

RESEARCH ARTICLE

The potential effects of climate-change-associated temperature increases on the metabolic rate of a small Afrotropical bird

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ABSTRACT

Studies have only recently begun to underline the importance of including data on the physiological flexibility of a species when modelling its vulnerability to extinction from climate change. We investigated the effects of a 4°C increase in ambient temperature (T_a), similar to that predicted for southern Africa by the year 2080, on certain physiological variables of a 10–12 g passerine bird endemic to southern Africa, the Cape white-eye *Zosterops virens*. There was no significant difference in resting metabolism, body mass and intraperitoneal body temperature between birds housed indoors at 4°C above outside ambient temperature and those housed indoors at outside ambient temperature. We conclude that the physiological flexibility of Cape white-eyes will aid them in coping with the 4°C increase predicted for their range by 2080.

KEY WORDS: Climate change, Avian resting metabolic rate, Evaporative water loss, Thermal PIT tags, Cape white-eye, *Zosterops virens*

INTRODUCTION

Birds on every continent have been directly affected by anthropogenic climate change (Møller, 2013; Parmesan, 2006; Şekercioglu et al., 2012; Wormworth and Mallon, 2006). One of the direct impacts of this rapid change in climate is an increased frequency of extreme heat events (Easterling et al., 2000; IPCC, 2012; Meehl and Tebaldi, 2004) to which birds are particularly vulnerable, because of their diurnal habits and small body sizes (Coumou and Rahmstorf, 2012; McKechnie et al., 2012; McKechnie and Wolf, 2010). Extreme weather events may drive local avian population dynamics (Parmesan et al., 2000) and can exert strong natural selection pressures (Bumpus, 1899), favouring the evolution of avian morphometric traits (Boag and Grant, 1984). Extreme heat events pose the most risk to species with narrower thermal ranges, and consequently, lower thermal tolerances (Jiguet et al., 2006; Khaliq et al., 2014).

In addition to surviving extreme heat events, birds will also need to cope with higher mean surface air temperatures (IPCC, 2013a), which, in turn, will increase the frequency of extreme heat events (NASA, 2012). An A2 emissions scenario, where emissions related to land use are expected to continue increasing rapidly (IPCC, 2000) for southern Africa (from the equator to 45°S and from 5° to 55°E), predicted a 3.7 to 4°C increase by the 2080s (Mlingwa, 2000), similar to the mean increase in surface temperature of 3.7°C predicted by a Representative Concentration Pathway 8.5 scenario by 2081–2100, relative to 1986–2005 (IPCC, 2013b). Mean

seasonal temperatures and dry periods are predicted to increase throughout sub-Saharan Africa, with El Niño southern oscillation effects, fires and severe weather anomalies likely to become more common in southern Africa (IPCC, 2013a; Müller et al., 2014). Indeed, Africa is projected to have ‘above-average’ climate change in the 21st century (IPCC, 2007) and therefore is the continent where global warming will have the greatest effects on biodiversity (Simmons et al., 2004). Distributions of southern African bird species are predicted to contract towards the Cape (IUCN, 2014), yet little else is known of how African birds may move or adapt in response to climate change (Parmesan, 2006; Simmons et al., 2004).

Species may cope with environmental changes through micro-evolutionary adaptation (Karell et al., 2011) and/or phenotypic plasticity; the latter in particular is potentially crucial for projections of extinction risk due to climate change (Chase, 2013; Hoffmann and Sgrò, 2011). Small birds generally cope with elevated temperatures through behavioural adaptation, and physiologically, by reversibly altering their metabolic rate (McKechnie, 2008; McKechnie et al., 2007), body temperature (T_b) (Tieleman and Williams, 1999) and evaporative water loss (EWL) (Williams and Tieleman, 2000). Attention to how the attributes of a species change with temperature will help to improve the forecasting on the impacts of climate change (McClelland, 2004) because physiological capabilities may buffer the predicted effects of global warming (Khaliq et al., 2014). Yet, the role of phenotypic plasticity and flexibility in species’ physiological responses has been relatively underappreciated in climate change modelling (Chown et al., 2010; Vedder et al., 2013). Thus, we investigated how a small passerine bird would cope with the sustained temperature increase predicted for its range by the year 2080.

We chose the 10–12 g southern African endemic Cape white-eye *Zosterops virens* (Sundevall, 1850; Thompson and Taylor, 2014) as our model species. This species has a large range across southern Africa (Hockey et al., 2005) and so should exhibit a fair degree of phenotypic flexibility in terms of its metabolic rate. We aimed to investigate how Cape white-eyes would perform metabolically with the sustained 4°C increase predicted for their range by the year 2080. We hypothesized that Cape white-eyes would alter their resting metabolic rate (RMR), T_b and EWL when faced with a 4°C increase over a protracted period of time. We predicted that RMR would be lower, and T_b and EWL higher, in birds acclimated to higher temperatures, than in control birds also housed indoors, but at outdoor ambient temperatures.

RESULTS

Mean, minimum and maximum monthly temperatures peaked in January and February, and dipped to their lowest points in June and July (Fig. 1). Mean monthly M_b of Cape white-eyes varied throughout the year, with lows in July and November–January, and a peak in March–April (Fig. 2). Male Cape white-eyes were significantly heavier than female birds ($\chi^2=205.4, P<0.001$); however, there was no

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List of abbreviations and symbols

BMR	basal metabolic rate
Control	birds housed indoors, at the outdoor ambient temperature (T_a)
Control+4°C	birds housed indoors, at 4°C above the outdoor ambient temperature ($T_a+4^\circ\text{C}$)
EWL	evaporative water loss ($\text{mg H}_2\text{O h}^{-1}$)
Group	birds were either housed in the 'control' group or in the 'control+4°C' group
M_b	body mass (g)
RMR	resting metabolic rate ($\text{ml O}_2 \text{h}^{-1}$)
T_a	ambient temperature ($^\circ\text{C}$)
T_b	intrapерitoneal body temperature ($^\circ\text{C}$)
TNZ	thermoneutral zone
\dot{V}_{CO_2}	volumetric rate of carbon dioxide produced by the bird ($\text{ml CO}_2 \text{h}^{-1}$)
\dot{V}_{O_2}	volumetric rate of oxygen consumed by the bird ($\text{ml O}_2 \text{h}^{-1}$)

significant difference in M_b between control birds and those housed at control+4°C ($\chi^2=2.7$, $P=0.101$, Tables 1 and 2).

