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Comparison of physiological responses to high temperatures in juvenile and adult Cape Rockjumpers *Chaetops frenatus*[§]

Krista N Oswald^{1,3*} , Alan TK Lee²  and Ben Smit^{1,3} 

¹ Department of Zoology, Nelson Mandela University, Port Elizabeth, South Africa

² Fitzpatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Cape Town, South Africa

³ Department of Zoology and Entomology, Rhodes University, Grahamstown, South Africa

* Corresponding author, email: knoswald@gmail.com

Concerns about climate change have led to an increase in studies on physiological mechanisms birds possess to cope with increasing temperatures. For range-restricted species such as Cape Rockjumpers *Chaetops frenatus*, whose population declines are correlated with habitat warming, we identified juvenile physiological responses to high temperature as a potential gap in current knowledge. We compared metabolic rate, evaporative water loss, evaporative cooling efficiency (calculated from evaporative water loss and resting metabolic rate) and body temperature in juveniles ($n = 5$) with adult birds ($n = 10$) to a ramped temperature profile (30–42 °C). Although juveniles exhibited no significant difference in cooling efficiency, they had higher evaporative water loss, resting metabolic rate and body temperature. This suggests that while juvenile birds show similar abilities to dissipate metabolic heat evaporatively, they face higher overall water and energy demands, and thus higher thermoregulatory costs in maintaining body temperature as overall temperatures continue to increase.

Comparaison des réponses physiologiques aux températures élevées chez les juvéniles et les adultes du Chétopse bridé *Chaetops frenatus*

Les préoccupations concernant le changement climatique ont conduit à une augmentation des études sur les mécanismes physiologiques que possèdent les oiseaux pour faire face à la hausse des températures. Pour les espèces à aire de répartition restreinte, telles que les Chétopses bridés *Chaetops frenatus*, dont le déclin de la population est corrélé au réchauffement de l'habitat, nous avons identifié les réponses physiologiques des juvéniles à des températures élevées comme une lacune potentielle dans les connaissances actuelles. Nous avons comparé le taux métabolique, la perte d'eau par évaporation, l'efficacité du refroidissement évaporatif (calculée à partir de la perte d'eau évaporative et du taux métabolique au repos) et la température corporelle chez les juvéniles ($n = 5$) avec des oiseaux adultes ($n = 10$) à un profil de température en rampe (30–42 °C). Bien que les juvéniles n'aient montré aucune différence significative dans l'efficacité du refroidissement, ils présentaient une perte d'eau par évaporation, un taux métabolique au repos et une température corporelle plus élevés. Cela suggère que, même si les oiseaux juvéniles présentent des capacités similaires à dissiper par évaporation la chaleur métabolique, ils sont confrontés à des besoins en eau et en énergie plus élevés et donc à des coûts thermorégulateurs plus élevés.

Keywords: avian physiology, climate change, climate relict, juvenile physiology, South Africa endemic

Concerns about effects of climate change have led to numerous studies examining the physiological mechanisms whereby birds cope with increasing temperatures (e.g. Williams and Tieleman 2005; McKechnie and Wolf 2010; Whitfield et al. 2015), yet the development of these physiological mechanisms in immature birds has been almost entirely overlooked. Immature birds may be more susceptible to warming habitats, especially for those species breeding in the hot summer months. Weathers and Sullivan (1989) found Yellow-eyed Juncos *Junco phaeonotus*

4–7 weeks post-fledging showed increased signs of energy expenditure compared with adults due to low foraging efficiency, so it is also possible juvenile individuals may experience increased physiological stress.

Of the six Fynbos-endemic passerines, Cape Rockjumpers *Chaetops frenatus* may be the most adversely affected by increasing temperature as shown by population declines correlated with areas of their habitat experiencing the greatest temperature warming (Milne et al. 2015). Combined with already low population size (Lee and Barnard 2016),

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this has led to the Cape Rockjumper being upgraded to Near Threatened on the IUCN Red List of Threatened Species, and so they serve as an excellent study species to examine physiological responses to high air temperatures.

We tested for differences in physiological responses to high temperatures comparing juvenile (<3 months old based on fledge date, plumage and gape) and adult Cape Rockjumpers, as low tolerance to high temperatures may point to a vulnerability for population persistence. To do this, we explored four physiological parameters: (1) heat dissipation in the form of evaporative water loss (mg h^{-1}), (2) the lowest rate of heat production, resting metabolic rate (watts; W), (3) body temperature ($^{\circ}\text{C}$), and (4) evaporative cooling efficiency (the ratio of evaporative heat loss [EHL; calculated from evaporative water loss] to metabolic heat production [MHP; calculated from resting metabolic rate]).

