



# Circannual rhythm of resting metabolic rate of a small Afrotropical bird



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## ABSTRACT

Seasonal variation in avian metabolic rate is well established in Holarctic and temperate species, while trends in Afrotropical species are relatively poorly understood. Furthermore, given the paucity of data on circannual rhythm in avian metabolism, it is not known whether seasonal measurements made in summer and winter correspond with annual peaks and troughs in avian metabolic rate. Thus, we investigated how mean body mass, resting metabolic rate (RMR) and evaporative water loss (EWL) of a small Afrotropical bird, the Cape white-eye (*Zosterops virens*), changed monthly over the course of a year at 20 °C and 25 °C. Mean body mass was  $12.2 \pm 1.0$  g throughout the study period. However, both EWL and RMR varied monthly, and peaks and troughs in RMR occurred in March and October respectively, which did not correspond to peaks and troughs in mean monthly outdoor ambient temperatures. These results suggest that measuring RMR at the height of summer and winter may underestimate the flexibility of which birds are capable in terms of their metabolic rate. We encourage further studies on this topic, to establish whether the lag between environmental temperature and RMR is consistent in other species.

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## 1. Introduction

Basal metabolic rate (BMR) is the ‘obligatory cost of living for endotherms’ (Barceló et al., 2009), and it is measured in resting, post-absorptive, non-reproductive, adult endotherms at thermo-neutrality during their inactive period (McKechnie et al., 2006; McNab, 1997). BMR is one of the most commonly measured physiological variables of endotherms (Bech et al., 1999; Rønning et al., 2007), and is a useful metric for comparing metabolic power output among avian taxa (Liknes and Swanson, 1996; McKechnie, 2008; McKechnie et al., 2006).

In birds, BMR is influenced by a multitude of factors (McKechnie and Swanson, 2010), however, it is not fixed, as was previously implied by studies that reported a single BMR value for a species (McKechnie, 2008; Speakman et al., 2004). On the contrary, avian BMR is now known to be a highly flexible trait (Piersma, 2002; Swanson et al., 2014; Van de Ven et al., 2013a; Vézina et al., 2006; Zheng et al., 2013), and changes in avian BMR are temporary, reversible and repeatable (McKechnie et al., 2007;

Piersma and Drent, 2003), which helps birds to adapt to spatially or temporally heterogeneous environments (DeWitt, 1998; DeWitt et al., 1998; Schlichting and Pigliucci, 1998; Tieleman et al., 2003; Via et al., 1995). For example, there are a plethora of studies showing seasonal flexibility in avian metabolic rate (Bech, 1980; Bush et al., 2008a; Cooper et al., 2002; Cooper and Swanson, 1994; Hart, 1962; McKechnie, 2008; Piersma et al., 1995; Pohl and West, 1973; Thabethe et al., 2013; Van de Ven et al., 2013b), and these changes in avian metabolism usually follow seasonal changes in energy expenditure (Dawson, 2003; Smit et al., 2008).

The higher winter metabolic rates of some avian species suggest increased thermogenic capacity, and are correlated with improved cold tolerance (Cooper and Swanson, 1994). For example, increased thermogenic capacity was found to be the main feature of winter acclimatization in American goldfinches (*Carduelis tristis*) (Carey et al., 1978; Dawson and Carey, 1976), and winter-acclimatized house sparrows (*Passer domesticus*) are more tolerant of low temperatures than summer-acclimatized birds (Davis Jr., 1955; Kendeigh, 1949; Nzama et al., 2010). Avian BMR may show significant seasonal adjustments of up to 64% and 120% for whole animal and mass-specific BMR respectively (McKechnie, 2008; Nzama et al., 2010), and in environments with extremely cold winters, birds usually have higher BMR, cold tolerance, metabolic capacity, standard and peak metabolic rates, and resting metabolic rate (RMR), in winter than in summer (Dawson and Carey, 1976; Dawson and Marsh, 1989; Downs and Brown, 2002; Hart, 1962;

**Abbreviations:** BMR, Basal metabolic rate; EWL, Evaporative water loss; RMR, Resting metabolic rate; RER, Respiratory exchange ratio;  $\dot{V}CO_2$ , Rate of  $CO_2$  production;  $\dot{V}O_2$ , Rate of  $O_2$  consumption

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McKechnie et al., 2007; Olson et al., 2010; Pohl and West, 1973; Weathers and Caccamise, 1978; Williams and Tieleman, 2000).