During overnight metabolic measurements, intraperitoneal T_b , RMR and EWL of Cape white-eyes generally dropped quickly in the first 3 h of darkness (from 18:00 h–21:00 h, Figs 3 and 4). Intrapерitoneal T_b and RMR rose again in the three hours before photophase, whereas EWL dropped continuously throughout the night. There was a weakly positive but highly significant correlation between T_b and whole animal RMR (Pearson's product-moment correlation, $t_{237}=2.905$, $r=0.185$, $P=0.004$).

During scotophase, mean hourly T_b measurements of individual Cape white-eyes ranged from 36.6°C (at 23:00 h, in April 2014, in a control bird, measured at 20°C) to 43.4°C (at 18:00 h, in March 2014, in a control bird measured at 25°C). T_b was $0.9\pm 0.4^\circ\text{C}$ lower in male birds than in females ($\chi^2=132.7$, $P<0.001$), but there was no significant difference in T_b between birds housed at $T_a+4^\circ\text{C}$ and those housed at T_a ($\chi^2=1.1$, $P=0.303$, Table 2, Fig. 5). Mean monthly T_b peaked in September–October and dropped to a minimum in November–December.

Mean whole-animal RMR of Cape white-eyes was lower in the austral winter and spring (August–December) than in summer and autumn (February–May, Figs 4 and 5). Whole-animal and

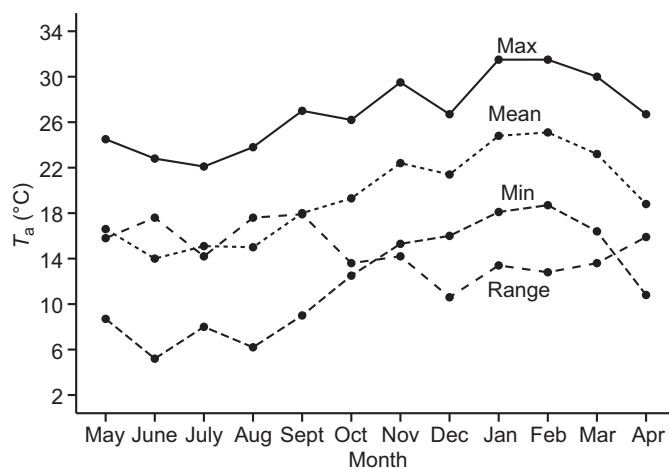


Fig. 1. Mean monthly maximum, minimum, mean and range of outdoor ambient temperatures. T_a ($^\circ\text{C}$) was recorded at the study site in Pietermaritzburg, South Africa, during the study period, May 2013 to April 2014.

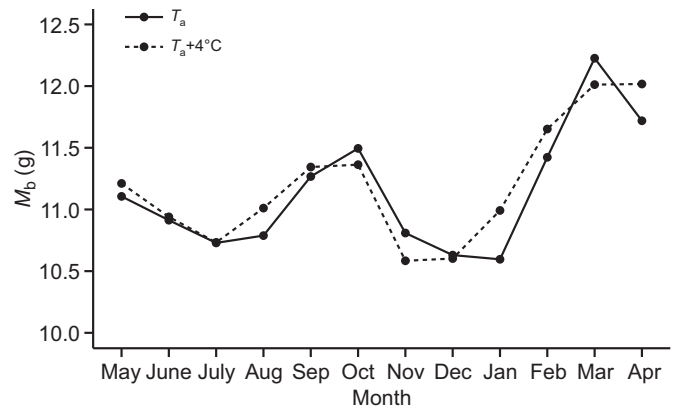


Fig. 2. Mean monthly body mass of Cape white-eyes from May 2013 to April 2014. Birds ($N=20$) were housed in the control group or in the control+4°C group and M_b was measured overnight.

mass-specific RMR showed very similar circannual rhythms, and predictive models for each of these variables included the same fixed effects (Table 1). Whole-animal RMR of male white-eyes was significantly lower than that of females ($\chi^2=495.8$, $P<0.001$) and the temperature at which birds were measured had a significant effect on whole-animal RMR ($\chi^2=177.2$, $P<0.001$), however the effect of 'group' on whole-animal RMR was not significant ($\chi^2=1.3$, $P>0.05$).

Mean monthly whole-animal EWL of Cape white-eyes showed distinct seasonal trends, being higher in September/October and March/April, than in May–July and November–February (Fig. 5). Whole-animal standard EWL was 2.313 $\text{mg H}_2\text{O h}^{-1}$ lower in males than in females (Table 2) and this difference was significant ($\chi^2=774.8$, $P<0.001$); however, there was no significant difference in whole-animal standard EWL between birds housed at control+4°C and control birds ($\chi^2=0.2$, $P=0.654$). Trends were similar for mass-specific standard EWL of Cape white-eyes (Table 2). Similarly, there was no significant difference in basal EWL of control birds and those housed at control+4°C ($\chi^2=2.8$, $P=0.096$); however, basal EWL was 0.015 $\text{mg H}_2\text{O h}^{-1}$ lower in males than in females (Table 2; $\chi^2=643.0$, $P<0.001$). Trends were similar for mass-specific basal EWL (Table 2).