Here we compare physiological responses of juvenile to adult Cape Rockjumpers during the summer season, collected as part of a study on adult Cape Rockjumper seasonal physiological flexibility (Oswald et al. 2018). Compared with the adult birds caught concurrently by Oswald et al. (2018), we hypothesised juvenile birds would have less ability to cope with high air temperatures, from which we predicted we would see steeper rates of increase – and higher overall values – of evaporative water loss, resting metabolic rate and body temperature. An increased ability to cope with high air temperature, which is shown by increased evaporative cooling efficiency, should result in a more stable body temperature (e.g. Marder and Arieli 1988; Ophir et al. 2002; Tieleman and Williams 2002; McKechnie and Wolf 2004); we thus also predicted lower rates of increase and overall values for evaporative cooling efficiency for juveniles.

This study took place at Blue Hill Nature Reserve (33.59° S , 23.41° E ; 1 000–1 530 m above sea level) in the Western Cape province, South Africa. During January 2016, 15 wild-living individuals were studied (four adult males, six adult females and five juveniles; mean mass (g) \pm SD: male = 55.52 ± 3.70 , female = 49.41 ± 1.20 , juvenile = 48.59 ± 2.01). Here we report evaporative water loss, resting metabolic rate, body temperature, and evaporative efficiency patterns measured for juvenile Cape Rockjumpers exposed to a ramped air temperature profile (30, 33, 36, 39 and 42°C) for 15–20 min at each temperature, with birds in chambers for 120–150 min in total. 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, Cape Town, South Africa). Birds were continuously monitored via live video feed with an infrared light source and closed-circuit security camera.

A BioMark PIT-tag reader was placed next to the chamber to continuously record body temperature (Gerson et al. 2014; Whitfield et al. 2015) using PIT-tags placed intra-peritoneally, with no recorded negative effects on Cape Rockjumpers (see Oswald et al. 2017). Chamber temperature (T_{air}) was measured using a thermistor probe (model TC100, Sable Systems, Las Vegas, NV, USA) inserted 1 cm through a small hole in the lid.

Data acquisition occurred by pulling subsampled air from the respirometry chambers through a water vapour analyser (RH-300, Sable Systems) before entering an O_2 and CO_2 analyser (Foxbox-C Field Gas Analysis System, Sable Systems). All the respirometry equipment, and flow-rate meters were regularly calibrated following Whitfield et al. (2015). The Foxbox produced an analog output, which was digitised and recorded at one-second intervals using Expedata Data Acquisition and Analysis Software (Sable Systems). We recorded baseline values of O_2 , CO_2 and water vapour pressure at the beginning of each experimental test, as well as between each air temperature and again at the end of each experimental test.

For gas-exchange analyses, we extracted data from the lowest V_{O_2} output present during the last 5 min at each air temperature, as metabolic rate was generally most stable at these times. Resting metabolic rate values are presented in watts (representative of metabolic heat production) and were calculated using a joule conversion of $20.1\text{ J mL}^{-1}\text{ O}_2$, using Table 4–2 in Withers (1992) from a calculated respiratory quotient of 0.76 (average = 0.76 ± 0.10); the maximum error associated with using this respiratory quotient does not exceed 6%. Evaporative heat loss (W) was calculated from evaporative water loss using latent heat of vaporisation 2.4 J mg^{-1} , and evaporative cooling efficiency was calculated as the ratio of EHL to MHP. Juvenile data were compared with the same measurements collected for adult birds as reported in Oswald et al. (2018), captured at the same study site during the same study period. For a more detailed experimental protocol see Oswald et al. (2018).

We explored the contribution that bird age (adult versus juvenile), mass, air temperature and the interaction of air temperature and age, had on physiological response parameters. We did this by fitting linear mixed-effects models using the lme4 package (Bates et al. 2013) in R version 3.1.2 (R Core Team 2016), with individual included as a random effect. We used the ANOVA function from the car package (Fox and Weisberg 2011) to examine models for significant parameters. Best models were found using the MuMin dredge function (Barton 2013) for models within two AICc (Akaike information criterion used to measure model goodness of fit, corrected for small sample size) of one another. We present beta parameters (slopes) as mean \pm standard error. Where more than one best model was found within two AICc, the model with the lowest AICc is presented in results. For the raw data see Supplementary Table S1.

There were no significant differences in body mass between males, females and juveniles ($F_{12} = 2.464$; $p = 0.127$; Table 1), and we found neither a sex nor mass effect for any physiological responses. Sex was thus

Table 1: Summary table of the linear model comparing mass (g) of male ($n = 4$), female (Intercept; $n = 6$), and juvenile ($n = 5$) Cape Rockjumpers from Blue Hill Nature Reserve, South Africa

Factor	Estimate	SE	<i>t</i> -value	df	<i>p</i> -value
Intercept	48.48	1.64	29.57		
Juvenile	−0.07	2.43	−0.03	12	0.98
Male	5.18	2.59	2.00	12	0.07

removed as a covariate, as per previous models fitted with only adult birds where we found no significant difference in these same response variables between sexes (Oswald et al. 2018). Moreover, the inclusion of sex along with age led to issues of collinearity, and so we excluded sex as a parameter in the present study.

