



# Seasonal physiological responses to heat in an alpine range-restricted bird: the Cape Rockjumper (*Chaetops frenatus*)

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## Abstract

Hot, dry summer conditions impose physiological stress on endotherms, yet we have a poor understanding of how endotherms seasonally adjust their costs of thermoregulation under hot conditions. We determined whether seasonal phenotypic plasticity in evaporative cooling capacity at high temperatures explained how the range-restricted Cape Rockjumper (*Chaetops frenatus*; hereafter ‘Rockjumper’), copes with hot and dry summer temperatures of the temperate mountain peaks of southwest South Africa. We measured evaporative water loss (EWL), resting metabolic rate (RMR), and body temperature at high air temperatures (30–42 °C) of individuals from a wild population of Rockjumpers during winter and summer ( $n = 11$  winter, 4 females, 7 males;  $n = 10$  summer, 6 females, 4 males). We found Rockjumper evaporative cooling in summer imposes higher EWL (i.e. greater water costs) compared to winter, although an accompanying lack of change in RMR resulted in increased summer cooling efficiency. These patterns are similar to those observed in species that inhabit regions where summer temperatures are routinely high but the species are not water stressed. Our findings indicate that avian seasonal physiological adjustments to heat can be diverse. Further seasonal studies on thermoregulation in response to heat will greatly improve our knowledge of the functional value of traits such as evaporative cooling efficiency and heat tolerance and how they contribute to the physiological stress organisms experience in heterogeneous environments.

**Keywords** Climate relict · Alpine species · Heat stress · Seasonal acclimatisation · Species vulnerability · Thermoregulation

## Zusammenfassung

### Saisonale physiologische Reaktionen auf Hitze bei einer alpinen Vogelart mit begrenztem Verbreitungsgebiet: der Kapfelsenspringer (*Chaetops frenatus*)

Heiße und trockene Bedingungen im Sommer bewirken physiologischen Stress bei warmblütigen Tieren. Dennoch haben wir ein begrenztes Verständnis, wie Endotherme die Kosten für die Thermoregulation unter Hitzebedingungen saisonal anpassen. Wir bestimmten, inwiefern die saisonale phänotypische Plastizität in der Fähigkeit zur Verdunstungskühlung bei hohen Temperaturen erklärt, wie die in ihrem Verbreitungsgebiet begrenzten Kapfelsenspringer (*Chaetops frenatus*) mit den heißen und trockenen Sommertemperaturen der gemäßigten Berggipfel im südwestlichen Südafrika zurecht kommen. Gemessen wurden der Wasserverlust durch Verdunsten, der Ruhestoffwechsel sowie die Körpertemperatur bei hohen Lufttemperaturen (30–42 °C) von Individuen einer Population von Kapfelsenspringern im Winter und im Sommer ( $n = 11$  Winter, 4 Weibchen, 7 Männchen;  $n = 10$  Sommer, 6 Weibchen, 4 Männchen). Wir stellten fest, dass die Verdunstungskühlung im Sommer einen höheren Wasserverlust (und damit höheren Wasserbedarf) im Vergleich zum Winter bedingt. Wenngleich eine damit einhergehende fehlende Veränderung im Ruhestoffwechsel in einer gesteigerten Kühleffektivität im Sommer resultiert. Diese Muster sind vergleichbar mit denen von Arten, die Regionen mit üblicherweise hohen Sommertemperaturen, aber ohne Wasserstress besiedeln. Unsere Ergebnisse zeigen, dass saisonale physiologische Anpassungsstrategien an Hitze bei

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Vögeln sehr divers sein können. Weitere saisonale Studien zu Thermoregulation bei Hitze würden die Kenntnisse über die funktionalen Eigenschaften wie zum Beispiel die Effizienz der Verdunstungskühlung und Hitzetoleranz deutlich erweitern und Informationen darüber liefern, wie diese Eigenschaften zum physiologischen Stress von Organismen in einer heterogenen Umwelt beitragen.

## Introduction

Many birds live in temporally heterogeneous environments where physiological phenotypes are adjusted seasonally to optimise the balance of energy (typically heat and chemical energy) and water. Whereas many studies to date have focussed on physiological adjustments to winter conditions (Swanson 1991, 2010; McKechnie et al. 2015), studies about adjustments to hot summer conditions are rare. Hotter summer conditions could impose physiological stress on endotherms through greater rates of environmental heat gain, decreased rates of metabolic heat dissipation, and often elevated evaporative water loss (EWL) rates (Wolf 2000). Loss of body water due to higher levels of EWL cannot be sustained indefinitely without risking dehydration (Tieleman et al. 2002a), so presumably there are strong selective pressures to minimise the costs of heat dissipation, especially in water-scarce environments.

Diurnal birds in exposed terrestrial environments cope with a high operative temperature, defined as an integrated temperature meant to reflect the overall thermal environment experienced by individuals (e.g. Wolf 2000; Tieleman 2002; Williams and Tieleman 2005). EWL is well documented as the primary physiological mechanism of heat dissipation in birds when air temperature ( $T_{\text{air}}$ ) exceeds normal body temperature ( $T_b$ ) (e.g. Tieleman 2002; Gerson et al. 2014), although behaviour may also be used as a thermal buffer (Boyles et al. 2011; Cunningham et al. 2015; Clauser and McRae 2017). Elevated water demands may therefore represent a primary thermoregulatory cost during summer.