DISCUSSION

This year-long study showed that a 4°C increase in housing temperature had no significant effect on intraperitoneal T_b , EWL or whole-animal RMR of Cape white-eyes, suggesting that the phenotypic flexibility of the Cape white-eye will be more than sufficient for coping physiologically with the mean temperature increase predicted across its range by 2080.

Mean M_b of Cape white-eyes showed no clear trend over the duration of the study, which was very similar to what was found in a group of 12 Cape white-eyes caught at the same study site and housed in outdoor aviaries for one year (Thompson et al., 2015b). Although white-eyes in this study increased their M_b prior to winter, there was nevertheless very little variation in M_b throughout the year, in stark contrast to circannual trends in M_b shown by migratory bird species (Zimmerman, 1965). The small fluctuations in M_b of Cape white-eyes between months may be due to variation in their diet in captivity, in that while certain fruits were available year round, others were not. Birds housed at T_a were 0.5 g heavier than those housed at $T_a+4^\circ\text{C}$, which may be due to increased food intake and increased fat deposits, although this was not investigated here. Although *Z. virens* is widely accepted as a sexually monomorphic

Table 1. Ranking of models predicting metabolic parameters of Cape white-eyes

Response variable	Fixed effects	<i>k</i>	AIC	AICWt	ΔAIC
T_b	' M_b '+'sex'+' T_a '+'group'	8	635.39	0.69	0.00
	' M_b '+'moult'+sex'+' T_a '+'group'	9	637.01	0.31	1.63
Whole-animal RMR	' M_b '+'moult'+sex'+' T_a '+'group'	9	2075.32	0.94	0.00
	' M_b '+'sex'+' T_a '+'group'	8	2080.85	0.06	5.53
M_b	'Moult'+sex'+group'	7	790.94	1.00	0.00
	' M_b '+'moult'+sex'+' T_a '+'group'	9	3625.1	1.00	0.00
Whole-animal standard EWL	' M_b '+'moult'+sex'+' T_a '+'group'	9	1705.3	0.99	0.00
Mass-specific standard EWL	' M_b '+'sex'+' T_a '+'group'	8	1715.3	0.01	9.95
Whole-animal basal EWL	' M_b '+'moult'+sex'+' T_a '+'group'	9	2961.11	0.00	1.00
Mass-specific basal EWL	' M_b '+'moult'+sex'+' T_a '+'group'	9	1273.32	0.00	1.00

All candidate models included 'individual' and 'date' as random effects; however, only those with an AICcWt>0 are presented. The number of parameters (*k*) and Akaike Information Criterion (AIC) scores for each respective model are given. Models were ranked on their Akaike weights (AICWt) and on the difference between the best model and each candidate model (ΔAIC). Models with ΔAIC<2 have considerable empirical support (Smit et al., 2011; Swanson and Garland, 2009) and are shown in bold. See list of abbreviations for meaning of fixed effects.

species (Hockey et al., 2005; Oatley, 2011; Skead, 1967), male Cape white-eyes were slightly heavier and had significantly lower whole-animal RMR than females.

Thermal PIT tags have been used in physiological studies on reptiles (Bittner et al., 2002; Roark and Dorcas, 2000) and small mammals (Cory Toussaint and McKechnie, 2012) but to our knowledge this is the first study in which these PIT tags have been

successfully used for a long-term study in small birds. Mean hourly intraperitoneal T_b of Cape white-eyes showed a marked circadian rhythm typical of small diurnal avian insectivores and nectarivores (Clarke and Rothery, 2008; McKechnie and Lovegrove, 2002).

Circannual rhythm in T_b did not seem to follow circannual rhythm in T_a , and there was little similarity between circannual trends in T_b and RMR in this study, even though T_b influences (and is influenced by) metabolic rate (Clarke and Rothery, 2008). The higher T_b levels shown in this study may be from nights when RMR fell earlier in the evening, since T_b usually took at least 3 h after dark to fall to minimal levels. We cannot explain the abrupt October–November crash in mean T_b of Cape white-eyes.

Sex may have a significant effect on T_b in passerines, presumably because of widespread sexual size dimorphism (Clarke and Rothery, 2008). Indeed, male Cape white-eyes had significantly lower T_b than females, possibly as a result of their marginally larger body size, although since the difference in M_b between the sexes was so little, we would not have expected a difference in T_b . Nevertheless the estimated effect of sex on T_b was double that of increasing the housing temperature by 4°C, suggesting that the 4°C increase in T_a , predicted for southern Africa by the year 2080, will have a negligible effect on core T_b in this population of Cape white-eyes. Similarly, the T_b of Cape white-eyes measured at 25°C was only 0.2°C different from that of birds measured at 20°C. This result is in line with the findings of Bucher (1981), who reported that a medium-sized parrot *Amazona viridigenalis* showed no significant difference in T_b between T_a values of 10 and 27°C. Since our birds were measured at ambient temperatures close to or below the lower critical limit of their TNZ (our unpublished data), water conservation should not have been of concern and thus there was no need for them to become hyperthermic (Tieleman et al., 1999).

Cape white-eyes in this study had lower whole-animal RMR in spring than in autumn. However, the RMR trend does not precisely fit that of outdoor T_a at the study site. Cape white-eyes housed at $T_a+4°C$ had a whole-animal and mass-specific RMR that was marginally lower than for birds housed at T_a . However, this difference was not a significant effect. Thus, it would seem that coping with the mean air temperature increase of 4°C predicted for southern Africa by 2080 (Mlingwa, 2000) should be well within the physiological capabilities for this species. However, although a 4°C increase induced very little change in RMR of Cape white-eyes, the long-term fitness consequences of this change are unknown (Burton et al., 2011).