However, avian metabolic rate does not always increase with cold acclimation (Vézina et al., 2006; Williams and Tieleman, 2000); reduction of fasting metabolic rate in winter may allow improved maintenance of body temperature independent of low ambient temperature (Weathers and Caccamise, 1978). Furthermore, the direction of seasonal change may depend on body size, with some smaller birds and mammals reducing their metabolic rates in winter, to conserve energy (Heldmaier, 1989; Lovegrove, 2005; Smit and McKechnie, 2010). For example, in the Afrotropics, where winters are generally mild, some species have been shown to conserve energy during winter acclimatization by lowering RMR (Bush et al., 2008b). However, in the southern subtropics, the direction of seasonal trends in metabolic rate are not yet well understood; Knysna turacos (*Tauraco corythaix*) and an inland population of southern red bishops (*Euplectes orix*) increased their BMR in winter (Van de Ven et al., 2013b; Wilson et al., 2011); no significant seasonal change in BMR was recorded in rufous-collared sparrows (*Zonotrichia capensis*), white-browed scrubwrens (*Sericornis frontalis*) and a coastal population of southern red bishops (Ambrose and Bradshaw, 1988; Maldonado et al., 2009; Smit and McKechnie, 2010; Van de Ven et al., 2013b); and white-browed sparrow-weavers (*Plocepasser mahali*), crimson-breasted shrikes (*Laniarius atrococcineus*), fork-tailed drongos (*Dicrurus adsimilis*), African scops-owls (*Otus senegalensis*) and pearl-spotted owlets (*Glaucidium perlatum*) all reduced their BMR in winter (Smit and McKechnie, 2010).

There are numerous studies on seasonal variation in avian metabolism (McKechnie, 2008), often comparing metabolic rate between two seasons (Versteegh et al., 2012). However, relatively few studies have investigated circannual rhythms in avian metabolic rate (Klaassen, 1995; Piersma et al., 1995; Vézina et al., 2011; West, 1960; Zheng et al., 2008), belying the possible importance of the finer-scale understanding of circannual rhythm in metabolic rate to be gleaned from more frequent, regular measurements. For example, Zheng et al. (2008) found distinct seasonal trends in BMR and body mass in freshly wild-caught Eurasian tree sparrows (*Passer montanus*), and yet their clustering of the data into seasonal values, rather than separation into monthly values, gives a coarser picture of circannual rhythm than it would had they presented monthly data, as did West (1960) and Vézina et al. (2011).

Given that seasonal metabolic adjustments in Afrotropical birds are relatively understudied and poorly understood compared to in temperate and Holarctic birds (Smit and McKechnie, 2010), and given the abovementioned scarcity of data on circannual rhythms in avian metabolic rate, we studied variation in RMR of a small Afrotropical bird monthly throughout the year at 20 °C and 25 °C. The genus *Zosterops* contains ~75 species (Van Balen, 2008), making it the most species-rich genus in the world (Oatley, 2011), and yet barring work on the Australian silvereye (*Z. lateralis*) (Jurisevic et al., 1999; Maddocks and Geiser, 1997, 1999, 2000) and the chestnut-flanked white-eye (*Z. erythropleura*) (Liu et al., 2005), relatively little is known about the metabolism of this group. We hypothesized that Cape white-eyes (*Zosterops virens*) (Sundevall, 1850; Thompson and Taylor, 2014), a southern African endemic species, would show a distinct circannual rhythm of metabolism, leading to seasonal differences in RMR, and we predicted that they would reduce their RMR in winter, in accordance with many other small Afrotropical species, as an energy conservation mechanism (Smit and McKechnie, 2010).