Our current understanding of the thermoregulatory costs associated with summer responses to higher temperature relies on a handful of acclimation (typically exposure to hot laboratory holding conditions) and more recently acclimatisation (adjusted to natural weather patterns in free-ranging and captive birds in outdoor holding conditions) studies. Acclimation studies often demonstrated that heat responses involved an increase in evaporative cooling efficiency (defined as the ratio of evaporative heat lost to metabolic heat produced) to better control  $T_b$  when organisms were exposed to hot conditions (Marder and Arieli 1988; Ophir et al. 2002; Tieleman and Williams 2002; McKechnie and Wolf 2004). This generally involved an ability to elevate total EWL rates (McKechnie and Wolf 2004), and/or reduce RMR (resting metabolic rate) at high temperatures

(Tieleman and Williams 2002) in order to regulate  $T_b$ . Alternatively, despite the potentially lethal risks of hyperthermia, birds may use some degree of facultative hyperthermia, allowing  $T_b$  to rise, presumably to promote savings in EWL (Tieleman and Williams 1999). We may expect facultative hyperthermia to be more beneficial in water-scarce environments, but it seems to be widely used by many bird species where the costs and benefits are not yet clear (Tieleman and Williams 1999; Williams and Tieleman 2005).

Seasonal studies on thermoregulation at high temperatures have thus far shown summer-acclimatised birds to generally increase evaporative cooling efficiency leading to improved regulation of normal  $T_b$  compared to winter-acclimatised birds. For example, captive-bred Houbara Bustards (*Chlamydotis macqueenii*) achieved greater evaporative cooling capacity during summer by increasing total EWL and decreasing RMR compared to winter (Tieleman et al. 2002b). Alternatively, free-ranging Freckled Nightjars (*Caprimulgus tristigma*) also achieved greater cooling capacity in late spring compared to winter, but solely through elevated total EWL rates (O'Connor et al. 2016). The mechanisms of seasonal variation in evaporative efficiency can also vary at an intra-specific level, with Noakes et al. (2016) showing that free-ranging White-browed Sparrow-weavers (*Plocepassar mahali*) from mesic sites increased total EWL and decreased RMR in summer compared to winter, unlike xeric Sparrow-weavers that focused on water conservation and maintaining low EWL. The emerging patterns from these studies suggest that seasonal variation in physiological stress and costs of evaporative cooling may vary at both intra- and inter-specific levels with local climate.

To date, the handful of studies reporting seasonal responses to high temperatures have focussed mostly on wide-ranging, predominantly desert species that routinely experience hot summer conditions across their range (e.g. Noakes et al. 2016; O'Connor et al. 2016), with Noakes et al. (2016) the only such study focusing on a free-ranging diurnal bird. To better understand the role of seasonal responses in evaporative cooling capacity at reducing physiological stress to warming conditions, we also need data from species that inhabit non-desert climates, or more sedentary species where dispersal may not be possible. Some examples would include dynamic climates where summers can be 60–80 °C warmer than winter (e.g. high-latitude continental climates), seasonally stable climates where mean temperatures vary by

less than 10 °C (e.g. some Mediterranean, warm temperate or cool tropical climates), and climates that vary greatly in seasonal aridity.

Our purpose was to assess seasonal adjustments in EWL, RMR,  $T_b$ , and evaporative cooling efficiency at high  $T_{air}$  (i.e. > 30 °C) in a ~ 50 g passerine bird, the Cape Rockjumper (*Chaetops frenatus*; hereafter 'Rockjumper'). Restricted to the high-elevation Cape Fold Mountains of South Africa, Rockjumpers are an interesting species in which to assess seasonal responses to heat as annual mean  $T_{air}$  across their range are generally mild [ $14.3 \pm 1.6$  °C (Lee and Barnard 2016)]. In addition, Rockjumpers provide a model for how seasonal physiological adjustments to heat may explain how climate relict species [see Woolbright et al. (2014) for discussion] respond to past and contemporary climate shifts. Diminishing habitat and population declines correlated with warming temperatures (Milne et al. 2015) have led to Rockjumpers being listed as 'near threatened' by the International Union for Conservation of Nature, with climate warming requiring Rockjumpers to cope with higher  $T_{air}$ . While Rockjumper habitat will periodically experience  $T_{air}$  that approaches or exceeds 40 °C when heat waves precede the landfall of mid-latitude frontal systems (Mucina and Rutherford 2006), these events are infrequent and of short duration, and the preferred mountain habitat of Rockjumpers has historically been climatically stable (Cowling et al. 2015). Thus, whether Rockjumpers possess the ability to adjust to hot temperatures above their proposed thermal niche may reveal how cool-climate species may adapt to sudden heat waves associated with climate warming.

Since summers in the Cape Fold Mountains are typically dry, we hypothesise that summer adjustments in EWL and  $T_b$  patterns centred on water conservation may have incurred a selective advantage in Rockjumpers, which we predict will result in lower summer EWL and RMR compared to winter. In addition, given the relatively mild climate of their habitat, we hypothesise that Rockjumpers may show a limited capacity to improve evaporative cooling efficiency during summer, which we predict will result in unchanged efficiency in summer compared to winter.