M_b , T_b and EWL all dipped around December, coinciding with an unseasonal drop in environmental temperature at the study site, when the range of temperatures was also the lowest. Since housing

Table 2. Estimate sizes of fixed effects contained in the best approximating model(s) fitted by restricted maximum-likelihood estimation (REML) for each respective response variable

Response variable	Fixed effect	Estimate size	s.e.m.
T_b	'Sex'	−0.85	0.40
	'Group'	0.44	0.42
	' T_a '	−0.20	0.15
	' M_b '	0.15	0.11
Whole-animal RMR	' T_a '	−7.33	0.38
	' M_b '	1.87	0.25
	'Sex'	−1.79	1.24
	'Group'	−1.27	1.26
	'Moult'	0.12	0.05
M_b	'Group'	−0.50	0.32
	'Sex'	0.33	0.32
	'Moult'	0.03	0.01
Whole-animal standard EWL	' T_a '	5.62	3.39
	' M_b '	3.39	1.64
	'Sex'	−2.31	3.73
	'Group'	1.83	4.33
	'Moult'	−0.88	0.33
Mass-specific standard EWL	' T_a '	0.50	0.30
	'Sex'	−0.23	0.33
	'Group'	0.22	0.38
	' M_b '	−0.15	0.15
	'Moult'	−0.08	0.03
Whole-animal basal EWL	'Group'	−5.21	3.22
	' T_a '	−0.98	2.57
	'Moult'	−0.80	0.19
	' M_b '	−0.69	1.07
Mass-specific basal EWL	'Sex'	−0.02	2.71
	'Group'	−0.41	0.31
	' M_b '	−0.33	0.11
	' T_a '	−0.10	0.25
	'Moult'	−0.08	0.02
	'Sex'	−0.02	0.26

In each case, ' T_a ' refers to metabolic measurement of birds at 25°C (as opposed to 20°C), 'sex' refers to male, and 'group' to the group of birds kept at $T_a+4°C$ (as opposed to those kept at T_a). The estimate sizes given above for T_b are the result of model averaging (Swanson and Garland, 2009). See list of abbreviations for meaning of fixed effects.

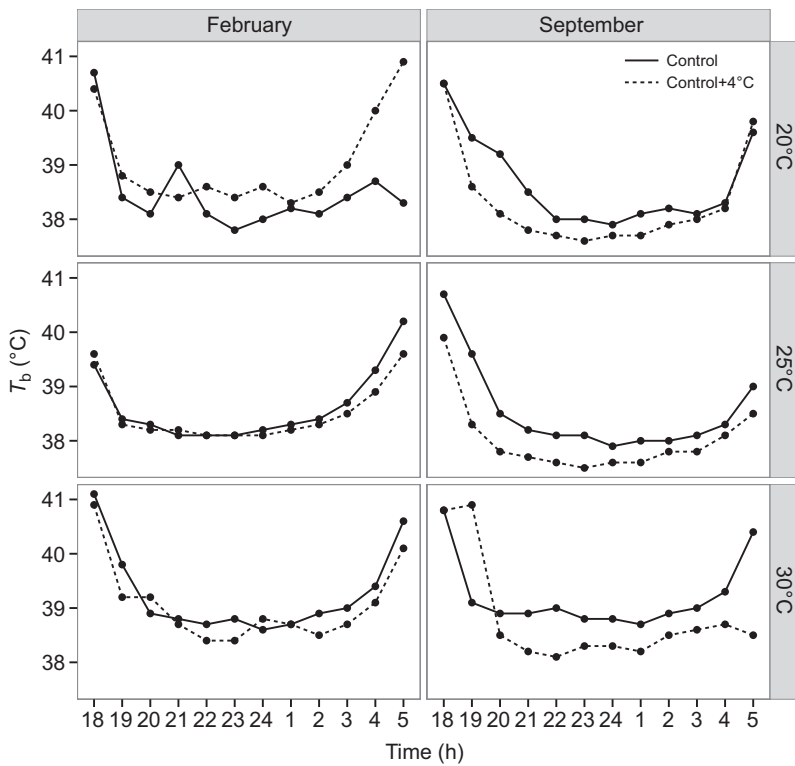


Fig. 3. Mean hourly intraperitoneal body temperature of Cape white-eyes housed at T_a and at $T_a+4^\circ\text{C}$. T_b of birds housed at T_a ($N=5$) and at $T_a+4^\circ\text{C}$ ($N=5$), measured at $T_a=20^\circ\text{C}$, 25°C and 30°C , in February 2014 and September 2013. Scotophase lasted from 18:00 h to 06:00 h.

birds at 4°C above T_a had a smaller effect on whole-animal and mass-specific standard EWL than either sex or of measuring at 25°C vs 20°C , we can conclude that the 4°C increase in temperature predicted for 2080 will have little direct effect on EWL in this population of Cape white-eyes.

In September, when temperatures were cooler, Cape white-eyes lost water at a faster rate overnight than they did in February, when temperatures were slightly higher. EWL showed a general increase

over the study period. This result goes against the notion of EWL having a circannual pattern, since start and end values were so different. We cannot explain what may have caused the overall increase in EWL over the study period, nor do we have any evidence to link the increase in EWL to any potential physiological effects of long-term captivity.

