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Seasonal metabolic variation over two years in an Afrotropical passerine bird

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ABSTRACT

Seasonal trends in metabolic parameters are well established in avian populations from highly seasonal environments, however, seasonal trends in metabolism of birds from lower latitudes (and of Afrotropical birds in particular) are not well understood. We investigated seasonal trends in metabolism for a small (10–12 g) Afrotropical bird, the Cape White-eye (*Zosterops virens*), using flow-through respirometry in two summers and two winters. There was no seasonal difference in body mass between consecutive seasons. The lower critical limit of thermoneutrality was lower in winter (23 °C) than in summer (28 °C), as expected for a small Afrotropical bird. In the first year of the study, mean whole animal basal metabolic rate (BMR) of Cape White-eyes was significantly lower in winter than in summer, while in the second year of the study this trend was reversed, and in the middle two seasons there was no significant difference in BMR. Differences in mean temperature and mean rainfall between seasons could not account for the seasonal trends in BMR. We conclude that seasonal trends in avian BMR may vary between years, within a population.

1. Introduction

Small birds have higher mass-specific rates of energy expenditure, thermoregulatory costs and surface-area-to-volume ratios than larger birds (Arens and Cooper, 2005; McNab, 2009; Sharbaugh, 2001). To cope with changing environments, they need to make physiological adjustments in metabolism or insulation, at a rate equalling that at which they gain and lose heat from/to their environment (Chaui-Berlinck et al., 2002; Williams and Tieleman, 2001). Small birds lose heat to their environments more rapidly than larger birds, however, they can only carry a limited amount of insulation before their movement is affected and the risk of predation increases (Calder, 1984). Thus, in winter, many small bird species show higher basal (Liknes et al., 2002; McKechnie, 2008; Pohl and West, 1973; Swanson and Olmstead, 1999), fasting (Southwick, 1980; Weathers and Caccamise, 1978) and summit/peak (Cooper and Swanson, 1994; Dawson and Marsh, 1989; Liknes and Swanson, 1996; O'Connor, 1995) metabolic rates, reflecting greater thermogenesis, and thus higher cold tolerance, in winter than in summer (Swanson, 1990).

Basal metabolic rate (BMR) is the minimum metabolic rate of postabsorptive homoeotherms, measured at thermoneutrality during their inactive phase (Daan et al., 1990). BMR is one of the most commonly measured physiological variables of endotherms (Bech et al., 1999; Rønning et al., 2007), making it extremely useful for comparisons between avian taxa (Liknes and Swanson, 1996; McKechnie, 2008, 2006). Seasonal differences in avian metabolism have been well-studied in Holarctic temperate climates, where BMR is generally higher in winter than in summer (Liknes et al., 2002). For example, House Sparrows (*Passer domesticus*) from Wisconsin increased their whole animal BMR by 64% in winter (Arens and Cooper, 2005), and Downy Woodpeckers (*Picoides pubescens*) from South Dakota increased their mass-specific BMR by 40% (Liknes and Swanson, 1996). These winter increases in BMR seem to follow seasonal changes in energy expenditure, and may reflect an up-regulation in the metabolic machinery necessary for improved cold tolerance, which increases the chances of survival in extremely cold winter conditions (Cooper and Swanson, 1994; Dawson, 2003; Piersma et al., 1995).

In contrast, birds resident in the Afrotropics, Australasia and Indomalaya are generally exposed to milder winters, although these may be punctuated by unpredictable cold periods and less predictable rainfall, than birds in the Holarctic region (Lovegrove, 2000; Sinclair et al., 2003). Although fewer studies have investigated seasonal changes in metabolism in these tropical and subtropical bird species (Van de Ven et al., 2013), their peak metabolic rates (Wells and Schaeffer, 2012) and BMR (Table 1) are often significantly lower in winter than in summer. For example, Australian Silvereyes (*Zosterops lateralis*) had significantly lower

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Table 1
Southern African avian species in which seasonal variation in metabolism has been investigated. Lower limit of the thermoneutral zone (T_{lc}), body mass (M_b), basal metabolic rate (BMR), and seasonal trends in winter (w) and summer (s) are presented.

Species	T_{lc} summer (°C)	T_{lc} winter (°C)	T_{lc}	Mean M_b (g) summer (n)	Mean M_b (g) winter (n)	M_b	BMR mass-specific	BMR whole-animal	Reference
Cape White-eye *Zosterops virens* (winter 2012, summer 2013)	28	23	w < s	11.7 (24)	11.7 (36)	w=s	w < s*	w < s*	1
Z. virens (winter 2013, summer 2013)	28	23	w < s	11.7 (24)	11.7 (36)	w=s	w=s	w < s*	1
Z. virens (winter 2013, summer 2014)	27	23	w < s	11.9 (24)	11.7 (36)	w=s	w=s	w=s	1
Southern Red Bishop *Euplectes orix* (inland site)	n/a	n/a	n/a	19.9 (14)	24.1 (18)	w > s*	w > s*	w > s*	2
E. orix (coastal site)	n/a	n/a	n/a	21.0 (17)	23.8 (18)	w > s*	w < s*	w=s	2
White-browed Sparrow-weaver *Plocepasser mahali*	26-29	26-29	n/a	40.6 (7)	40.6 (6)	w=s	w < s*	w < s*	3
Crimson-breasted Shrike *Laniarius atrococcineus*	26-29	26-29	n/a	43.0 (6)	41.0 (5)	w=s	w < s*	w < s*	3
Fork-tailed Drongo *Dicrurus adsimilis*	26-29	26-29	n/a	44.8 (8)	42.6 (7)	w=s	w < s*	w < s*	3
African Scops-owl *Otus senegalensis*	26-29	26-29	n/a	62.2 (7)	55.4 (7)	w < s*	w < s*	w < s*	3
Pearl-spotted Owlet *Glaucidium perlatum*	26-29	26-29	n/a	66.4 (5)	70.3 (3)	w=s	w < s*	w < s*	3
Rose-ringed Parakeet *Psittacula krameri*	20	15	w < s	123.0 (10)	123.5 (10)	w=s	w < s*	n/a	4
House Sparrow *Passer domesticus*	25	25	w=s	n/a	n/a	w=s	w > s*	w > s*	5
Red-winged Starling *Onychognathus morio*	15	30	w > s	n/a	n/a	w > s*	w > s*	n/a	6
Southern White-faced Scops-owl *Ptilopsis granti*	20	28	w > s	221.1	221.1	w=s	w=s	w=s	7
Knysna Turaco *Tauraco corythaix*	10	20	w > s	n/a	n/a	w=s	w > s*	w > s*	8
Rock Kestrel *Falco rupicolis*	20	15	w < s	214	214	w=s	n/a	n/a	9
F. rupicolis	21	21	w=s	214	214	w=s	w=s	n/a	9