## Methods

### Study site and species

This study took place at Blue Hill Nature Reserve (33.59 S, 23.41 E; 1000–1530 m a.s.l.) in the Western Cape Province, South Africa, which consists primarily of mountain fynbos. Rockjumpers occur on the highest ridges and slopes of the reserve, with family groups of two to five individuals occurring at comparatively low densities [ $0.56$ – $1.02$  individuals  $\text{km}^{-2}$  (Lee and Barnard 2016)]. The

average daily temperature (°C  $\pm$  SD) in winter (24 July–31 August 2015) and summer (1–31 January 2016) was  $8.7 \pm 6.0$  and  $20.5 \pm 5.9$ , respectively. Temperature minima and maxima occurring over the study period were  $-2.6$  and  $27.5$  °C in winter, and  $6.9$  and  $35.4$  °C in summer. The specific territories occupied by Rockjumpers used in this study ranged from 1100 to 1500 m a.s.l. Rainfall and temperature data were collected every 30 min using an on-site weather station (Vantage Vue; Davis Instruments, USA). Average dew point temperatures, measured at maximum  $T_{air}$  (a direct proxy of absolute humidity) over a 3-year period (2013–2015) at Blue Hill Nature Reserve are  $2.1$  °C for July and  $12.0$  °C for January (A. T. K. L., unpublished data); these humidity levels result in mean water vapour pressure deficits of ~ 1 and 2.4 kPa in July and January, respectively, and around 5 kPa on the hottest summer days.

During winter 16 individuals were captured (nine males, seven females), and during summer 16 individuals were captured (five males, six females, five juveniles) using snap traps (non-lethal, spring-loaded trap made from a metal frame covered in netting, and activated with a baited hair-pin trigger). After capture, birds were kept in captivity for a maximum 48-h period after which they were released at the point of capture. After all experimental runs (see section below) birds were weighed and returned to holding cages and provided with tenebrionid beetle larvae ad libitum. Body mass ( $M_b$ ) was measured to within 0.1 g before and after each experiment, with experimental runs occurring only for birds maintaining mass within 5% capture mass [average  $M_b$  (g): winter =  $54.4 \pm 3.2$ , summer =  $52.3 \pm 3.1$ ]. We removed two males and three females from the experiment in winter (one male with  $M_b$  loss of > 5%, the other one male and three females due to the presence of brood patches) and one female in summer (due to prolonged agitation at  $T_{air} > 39$  °C), making the sample size 11 in winter (seven males, four females) and ten in summer (four males, six females); in Rockjumpers, both sexes share in parental duties including brooding and incubation (Holmes et al. 2002). Juveniles were removed from the current study and analysed as part of a separate study comparing adult and juvenile physiology in summer (unpublished data).

We measured physiological responses to heat (current study), and physiological responses to cold and basal metabolism (unpublished data), in each individual during the captive period. We allowed birds to rest in holding cages for at least 5 h between experiments. Measurements at high temperature therefore occurred either on the day of capture (if caught before 1500 hours) or the day after capture (if caught after 1500 hours); the exact time of measurement depended on the number of birds caught on a given day ( $n = 1$ – $4$ ), with one to three experimental heat runs per day.

## $T_b$ measurements

Individual birds were injected with a small, temperature-sensitive, passive integrated transponder (PIT) tag intraperitoneally to measure  $T_b$  throughout our experiments. Injections were made into the peritoneum after first sterilizing the PIT tag and a 3.17-mm non-replaceable sterile needle, with the puncture hole sealed using cyanoacrylate adhesive. This procedure took less than 1 min per individual. PIT tags provide  $T_b$  information while minimising handling effects, with no significant alteration of individual condition for birds (Gerson et al. 2014; Ratnayake et al. 2014), and no significant negative long-term effects amongst Rockjumpers specifically (Oswald et al. 2018).

## Metabolic measurements

Respirometry chambers were placed in a custom-made environmental chamber consisting of a 100-L cooler box lined with copper tubing through which temperature-controlled water was pumped from a circulating water bath (FRB22D; Lasec, South Africa). A small fan was placed inside the 100-L environmental chamber to ensure a uniform distribution of  $T_{air}$ . Continuous monitoring of each bird was provided by an infrared light source and closed-circuit security camera with live video feed. A BioMark PIT tag reader was placed next to the chamber to record  $T_b$  every minute (Gerson et al. 2014; Whitfield et al. 2015).

