of this study is that variation in residual BMR is not consistent across latitude, with significant heteroscedasticity reflecting greater variation in the winter and summer residual BMR of tropical/subtropical species compared to temperate species. For instance, whereas most species from temperate latitudes show marked winter increases in BMR, among tropical/subtropical species winter mass-specific BMR expressed as a percentage of summer values varies from 66 % (Fork-tailed Drongo *Dicrurus adsimilis*; Smit and McKechnie 2010) to 163 % (Amethyst Sunbird *Chalcomitra amethystina*; Lindsay et al. (2009a, b) (Fig. 3). This pattern is reminiscent of the global pattern in avian field metabolic rate (FMR, or daily energy requirements) identified by Anderson and Jetz (2005), where there is considerably more variation in residual FMR at lower latitudes compared to higher latitudes. These authors

interpreted this pattern as reflecting a greater diversity of metabolic niches at lower latitudes, with decreasing environmental temperature and increasing day length being key drivers of lower interspecific variation in FMR in higher-latitude environments. Our finding that the direction and magnitude of seasonal BMR adjustments is more variable at lower latitudes is broadly consistent with the arguments made by Anderson and Jetz (2005). A functional link between avian BMR and FMR has yet to be convincingly demonstrated (Ricklefs et al. 1996; Careau et al. 2008). However, compared to higher latitudes characterized predominantly by relatively predictable seasonal cycles, one might a priori expect more variable patterns of phenotypic flexibility in baseline energy requirements among species inhabiting latitudes where habitats range from hyperarid deserts to wet rainforests, and where phenomena such as the El Niño Southern Oscillation exert a strong and unpredictable influence on climate (Lovegrove 2000).

The ecological relevance of M_{sum} is perhaps more intuitively obvious than that of BMR, as M_{sum} is a measure of the maximum capacity of an individual to defend a body temperature setpoint during cold weather. Several studies have found that avian M_{sum} is generally lower in species from warmer tropical and subtropical environments compared to colder, temperate environments (Swanson and Garland 2009; Wiersma et al. 2007a). Our finding that winter residual M_{sum} is significantly higher among temperate-zone species compared to tropical/subtropical species is consistent with this overall picture, as is the corresponding difference in W/S ratios. Moreover, the absence of a corresponding difference in summer residual M_{sum} supports the notion that the global variation in winter M_{sum} adjustments is driven primarily by a link between M_{sum} and thermogenic requirements during winter. These patterns are strikingly illustrated in Fig. 4, where the divergence in winter M_{sum} between tropical/subtropical and temperate species, but lack thereof in summer, is readily apparent. Our analysis is, however, constrained by the paucity of seasonal M_{sum} data from the subtropics (just five data points representing two Afrotropical species) and tropics (seven species at a single site in Panama; Wells and Schaeffer 2012).

The data that are currently available also highlight the need for more studies examining variation among and within populations of a particular species. It is striking, for instance, that within both a north-temperate species (Black-capped Chickadee, *Poecile atricapillus*) and a southern subtropical species (White-browed Sparrow-weaver, *Plocepasser mahali*) the direction of winter changes in BMR varies among populations from winter decreases to winter increases (Table 1). In the case of *P. atricapillus*, W/S values range from 0.807 to 1.187 (Cooper and Swanson 1994; Sharbaugh 2001), whereas in *P. mahali* the

corresponding range is 0.838–1.490 (Smit and McKechnie 2010; Noakes and McKechnie, unpublished). These data for *P. atricapillus* raise the possibility that some temperate-zone species may in fact show more variable seasonal adjustments in BMR than suggested by the strong correlations with temperature that emerged in the interspecific analysis, and highlight the need for more data to test the generality of the patterns identified in the present analysis.

A related question that remains largely unanswered, but which is potentially important for understanding observed patterns in intra- and interspecific variation in seasonal metabolic adjustments, concerns the extent to which seasonal changes within populations are flexible and are modulated by environmental conditions. Data for several north-temperate species reveal that M_{sum} closely tracks short-term fluctuations in temperature, suggesting a proximate influence of temperature (Swanson and Olmstead 1999; Petit and Vezina 2014). But the intraspecific variation in seasonal BMR adjustments highlighted in the preceding paragraph raises the possibility that not just the magnitude but also the direction of seasonal metabolic adjustments may vary among seasons. For instance, Smit and McKechnie (2010) observed a winter reduction of 17 % in the mass-specific BMR of White-browed Sparrow-weavers at a site in the Kalahari Desert. However, more recent data for the same species provide a different picture, with three populations increasing BMR during winter, with a 45 % winter increase in mass-specific BMR in another Kalahari Desert population (Noakes and McKechnie, unpublished data). Smit and McKechnie's (2010) winter data were collected following a relatively dry rainy season, whereas the more recent unpublished winter data were collected following a summer with above-average rainfall. These contrasting results within a species raise questions about environmental drivers of seasonal metabolic adjustments (Swanson and Olmstead 1999), and it may be that the direction of seasonal changes within populations are modulated by year-to-year differences in temperature and/or food availability. The functional significance of these variable adjustments may reflect the continuum from energy conservation to enhanced cold tolerance proposed by Smit and McKechnie (2010), a possibility that can be evaluated by examining correlations between metabolic adjustments and temporal variation in temperature and food availability. Moreover, birds are not the only endotherms in which the direction and/or magnitude of seasonal metabolic adjustments appears to vary widely within species at subtropical latitudes. Two populations of Wahlberg's Epauletted Fruit Bats (*Epomophorus wahlbergi*) from South Africa showed seasonal changes in BMR in opposite directions, with one population decreasing whole-animal BMR by 16–25 % but another increasing it by 40 % (Minnaar et al. 2014; Downs et al. 2012).

In conclusion, the analyses presented here reveal that global patterns of variation in seasonal adjustments of avian resting metabolic rates are more complex than the linear relationships with latitude and temperature reported by Smit and McKechnie (2010), reflecting several recent studies showing winter increases in BMR among species from subtropical regions. Seasonal changes in BMR are more variable in subtropical latitudes compared to temperate latitudes. Far less information is available for M_{sum}, particularly in tropical and subtropical species, but the few data that are available suggest that winter adjustments in this variable are strongly linked to temperature, with winter decreases or smaller increases in tropical and subtropical specues compared to those observed in species from higher latitudes. Our study also highlights the almost complete lack of data on seasonal adjustments for species from the tropics, where most avian diversity occurs; although the number of tropical species for which BMR measurements exist is rapidly increasing (Wiersma et al. 2007b; Londoño et al. in press), none of these studies involved measurements across seasons. In the case of seasonal adjustments in M_{sum}, the data available for tropical species are currently limited to seven species (Wells and Schaeffer 2012).

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