Mean BMR of captive Cape white-eyes housed indoors in the room set to T_a ($41.235\pm 3.380 \text{ ml O}_2 \text{ h}^{-1}$, mean \pm s.d., $N=12$) was

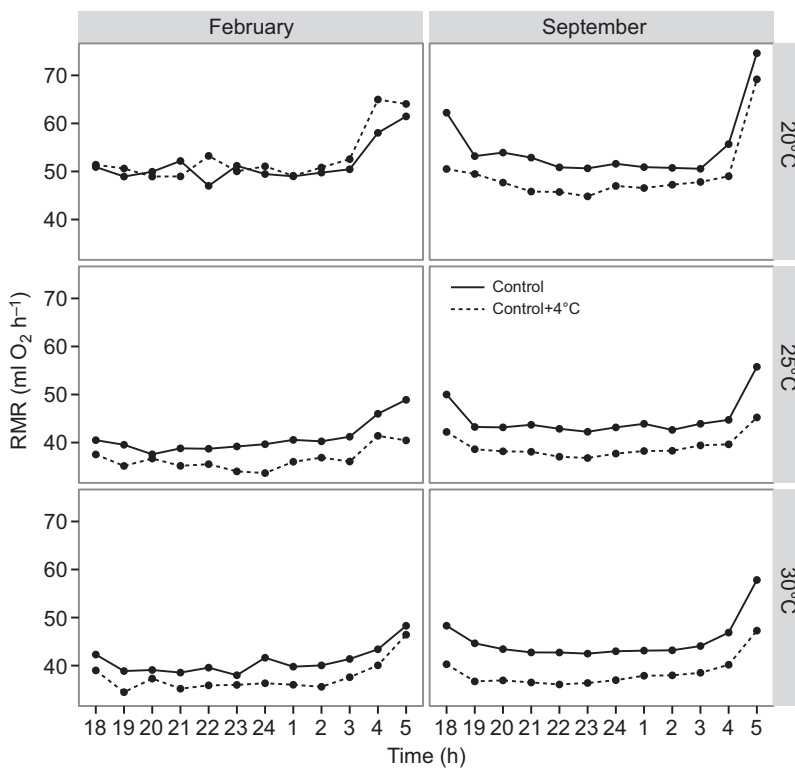


Fig. 4. Mean hourly resting metabolic rate of Cape white-eyes housed at T_a and at $T_a+4^\circ\text{C}$. RMR of birds housed at T_a ($N=10$) and at $T_a+4^\circ\text{C}$ ($N=10$), measured at $T_a=20^\circ\text{C}$, 25°C and 30°C , in February 2014 and September 2013. Scotophase lasted from 18:00 h to 06:00 h.

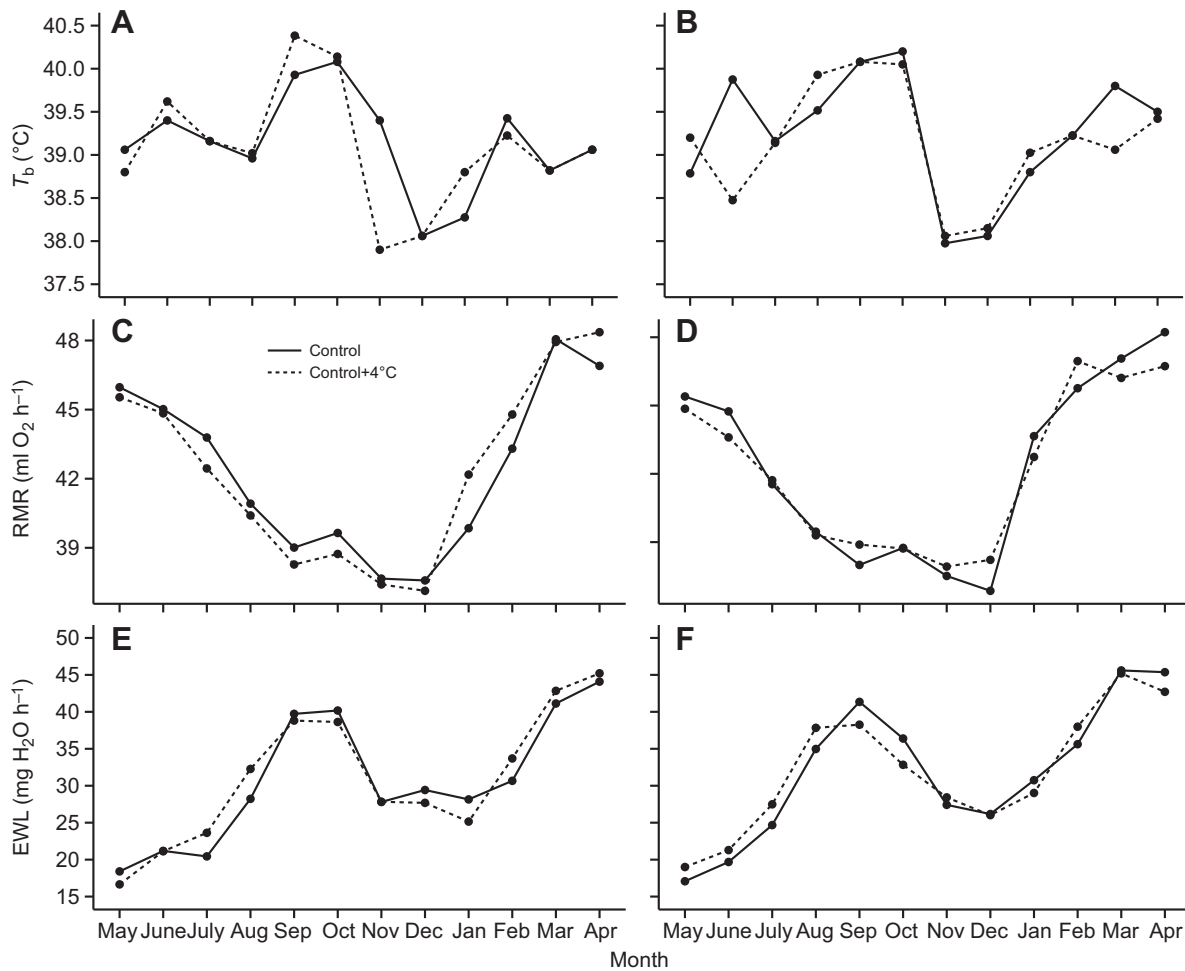


Fig. 5. Mean monthly intraperitoneal body temperature, resting metabolic rate and standard evaporative water loss for Cape white-eyes. T_b (A,B), RMR (C,D) and EWL (E,F) were measured for birds housed in the control group and in the control+4°C group. Birds were measured at $T_a=20^{\circ}\text{C}$ (A,C,E) and $T_a=25^{\circ}\text{C}$ (B,D,F) each month.