We followed the experimental procedure of Whitfield et al. (2015) by measuring EWL, metabolic rate, and  $T_b$  in birds being exposed to a ramped  $T_{air}$  profile. Birds typically spent between 2 and 24 h in captivity before physiological responses were measured at high temperatures. Birds were placed individually in a 4-L airtight plastic chamber (Lock & Lock, India) fitted with a wire-mesh platform raised 15 cm from the floor to ensure normal perching posture. To determine that water vapour absorption within the plastic respirometry chambers was negligible, we followed Whitfield et al. (2015) by comparing rates of change in  $CO_2$  and water vapour by switching air streams that varied considerably in  $CO_2$  and water vapour. A thin layer of mineral oil was used to ensure faecal water did not factor into EWL measurements. Chamber temperature ( $T_{air}$ ) was measured using a thermistor probe (TC100; Sable Systems, USA) inserted 1 cm through a small hole in the lid. Birds were habituated to the chamber for 10–15 min before the experiment started. This period of acclimation to the respirometry chamber was shorter than in the study of Whitfield et al. (2015) as we aimed to shorten the time Rockjumpers were exposed to high temperatures. We observed that birds were very calm when placed in the respirometry chambers and that gas traces typically stabilised within the first 10 min that they were in the chamber. After the acclimation period,

EWL and RMR [measured indirectly as oxygen consumption ( $\dot{V}_{O_2}$ ) and carbon dioxide emission ( $\dot{V}_{CO_2}$ )] were measured (millilitres per minute) using a portable open-flow respirometry system. For all measurements, flow rate of atmospheric air through bird chambers was controlled using FMA-series mass flow controllers (Omega, USA) calibrated using a 1-L soap bubble flow metre (Baker and Pouchot 1983). Atmospheric air was supplied at flow rates around  $3 \text{ L min}^{-1}$  (occasionally as low as  $1.75 \text{ L min}^{-1}$ ) to ensure  $[O_2]$  to the chamber remained within 0.5% of incurrent  $[O_2]$ . This allowed 95% wash-out rates, calculated using the corrected Eq. 8.1 in Lighton (2008), of around 4 min at our maximum flow rates. Our air pump did not allow for flow rates greater than  $3 \text{ L min}^{-1}$ , and chamber humidity levels (including those due to the bird) were thus higher than those used by Whitfield et al. (2015) for desert passerines. However, our aims were not to determine thermal tolerance limits as in Whitfield et al. (2015), but rather to test thermoregulatory responses similar to the extreme maxima  $T_{air}$  and humidity levels these birds are likely to experience in their natural environment.

Atmospheric air was scrubbed of water vapour using columns of silica gel and Drierite, so that air entering the bird chamber was low in water vapour (baseline values of 1.5–9 p.p.t.). We adjusted flow rates to maintain chamber humidity levels at water vapour levels of 10 p.p.t. (range 6–14 p.p.t.), equivalent to an average dew point temperature of around  $8 \text{ }^\circ\text{C}$ . The chamber humidity levels that Rockjumpers experienced were low enough to ensure high water vapour pressure deficits ( $\sim 7.1 \text{ kPa}$ ) and effective evaporative cooling (see Gerson et al. 2014). Subsampled air was then pulled from the bird chamber through a water vapour analyser (RH-300; Sable Systems) before entering  $O_2$  and  $CO_2$  analysers (Foxbox-C Field Gas Analysis System; Sable Systems). The Foxbox included a subsampling pump and allowed for analog outputs to be digitized and recorded at 1-s intervals using Expedata Data Acquisition and Analysis Software (Sable Systems).

## Experimental protocol

Heat tolerance measurements were taken during the active diurnal phase of birds within 48 h of capture. Birds were in chambers for a mean  $\pm$  SD of  $106.5 \pm 12.9$  contiguous minutes, with no birds kept in the chamber more than 130 min. Birds were subjected to a continuous ramped series of  $T_{air}$  ( $\approx 30, 33, 36, 39, 42 \text{ }^\circ\text{C}$ ) for 15–20 min each. Roughly 5 min was required for each chamber to reach a  $3 \text{ }^\circ\text{C}$  increase in  $T_{air}$ , meaning birds spent 10–15 min at each target  $T_{air}$ . Baseline values of  $O_2$ ,  $CO_2$ , and water vapour pressure, were recorded for a minimum of 5 min at the beginning of each experimental test, as well as between each  $T_{air}$  and again at the end of the run. Birds were held at the final  $T_{air}$  of  $42 \text{ }^\circ\text{C}$  for up to 20 min to allow a thorough assessment of RMR,

EWL, and  $T_b$  regulation at a  $T_{air}$  close to  $T_b$  (Marras et al. 2015; Whitfield et al. 2015). Although these  $T_{air}$  are higher than Rockjumpers likely experience in their natural environment, operative temperatures can be 10–20 °C above  $T_{air}$  when Rockjumpers are directly exposed to the sun and/or near the soil surface (Tieleman 2002). Moreover, the maximum test  $T_{air}$  of around 42 °C allowed us to determine thermoregulatory responses at  $T_{air}$ s near expected normal avian  $T_b$  [ $\sim 41.6$  °C (Prinzinger et al. 1991)] where evaporative cooling demands become a necessity for maintaining heat balance (Wolf 2000).