This table only includes studies on species currently found in the wild in South Africa, and work done on birds that were either freshly wild-caught, or held in semi-natural conditions in outdoor aviaries prior to measurements being taken. 'n/a' indicates that a certain variable was not presented in a specific study, and 'w=s' shows that there was no significant seasonal variation in a certain variable. 1=this study, 2=Van de Ven et al. (2013), 3=Smit and McKechnie (2010), 4=Thabethe et al. (2013), 5=Nzama et al. (2010), 6=Chamane and Downs (2009), 7=Smit et al. (2008), 8=Wilson et al. (2011), 9=Bush et al. (2008). We have included mass-specific BMR measurements because in some studies M_b was not provided. Note that strictly speaking, our summer measurements on Cape White-eyes should be classed as RMR not BMR, since birds showed some primary feather moult.

* Indicates statistical significance.

BMR in winter than in summer (Maddocks and Geiser, 2000), and White-browed Scrubwrens (*Sericornis frontalis*) from arid Western Australia had significantly lower standard metabolic rates in winter than in summer (Ambrose and Bradshaw, 1988). Similarly, Southern Red Bishops (*Euplectes orix)* from a milder, more predictable, coastal environment in South Africa's Eastern Cape province reduced their BMR in winter (Van de Ven, 2012). However, not all southern African birds follow this general trend of reducing their BMR in winter; Rock Kestrels (*Falco rupicolus*) showed no significant seasonal difference in BMR (Bush et al., 2008), while Kynsna Turacos (*Tauraco corythaix*) and Red-winged Starlings (*Onychognathus morio*) elevated their BMR in winter, suggestive of thermogenesis rather than energy conservation (Chamane and Downs, 2009; Wilson et al., 2011). It may be that timing of seasonal metabolic measurements influences the direction and magnitude of seasonal change (Thompson et al., 2015a, c).

In light of the seeming disparity regarding seasonal trends in BMR of southern African bird species (Table 1), we investigated seasonal effects on BMR in a 12 g Afrotropical bird, the Cape White-eye (*Zosterops virens*; Sundevall, 1850; Thompson and Taylor, 2014). This southern African endemic species has an extremely large range (Hulley et al., 2004; Smith and Bowie, 2005), and we anticipated that its ability to tolerate a diverse range of habitats could reflect a high degree of flexibility in its BMR, making it an ideal candidate for showing seasonal variation in BMR.

We hypothesised that Cape White-eyes would show seasonal variation in BMR, evaporative water loss (EWL) and the lower critical limit (T_{lc}) of the thermoneutral zone (TNZ). We hypothesised that there would be no seasonal difference in body mass (M_b), since small birds generally do not rely on increased plumage insulation or subcutaneous fat for improved cold tolerance in winter (Zheng et al., 2014). We predicted that the BMR and T_{lc} of Cape White-eyes would be lower in winter than in summer, to conserve energy, as in a variety of other small southern African bird species in winter (Smit and McKechnie, 2010; Table 1). Since ambient temperatures are lower in winter than in summer, evaporative cooling should not be as important for thermoregulation in winter, and so we predicted that EWL would be lower in winter than in summer. Moreover, since the Cape White-eye is a sexually monomorphic species (Oatley, 2011), we predicted that sex would not affect BMR, M_b or EWL.

2. Materials and methods

2.1. Experimental animals

Twelve Cape White-eyes were caught in February 2012 at the Darvill Bird Sanctuary, Pietermaritzburg, KwaZulu-Natal, South Africa (29°36′S, 30°26′E), using mist nets (Ecotone, Gdynia, Poland). Birds were transported 2.5 km to the Animal House of the University of KwaZulu-Natal, Pietermaritzburg, where they were housed in groups of four in outdoor aviaries ($1 \times 3 \times 2$ m^3). These aviaries permitted limited flight, and they ensured that the birds used in the study experienced the same environmental conditions encountered by wild birds in the same area. Fresh fruits (oranges, papayas, bananas and apples) and softbill pellet supplements (Aviproducts, Durban, South Africa) were supplied daily, and water was given *ad libitum*. Breeding was discouraged with a lack of nesting materials. After the study, birds were released at their capture sites. A permit to capture, ring, transport, monitor and release Cape White-eyes was granted by Ezemvelo KwaZulu-Natal Wildlife, number OP 5122/2012. Ethical approval for this study was granted by the Animal Ethics Sub-committee of the University of KwaZulu-Natal, reference 071/13/Animal. Mean maximum monthly temperatures at the study site ranged from 30 °C in