very similar to that of conspecifics housed in outdoor aviaries ($42.405 \pm 3.139 \text{ ml O}_2 \text{ h}^{-1}$, $N=13$), when both groups were measured at 30°C (which is within the TNZ for this population of Cape white-eyes) in the same month. However, long-term captivity in outdoor aviaries is linked to a significant increase in whole-animal BMR of Cape white-eyes (Thompson et al., 2015a) and so we can assume that RMR values for wild Cape white-eyes would be lower than those presented in this study. Indeed, the ecological relevance of laboratory studies has been questioned (Chown et al., 2010), so ideally, this experiment should be repeated with birds housed in large outdoor temperature-controlled aviaries. In addition, field metabolic rate measured during the day may be of more use than BMR or RMR in determining the effects of increased temperature associated with climate change on avian physiology. Although extreme heat events will undoubtedly pose a greater risk to survival than the smaller temperature increase experienced globally over time, it is also important to quantify the effects of the increased temperature associated with climate change on physiological variables of animals most at risk on temperature increases (that is, small animals), in regions most at risk from climate change.

Moreover, although we acclimated the birds to indoor conditions and to their different temperature regimes, in reality, birds are unlikely to experience such an immediate and continual 4°C increase in T_a , thus we accept that the responses of wild birds to

climate change may be somewhat different from the trends we observed here. While smaller bird species are more at risk from climate change because of their higher metabolic rates and reduced ability for fat storage (Simmons et al., 2004), we nevertheless feel that since all of our study birds coped with an abrupt increase of 4°C , they should be more than capable of coping with a far more gradual temperature increase associated with climate change in the coming decades. Indeed, when the constant-environment rooms overheated one night, maintaining a T_a of 43°C and 39°C for $\sim 16 \text{ h}$ in the control+4°C and control groups, respectively, only 2 of the 22 birds expired. That most of the birds could survive something akin to an ‘extreme heat event’ is testament to their great physiological flexibility, and this, along with their generalist feeding habits (Fry et al., 2000) and their use of a wide range of habitats (Hulley et al., 2004; Smith and Bowie, 2005), should be in their favour in the face of ongoing anthropocentric climate change (Jiguet et al., 2007; Julliard et al., 2003; Knowlton and Graham, 2010; Schwartz et al., 2006; Thomas et al., 2004).

During the study period, mean monthly temperatures were lowest in July and highest in February, corresponding with austral winter and summer, respectively. Had we elected to measure our birds only in these 2 months, for a study on a seasonal variation in metabolic parameters, we would have concluded that our birds reduced their RMR and T_b in winter, which would suggest that birds were

conserving energy in winter (Smit and McKechnie, 2010). Yet, the observed peaks and troughs in RMR and T_b did not correspond to the peaks and troughs in housing temperature. Instead, T_b was lowest around November–December and highest in September–October, while RMR was lowest in December and highest in April. This suggests that studies that investigate RMR only in summer and winter may not be recording the full range of values exhibited by the study animals, in agreement with the conclusions of Thompson et al. (2015b).

Conclusions

Species may adjust to global warming through phenotypic plasticity in their thermal responses or through alterations in the genetic composition of populations (Pulido and Berthold, 2004). Currently, there is no documented case of a genetic shift towards increased thermal tolerance in any bird population (Bradshaw and Holzapfel, 2006, 2010; Gienapp et al., 2008). The adaptive capacity (*sensu* Dawson et al., 2011) of Cape white-eyes seems to be high. In conclusion, our results support the ideas of McClelland (2004) and the results of Khaliq et al. (2014) and of Vedder et al. (2013). As the temperature increase forecast for our study area by 2080 is within the range of temperature tolerance of our population of Cape white-eyes, the direct effect of increased air temperature alone may not pose a severe threat to this southern African endemic species.

MATERIALS AND METHODS

Capture and maintenance

All research was conducted at the University of KwaZulu-Natal (UKZN), Pietermaritzburg, South Africa (29°37'S 30°24'E). Cape white-eyes *Zosterops virens* Sundevall 1850 were caught in the UKZN botanical garden using mist nets (Ecotone, Gdynia, Poland) and baited walk-in traps from November 2012 to January 2013 and moved to the UKZN Zoology building. Birds were then randomly assigned to one of two groups: (1) a control group ($N=10$, including five males and five females), housed in a room with T_a set to match the outdoor temperature of the previous day, and (2) an experimental group ($N=10$, including two females, six males, and two of unknown sex), housed in a room with T_a set to 4°C higher than the outdoor temperature from the previous day ('control+4°C'). Only 10 birds from each room were used in experiments; but two additional birds were caught with the original group, and one housed in each of the two rooms as a 'spare', so that there were 22 birds indoors in total, but only 20 were used in the experiments. Both rooms were artificially lit with a 12 h:12 h light:dark cycle, which remained constant throughout the year, since we were primarily interested in the effect of a 4°C difference in housing temperature. Although change in day length is closely tied to change in season (Bradshaw and Holzapfel, 2010), temperature, rather than photoperiod, seems to be the main driver of flexibility in avian metabolic rate (Swanson et al., 2014). Primary moult in the birds used in this study occurred from February to June, which corresponded with the timing of moult in birds from the same population housed at the study site in outdoor aviaries, and with moult in other populations of Cape white-eyes in the same province (Earlé, 1981; Symes et al., 2001). Thus the timing of primary moult did not change when birds were brought into captivity, even though the photoperiod of the rooms they were housed in was slightly different from the natural photoperiod when the birds were caught.