Expedata data files were corrected for O<sub>2</sub> drift in baselines using the relevant algorithms in Warthog LabHelper (<http://www.warthog.ucr.edu>). All measurements were taken as the minimum  $\dot{V}_{O_2}$  over a 60-s interval during the last 5 min at each  $T_{air}$  for calm birds to ensure the most accurate measurements of RMR. We calculated total metabolic rates, as it has been suggested they are more informative than mass-specific values for seasonal comparisons (Swanson 1991; Cooper 2002). Outgoing flow rate and rates of  $\dot{V}_{O_2}$ ,  $\dot{V}_{CO_2}$ , and  $\dot{V}_{H_2O}$  were calculated using Eqs. 9.3, 9.4, 9.5, and 9.6 from Lighton (2008), respectively. RMR values are presented in watts [also representative of metabolic heat production (MHP)] and calculated using a Joule conversion of 20.1 J mL<sup>-1</sup> O<sub>2</sub> (Walsberg and Wolf 1995). We calculated an average respiratory quotient of 0.76 using our measured  $\dot{V}_{O_2}$  and  $\dot{V}_{CO_2}$  values (winter average = 0.76 ± 0.01, summer average = 0.76 ± 0.10). Evaporative heat loss (EHL; watts) was calculated from EWL using the latent heat of vaporisation, 2.4 J mg<sup>-1</sup>, and evaporative cooling efficiency was calculated as the ratio of EHL to MHP.

## Statistical analysis

For each heat-response parameter the data spread was inspected in response to increasing  $T_{air}$  for possible inflection points in the response variable, as significant inflection points were found for similar heat parameters in Milne et al. (2015). Where inflection was suspected (EWL,  $T_b$ , EHL/MHP), the breakpoint value was assessed using the segmented function in the segmented package (Muggeo 2003) by testing linear models of the parameter of interest as a function of  $T_{air}$  and season, with multiple parameters for inflection point possibilities, selecting the best model by Akaike information criterion corrected for small sample size (AICc) as has been done in similar studies (Milne et al. 2015; Whitfield et al. 2015; McKechnie et al. 2016; Noakes et al. 2016).

To explore the contribution of potential predictor variables (i.e.  $M_b$ , sex,  $T_{air}$ , and season) on response parameters (EHL/MHP, EWL, RMR,  $T_b$ ), linear mixed-effects models were fitted using the lme4 package (Bates et al. 2015) in R version 1.1.447 (R Core Team 2017), with individual

included as a random effect (see Supplementary file Table S1 for raw data). We used the ANOVA function from the car package (Fox et al. 2011) to examine models for significant parameters as suggested by (Zuur et al. 2010).

For all parameters, significance did not vary with whole-animal vs. mass specific values, so we only report whole-animal values. We created a base model for each response parameter including  $T_b$ , sex, mass, and the interaction between  $T_{air}$  and season as covariates. Best models were found by sorting through a list of competing models created from the dredge function using MuMIn (Barton 2018) based on AICc. We present results for all models within 2Δ AICc of the top model. For all parameters, sex and mass were not included as important factors in the best models. Values are presented as mean ± SE except where indicated otherwise.

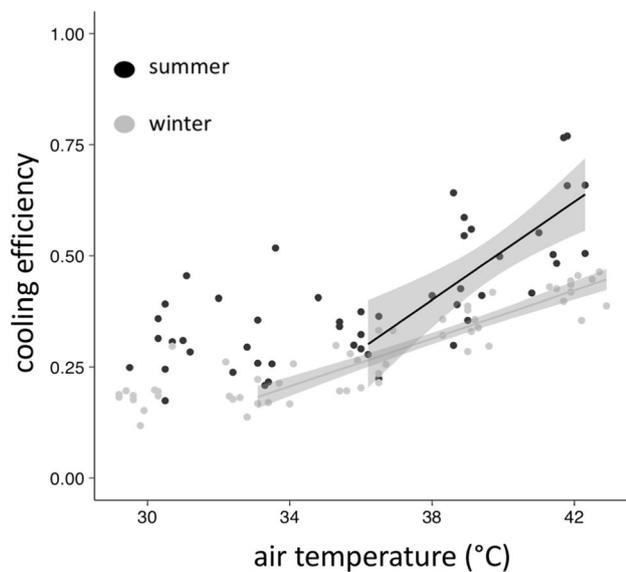
## Results

### Evaporative cooling efficiency

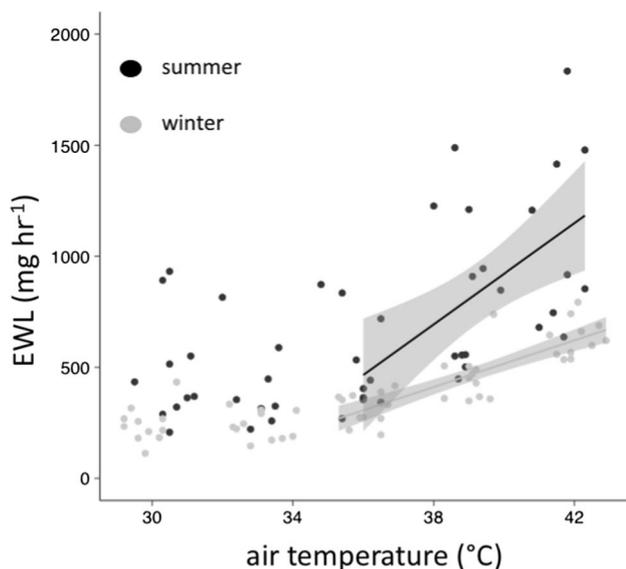
The estimated EHL/MHP inflection point was 37.3 ± 0.8 °C in summer and 33.5 ± 0.8 °C in winter. Above these inflection points EHL/MHP increased significantly with increasing  $T_{air}$  (mean slope ± SD: summer = 0.05 ± 0.01 EHL/MHP °C<sup>-1</sup>, winter = 0.03 ± 0.00 EHL/MHP °C<sup>-1</sup>;  $\chi^2_{1,50} = 83.43$ ;  $p < 0.01$ ) and the interactions of  $T_{air}$ \*season was significantly different between seasons ( $\chi^2_{1,50} = 23.95$ ;  $p < 0.01$ ; Fig. 1; see supplementary materials Table S2). There was a seasonal effect for EHL/MHP, with EHL/MHP higher in summer compared to winter for the experimental range of  $T_{air}$  (mean EHL/MHP ± SD: summer = 0.4 ± 0.14, winter = 0.28 ± 0.1), as well EHL/MHP was higher above average  $T_b$  (i.e.  $T_{air} > 40$  °C) in summer compared to winter (mean EHL/MHP ± SD: summer = 0.79 ± 0.09, winter = 0.69 ± 0.03).