## 2. Methods

### 2.1. Study animals and housing

Twelve Cape white-eyes were trapped as adults in February 2012 using mist-nets (Ecotone, Gdynia, Poland) in a garden in Pietermaritzburg, KwaZulu-Natal, South Africa (29°36'S, 30°26'E). Birds were housed in groups of 4, in outdoor aviaries (1 m wide x 3 m long, and 2 m tall), with cement floors, and walls and roofs of wire mesh. One third of each roof was covered in shade cloth to provide shelter from the sun, and each aviary was equipped with two wooden perches, but no nesting material, to discourage breeding. There were no refugia within cages. Each morning, birds were given a variety of fresh grated and whole fruit supplemented with softbill pellets (Avi-products, Durban, South Africa). Water was provided *ad libitum*.

### 2.2. Gas exchange measurements

Respirometry measurements were conducted in the first week of each month, from September 2012 to August 2013 inclusive. Four birds were run each night, at a constant temperature of either 20 or 25 °C all night, from 15:00 until 06:30 the following morning, with 12 minutes per hour spent recording data from a reference chamber, and then from each bird in turn. Scotophase was set from 18:00 to 06:00, and all data recorded before 18:00 each evening were discarded, as live infrared video camera feeds (CCTV camera Jiange® model JG-811CM, China) revealed that birds were awake and active while the lights were on in the temperature-controlled environmental chamber (Convicon, Winnipeg, Canada), but that within about 1 min of the lights going off, they closed their eyes and generally remained inactive. These differences in levels of physical activity between scotophase and photophase were reflected in the  $\dot{V}O_2$  traces. All 12 birds were run once a month, every month, at both 20 °C and 25 °C, with a break of at least one night in between measurements. One bird died part-way through the study and was replaced. These temperatures (20 °C and 25 °C) were chosen on the assumption that they would fall within the thermoneutral zone of this population of Cape white-eyes. However, subsequent measurements on Cape white-eyes from the same population showed the lower critical limit of the thermoneutral zone to be 28 °C in summer, and 23 °C in winter (Thompson et al., 2015c). Thus, we refer to our  $\dot{V}O_2$  values as  $RMR_{Ta}$  where ambient temperature inside the environmental chamber ( $T_a$ ) was either 20 or 25 °C. Similarly  $EWL_{20}$  and  $EWL_{25}$  indicate evaporative water loss (EWL) values when birds were measured overnight at 20 and 25 °C respectively.

Details of the respirometry setup have previously been described (Thompson et al., 2015a,b). Briefly, birds were placed into 2.8 L Perspex respirometers inside a temperature-controlled environmental chamber (CMP2244, Convicon, Winnipeg, Canada), set to 12L:12D. Open-flow, push mode respirometry was used to measure metabolic rate. Environmental air was drawn from outside the building, and water vapor and CO<sub>2</sub> were removed with silica gel and soda lime respectively (Withers, 2001). This air was then pumped (model PP2, Sable Systems, Las Vegas, Nevada, USA) through a flow measurement system (model FB8, Sable Systems), with flow rates set to approximately 800 mL min<sup>-1</sup> for each channel, maintaining the depletion in O<sub>2</sub> concentration in each chamber between 0.1% and 0.5%, following Lighton (2008). Effluent air then flowed through a multiplexer (model MUX, Sable Systems) and a subsampler (model SS4, Sable Systems), whereafter 200 mL min<sup>-1</sup> of the effluent airstream passed into a water vapor analyzer (model RH300, Sable Systems), before being dried with minimal quantities of Drierite (Hammond Drierite Co. Ltd., Xenia, Ohio). Air then flowed through a CO<sub>2</sub> analyzer (model CA-

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