No one entered the rooms except the same individual who fed the birds each morning, cleaned cages once a week and handled the birds for metabolic measurements. Temperatures in the two rooms were controlled by manually programming an Alerton® global controller (Redmond, WA). Each morning, a maximum and minimum temperature reading from the previous day was read from a max/min thermometer placed inside a Stevenson screen in UKZN grounds, Pietermaritzburg. Four times a day, every day, for a year, T_a in the control room was manually changed, to match the (1) minimum, (2) mean (of the minimum and maximum), (3) maximum and (4) mean (of the minimum and maximum, again) temperatures of the previous day (Fig. 1). Where possible, maximum T_a was set just after

midday, minimum in the early hours of the morning, and the two means approximately half-way in between. At the same time, T_a in the experimental room was set at 4°C higher than T_a in the control room. In this way we hoped that the birds would experience the same range of T_a as they would in the wild, whilst maintaining one group of birds 4°C higher than the control group. Cape white-eyes were acclimated for 8 weeks, which is more than enough time for birds from this population to acclimate to captivity, in terms of their body mass, resting metabolic rate, evaporative water loss and respiratory quotient (our unpublished data). During this acclimation period, the resting metabolic rates of all birds were measured weekly (our unpublished data), thus avoiding stress-related elevations in RMR in this study (Jacobs and McKechnie, 2014). We then kept the birds for a year, to avoid biasing our results to one particular season, since recent, rapid climate change is having a greater effect on winter temperatures than on summer temperatures (Bradshaw and Holzapfel, 2008, 2010).

Within the two rooms, birds were housed in cages (90×40×100 cm) in groups of 3 or 4. Since Cape white-eyes show no sexual dimorphism (Hockey et al., 2005; Oatley, 2011; Skead, 1967), we could not determine sex by looking at the birds, and so in some instances males and females were housed together. A variety of fruit and softbill pellet supplements (Avi-products, Durban, South Africa) were supplied daily, and water was given *ad libitum*. Breeding was discouraged with a lack of nesting materials. After all metabolic trials were completed, blood (<100 µl) was drawn from the jugular vein of each Cape white-eye using a disposable Healthase® syringe and 29G×½" (0.33×13 mm) needle (Neomedic Pty Ltd., Riverhorse Valley East, South Africa), and sent to Molecular Diagnostics Services Pty Ltd. (Westville, South Africa) for molecular DNA sexing. Birds were moved into outdoor aviaries for 3 weeks, and then soft-released at their capture sites. Birds were captured, transported, ringed, monitored and released under permit (number OP 5122/2012) from Ezemvelo KwaZulu-Natal Wildlife, and ethical approval for this study was granted by UKZN's Animal Ethics Sub-committee (reference: 071/13/Animal).

Body temperature measurements and moult score

Intraperitoneal T_b of Cape white-eyes were measured to the nearest 0.1°C using 12 mm×2.1 mm, 0.06 g, temperature-sensitive passive integrated transponder devices (PIT tags, Biomark, Boise, Idaho, USA), injected into the intraperitoneal cavity of each bird using a 12-gauge needle. Signals from the tags were detected using two racket antennae (Model FS2001F-ISO, Biomark) positioned next to metabolic chambers. These antennae, in turn, were connected to PIT tag readers (Destron Fearing, St. Paul, MN, USA), programmed to record data every 15 min. These data were then used to obtain mean hourly T_b measurements. Only five birds from each of the two rooms were injected with PIT tags. Thus, of the four birds placed into the temperature-controlled cabinet each night, only two contained PIT tags; more than this caused the tags' signals to interfere with each other.

A sample of ten PIT tags was calibrated in a circulating water bath following Cory Toussaint and McKechnie (2012), from 5 to 45°C, using a mercury-in-glass thermometer with a measurement precision of 0.1°C, and accuracy traceable to the US National Bureau of Standards. A linear regression was applied to the data, giving the following equation: $y=1.015x-0.983$ ($R^2=0.9993$), where y is actual temperature in °C, and x is measured temperature in °C. The variation between the tags was low, with standard deviation ranging from 0.148 at 44.9°C to 0.196 at 39.9°C.

Moult is energetically expensive and thus likely to increase metabolic rate (Cyr et al., 2008; Lindström et al., 1993; Portugal et al., 2007), and so each Cape white-eye was scored for primary feather moult immediately prior to metabolic trials, using methods described by De Beer et al. (2001). The score for each feather ranged from 0 (for an old feather) to 5 (for a new feather). The sum of the scores for all nine primaries was then divided by 4.5 to give an index ranging from 0 to 10.

Gas exchange measurements

Birds were fasted for 3 h before measurements started, to ensure that they were post-absorptive (Wellmann and Downs, 2009) and to reduce the possible effects of handling stress. From 15:00 h until 07:00 h the next morning, flow rate (ml min⁻¹), O₂ and CO₂ concentrations (%), and water vapour density (µg ml⁻¹) were recorded every 5 s. An interrupted sampling

regime was used (Thompson et al., 2015a), beginning with a baseline measurement for 6 min, and then four birds for 6 min each. This sequence was repeated so that each bird was measured twice (for 12 min in total) per hour. All birds were measured once a month, at both 20 and 25°C, for 1 year, with at least one night between measurements. These temperatures were chosen on the assumption that they would fall below and within the thermoneutral zone [TNZ, the range of ambient temperatures over which temperature regulation is achieved without changes in metabolic heat production or evaporative heat loss (IUPS Thermal Commission, 2001)] respectively, for this population. However, the lower critical limit of the TNZ of this population of Cape white-eyes was subsequently found to be 23°C in winter (our unpublished data), and so the measurements we made at 20°C and 25°C are likely to be below or close to the lower critical limit of the TNZ; hence, we refer to them as RMR. We therefore included metabolic measurements in summer and winter at 30°C, which is within the TNZ of this population of Cape white-eyes (our unpublished data), for a seasonal comparison of basal metabolic rate (BMR); that is, the minimum maintenance energy requirements of non-reproductive, post-absorptive, resting, adult normothermic endotherms (McKechnie et al., 2006; McNab, 1997) and to provide BMR values that may then be compared with other studies.