### Evaporative water loss

Summer improvements in evaporative cooling efficiency were corroborated by increased EWL at high  $T_{air}$  during summer. The estimated EWL inflection point was 36.0 ± 1.6 °C in summer and 34.7 ± 0.9 °C in winter. Above inflection points EWL (mg h<sup>-1</sup>) increased significantly with increasing  $T_{air}$  (mean slope ± SD: summer = 90.41 ± 14.20 mg h<sup>-1</sup> °C<sup>-1</sup>, winter = 49.82 ± 3.66 mg h<sup>-1</sup> °C<sup>-1</sup>;  $\chi^2_{2,67} = 97.02$ ;  $p < 0.01$ ), with a notable difference in seasons: the summer mean EWL was significantly higher in this temperature range (mean EWL ± SD: summer = 783 ± 397 mg h<sup>-1</sup>, winter = 447 ± 166 mg h<sup>-1</sup>,  $\chi^2_{2,67} = 9.75$ ;  $p < 0.01$ ; Fig. 2; see supplementary materials Table S3). The slope for EWL (mg h<sup>-1</sup>) was also significantly greater in summer compared



**Fig. 1** Evaporative cooling efficiency (evaporative heat loss/metabolic heat production) data over a range of air temperatures ( $T_{\text{air}}$ ) ( $\approx 30, 33, 36, 39, 42$  °C) collected for Cape Rockjumpers (*Chaetops frenatus*) captured in summer ( $n=10$ ) and winter ( $n=11$ ) at Blue Hill Nature Reserve, South Africa. A significant difference was found above an inflection point of  $36.2$  °C, with separate seasonal *trendlines* above inflection points and 95% confidence intervals (CI) shown. Each individual is represented at each of the five temperatures



**Fig. 2** Evaporative water loss (EWL;  $\text{mg h}^{-1}$ ) over a range of  $T_{\text{air}}$  ( $\approx 30, 33, 36, 39, 42$  °C) for Cape Rockjumpers (*C. frenatus*) captured in summer ( $n=10$ ) and winter ( $n=11$ ) at Blue Hill Nature Reserve, South Africa. A significant difference was found above an inflection point of  $33.5$  °C, with *trendlines* indicating best model fit above inflection points and 95% CI for each season. Each individual is represented at each of the five temperatures. For other abbreviations, see Fig. 1

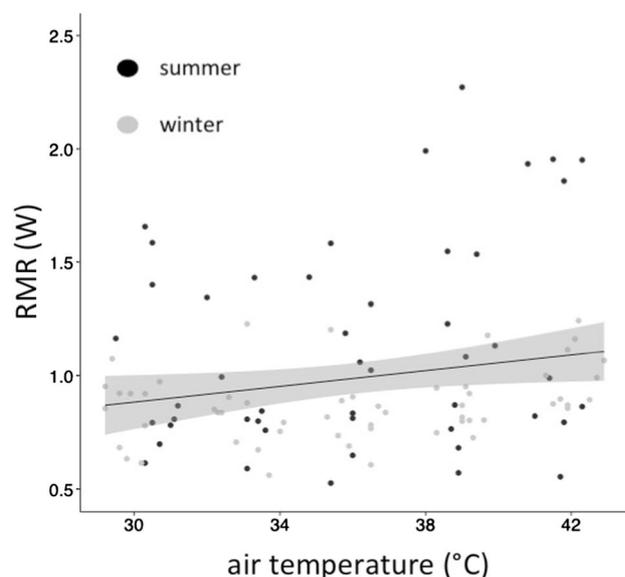
to winter ( $\chi^2_{2,67}=0.00$ ;  $p<0.01$ ; see supplementary materials Table S3).