Metabolic rate was indirectly measured every month, from May 2013 to April 2014 inclusive, using open-flow, push-mode respirometry. At 15:00 h, after being weighed to the nearest 0.01 g using digital scales (model: AFB-3100L, Adam Equipment S.A. Pty Ltd, Johannesburg), Cape white-eyes were placed onto wooden perches inside 2.8 l Perspex respirometers, within a temperature-controlled environmental chamber (CMP2244, Conviron, Winnipeg, Canada), set to 12 h:12 h light:dark. Inside each respirometer, a plastic mesh platform was positioned 10 cm above a 1 cm layer of liquid paraffin/mineral oil (AlphaPharm, Pietermaritzburg), to eliminate evaporation from excreta.

Water vapour and CO₂ were removed from environmental air with silica gel, soda lime and more silica gel. This air was then pumped (model PP2, Sable Systems, Las Vegas, NV, USA) into five inlets of a flow measurement system (model FB8, Sable Systems). Flow rates were set to ~800 ml min⁻¹, to maintain O₂ depletion in each respective chamber between 0.1 and 0.5% (Lighton, 2008). In each respirometer, the air inlet was located near the bottom, and the outlet near the top, to aid mixing of air inside the chamber. Effluent air flowed through a flow multiplexer (model MUX, Sable Systems) and then excess air escaped through a manifold, while the remainder was pumped through a subsampler (model SS4, Sable Systems) at 200 ml min⁻¹. This air then flowed through a water vapour analyser (model RH300, Sable Systems), which was regularly spanned using a nearly saturated airstream and zeroed using N₂. Air was then dried with minimal quantities of Drierite (Hammond Drierite Co. Ltd, Xenia, Ohio), that had previously been recharged to reduce its affinity for CO₂ and therefore to reduce CO₂ washout time (White et al., 2006). Air then flowed through a CO₂ analyser (model CA-10, Sable Systems) and an O₂ analyser (model FC-10, Sable Systems). The CO₂ analyser was regularly zeroed with N₂, and spanned with a certified gas of 964 ppm CO₂ in N₂ (AFROX, Pietermaritzburg, South Africa). The flow meter and gas analysers were connected to a Universal Interface (model UI2, Sable Systems), which transferred data to a computer using ExpeData data acquisition software (Sable Systems). Temperatures within each respirometry chamber were recorded every 15 min with i-Buttons[®] at a resolution of 0.0625°C (model DS1922L-F5, Thermochron[®], Maxim, CA, USA). All i-Buttons[®] were calibrated before use in a circulating water bath, from 7–36°C, with a mercury-in-glass thermometer (measurement precision=0.1°C), with accuracy traceable to the US National Bureau of Standards.

Lag and drift correction were performed in ExpeData using a macro, and a 95% equilibration time of 11 min was calculated using the equation of Lasiewski et al. (1966). Therefore, rates of O₂ consumption (\dot{V}_{O_2}), CO₂ production (\dot{V}_{CO_2}) and EWL were Z-transformed (Lighton, 2008; Lighton and Halsey, 2011; Tøien et al., 2011) before hourly means were calculated. We also checked the washout characteristics of our system for water vapour without a bird in the respirometer, since water may adhere to Perspex. For each night, the lowest hourly \dot{V}_{O_2} reading was taken as the RMR. \dot{V}_{CO_2} and \dot{V}_{H_2O} (hereafter termed standard EWL) were taken at the same time as RMR

was recorded. The basal EWL measurement of each night was also recorded, since the time of minimum EWL and minimum \dot{V}_{O_2} usually did not coincide. \dot{V}_{O_2} , \dot{V}_{CO_2} and EWL were calculated in accordance with the configuration of the system, following Withers (2001). Body mass (M_b , g) and standard EWL were taken at the same time as RMR each night.

Data analyses

Statistical analyses were conducted using the base program in R version 3.1.0 (R Core Team, 2014), and figures were produced using the R package ‘ggplot2’ (Wickham, 2009). We defined a set of candidate models *a priori*, following Burnham and Anderson (2002) and linear mixed-effects models were performed with the ‘lme4’ package in R (Bates et al., 2014) to determine the effects of various predictor variables on RMR, standard EWL, T_b and M_b . Fixed effects included ‘ T_a ’ (temperature at which birds were measured overnight, either 20°C or 25°C), ‘group’ (whether birds were housed at T_a or at $T_a+4^\circ\text{C}$), ‘ M_b ’, ‘moult’ (ranging from 0 to 10), and ‘sex’ (male, female or unknown). ‘Date’ (on which metabolic measurement was done) and ‘BirdID’ (individual) were included as random effects, the latter to control for repeated measures. Predictors with possible biological importance were included in the global model regardless of whether they were statistically significant or not (Cheng et al., 2010). Visual inspection of residual plots showed no deviations from homoscedasticity or normality. Akaike’s information criterion weights (AICw), and delta AIC values, (ΔAIC , the differences between each respective candidate model and the best approximating model) produced using the R package ‘AICcmodavg’ (Mazerolle, 2013), were used to select the best approximating models, following Burnham and Anderson (2002) and Wagenmakers and Farrell (2004). Models with $\Delta\text{AICc}<2$ were averaged for multimodel inference using the R package ‘MuMIn’ (Bartoń, 2013). The significance of fixed effects was determined using analyses of variance in R (Knoblauch and Maloney, 2012).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

L.J.T., M.B. and C.T.D. designed the study. L.J.T. collected and analysed data, and wrote the manuscript. M.B. and C.T.D. provided comments on the manuscript.

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