### Resting metabolic rate

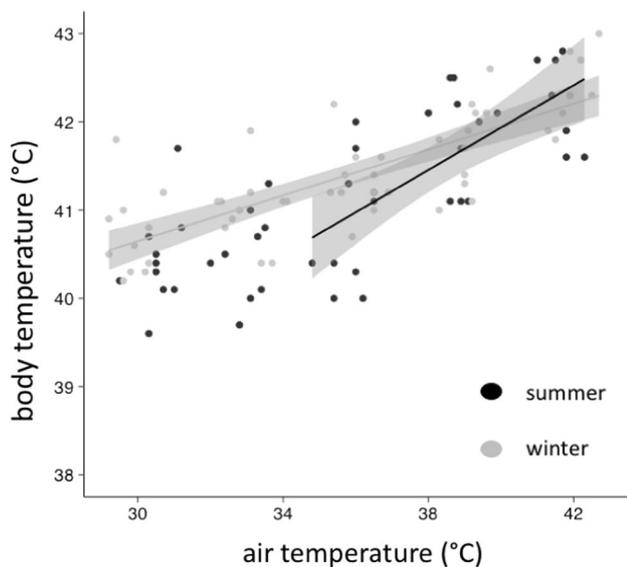
There were no significant inflection points for the relationship between RMR and  $T_{\text{air}}$  in either season. Despite increased EWL in summer we did not observe systematically higher summer RMR (watts) at high  $T_{\text{air}}$ . The only variable maintained in the best model explaining RMR was  $T_{\text{air}}$ , where a significant increase in RMR was observed with increasing  $T_{\text{air}}$  (slope =  $0.02 \pm 0.00$   $\text{W } ^\circ\text{C}^{-1}$ ;  $\chi^2_{2,67}=26.38$ ;  $p<0.01$ ; Fig. 3; see Supplementary materials Table S4). We did find higher variance in summer values compared to winter [mean RMR (watts)  $\pm$  SD: summer =  $1.11 \pm 0.46$ , winter =  $0.87 \pm 0.16$ ].

### Body temperature

The calculated  $T_b$  (°C) inflection point was  $34.8 \pm 2.0$  °C in summer, with no significant inflection point found in winter. Despite the difference between seasons,  $T_{\text{air}} \times$  season was not included in our top model, with the only significant effect on  $T_b$  that of increasing  $T_{\text{air}}$  (mean slope  $\pm$  SD: summer =  $0.30 \pm 0.04$   $^\circ\text{C } ^\circ\text{C}^{-1}$ ; winter =  $0.14 \pm 0.01$   $^\circ\text{C } ^\circ\text{C}^{-1}$ ;



**Fig. 3** Resting metabolic rate (RMR; watts; W) data over a range of  $T_{\text{air}}$  ( $\approx 30, 33, 36, 39, 42$  °C) for Cape Rockjumpers (*C. frenatus*) captured in summer ( $n=10$ ) and winter ( $n=11$ ) at Blue Hill Nature Reserve, South Africa. There were no significant differences between seasons with the *trendline* indicative of best model fit with 95% CI for both seasons combined. Each individual is represented at each of the five temperatures. For other abbreviations, see Fig. 1



**Fig. 4** Body temperature ( $T_b$ ; °C) data over a range of  $T_{air}$  ( $\approx 30, 33, 36, 39, 42$  °C) for Cape Rockjumpers (*C. frenatus*) captured in summer ( $n=10$ ) and winter ( $n=11$ ) at Blue Hill Nature Reserve, South Africa. No significant difference in season was found above an inflection point of  $34.3$  °C in summer, with *trendlines* indicating best model fit above the inflection point and 95% CI for each season. Each individual is represented at each of the five temperatures. For other abbreviations, see Fig. 1

$\chi^2_{1,63} = 10.47$ ;  $p < 0.01$ ; Fig. 4; see supplementary materials Table S5).

## Discussion

Despite the dry summer conditions, seasonal thermoregulatory adjustments to heat in Rockjumpers were centered on elevated EWL rates in summer compared to winter, with no clear seasonal change in RMR or  $T_b$ . Indeed, the lack of seasonal difference in RMR in summer compared to winter was unexpected, as a lower RMR in summer should help maintain a lower  $T_b$  if birds were acclimatised to summer heat (Williams and Tieleman 2000, 2005). The higher summer evaporative cooling efficiency in Rockjumpers was facilitated by higher EWL rates, contrary to our predictions that seasonal EWL adjustment would be centred on water conservation. The seasonal patterns of EWL in Rockjumpers' are qualitatively similar to patterns found in other species, despite the latter occupying habitats that are much warmer during summer. Species such as the Houbara Bustard (Tieleman et al. 2002b), Freckled Nightjar (O'Connor et al. 2016) and mesic populations of Sparrow-weavers (Noakes et al. 2016) also have elevated summer water demands, suggesting that certain species may use similar adaptations to deal with high temperatures irrespective of their particular habitat.

We expected adjustment in metabolic heat production to play an important role in seasonal heat balance (Noakes et al. 2016), but this did not have an overriding effect on evaporative efficiency in the Rockjumpers we studied. While we did not find a statistical difference in seasonal RMR, some individuals had RMR nearly twofold higher than average. We do not know the reasons for this variation among individuals, but also found higher variance among individuals in summer compared to winter in a concurrent study examining overnight basal metabolic rates (unpublished data). One potential reason for this is that summer birds were at the tail end of the breeding season, with some individuals still provisioning juveniles during the study period (K. N. O., personal observation). Yet, individuals with much higher RMR also had compensatory elevations in EWL and thus evaporative cooling efficiency remained higher in summer.

The elevated EWL rates of Rockjumpers in summer compared to winter are in direct contrast to summer water conservation patterns observed in arid-zone Sparrow-weavers (Noakes et al. 2016). However, as with the present study, two mesic populations of Sparrow-weaver (Noakes et al. 2016) and a mesic population of nightjars (O'Connor et al. 2016) had increased EWL in summer compared to winter. We argue that summer elevations in EWL are likely feasible in these mesic populations compared to Rockjumpers, given the differences in seasonal water bottlenecks we expect in their respective ranges; Sparrow-weavers and nightjars occupy a summer rainfall region where the availability of water-rich food or surface water should increase during summer, and elevated EWL will be balanced easily by higher water acquisition rates (Smit and McKechnie 2015). By contrast, Rockjumpers experience dry summers and will need to balance water loss by obtaining water-rich food on hot days. It may be that Rockjumpers have either not evolved the necessary flexibility to reduce water loss or can cope with water stress on the extremely rare occasions they experience extreme temperatures. A better understanding of water intake rates at increasing temperatures are needed to properly predict dehydration risks in Rockjumpers under the dry summer conditions they experience naturally.

Rockjumper average cooling efficiency at  $T_{air} \approx 42$  °C in summer remained considerably lower than both seasonal averages for Sparrow-weavers [summer = 1.32, winter = 1.04 (Noakes et al. 2016)]. This means that at  $T_{air}$  near  $T_b$  Sparrow-weavers dissipated more than 100% of their metabolic heat evaporatively, compared to only  $\approx 50\%$  for Rockjumpers, suggesting Rockjumpers face a net heat gain at  $T_b \approx T_{air}$ . Seasonal patterns in Rockjumper  $T_b$  regulation were also contrary to expected patterns of lower  $T_b$  at high  $T_{air}$  in summer. During both summer and winter  $T_b$  increased significantly as  $T_{air}$  increased from  $34.2$  to  $42$  °C, suggesting that Rockjumpers do not regulate a constant set point  $T_b$  under hot conditions. However, it is unlikely we tested

Rockjumpers near their thermal endpoint, as was attempted in Whitfield et al. (2015). It is also possible that Rockjumpers rely on behaviour to thermoregulate during rare occasions of high temperatures, as behavioural adjustments can be used as buffers in such extremes (Adolph 1990; Boyles et al. 2011; Buckley et al. 2015).

At  $T_b$  near  $T_{air} \approx 42$  °C, Rockjumper average  $T_b$  was quantitatively similar to that of Sparrow-weaver's (summer = 42.0 °C, winter = 42.4 °C), and does not seem indicative of  $T_b$  above normothermy. However, the benefits, if any, of elevating  $T_b$  for Rockjumpers are not clear. Many authors have suggested that allowing  $T_b$  to rise above normothermic levels is a mechanism for storing metabolic heat (i.e. facultative hyperthermia) to combat risks of dehydration stemming from evaporative cooling (Tieleman and Williams 1999; Wolf 2000; Smit et al. 2013). The adaptive benefit of facultative hyperthermia is generally centred on water savings from decreasing EWL (e.g. Maloney and Dawson 1998), which were not found for Rockjumpers. Our emphasis on seasonal variation in thermoregulation as evidence of acclimatisation does not account for changes in breeding condition, diet, or water availability. Additionally, although we added individual as a random effect in our mixed models, the extent to which repeated measures affected our results may have been underrepresented.

## Conclusion

Past studies have identified a number of traits that increase Rockjumpers' vulnerability to climate change. These include a relatively small and declining climatic space, a fragmented range, and overall low abundance (Lee and Barnard 2016). Additionally, recent population declines have been linked to a warming climate, and relatively low  $T_{air}$  inflections for increasing EWL in Rockjumpers were found compared to other species in a previous study (Milne et al. 2015), suggesting Rockjumpers may be climate relicts (see Woolbright et al. 2014) restricted to alpine peaks by their susceptibility to warmer temperatures and perhaps drier climates. Milne et al. (2015) argued low  $T_{air}$  inflections substantially elevate the costs of evaporative cooling in warmer parts of the Rockjumper range, potentially providing a causal explanation for why population declines of this species are greater in parts of their range where mean annual temperatures are rising.

Surprisingly few studies have quantified physiological responses to weather extremes in species defined as climate relicts (Woolbright et al. 2014). Woolbright et al. (2014) argue that climate relicts serve as natural laboratories for studying climate change responses. Our study on seasonal physiological responses to heat show that Rockjumpers had elevated water demands even throughout the hotter and drier summer. If these physiological responses result in a seasonal water bottleneck, our findings may partially

explain declining populations in species with a restricted and well-defined climatic niche. However, to fully understand the effects on water budgets resulting from elevated EWL demands will require a more mechanistic approach such as was attempted for Sparrow-weavers (Smit and McKechnie 2015) and Night Parrots (*Pexoporus occidentalis*) (Kearney et al. 2016). Indeed, for Rockjumpers a modelling approach using closely related, more common species, may be the only alternative. Finally, our findings show again that avian seasonal physiological adjustments to heat may be as diverse as their adjustments to the cold. Seasonal studies on thermoregulation in the heat will greatly improve our knowledge of the functional (or adaptive) value of traits such as evaporative cooling efficiency and heat tolerance, and how they contribute to the physiological stress organisms experience in heterogenous environments.

## Data accessibility

Our raw data has been made accessible as an online file, Table S1.csv, under the associated supplementary materials.

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