Evaporative water loss was significantly higher for juveniles compared with that of adults (pooled average: adults = $666 \pm 381 \text{ mg h}^{-1}$, juveniles = $905 \pm 415 \text{ mg h}^{-1}$,

$\chi^2_{65} = 8.42$, $p < 0.05$) and increased significantly for both age classes at increasing air temperature ($\chi^2_{65} = 0.44$, $p < 0.05$; Figure 1a, Table 2). Although mass and the interaction of air temperature and age were included in the best model, results from the ANOVA found these effects were not significant (mass: $\chi^2_{65} = 0.95$, $p = 0.331$; air temperature*age: $\chi^2_{65} = 0.44$, $p = 0.506$, adult slope = $58.07 \pm 7.07 \text{ mg h}^{-1} \text{ }^\circ\text{C}^{-1}$, juvenile slope $67.24 \pm 22.59 \text{ mg h}^{-1} \text{ }^\circ\text{C}^{-1}$; Figure 1a, Table 2).

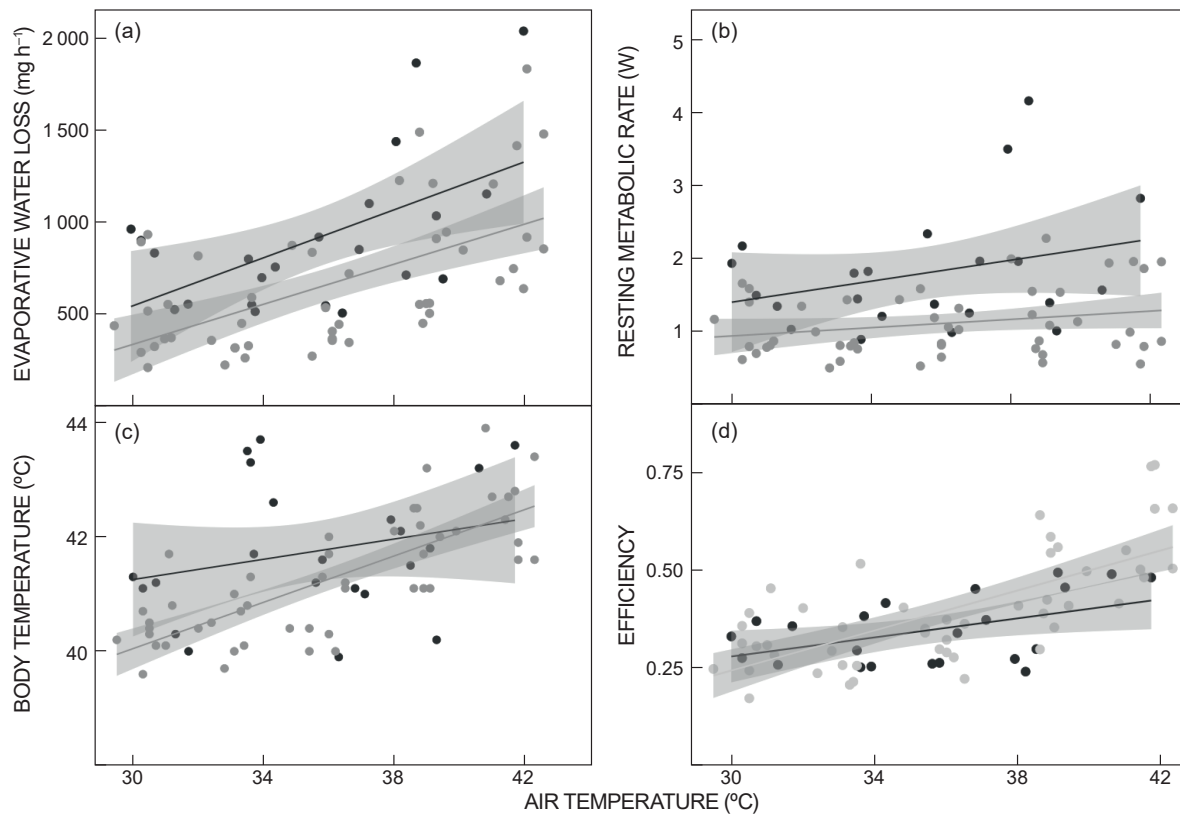


Figure 1: Physiological data collected from adult ($n = 10$; grey) and juvenile ($n = 5$; black) wild-living Cape Rockjumpers captured in January 2016 at Blue Hill Nature Reserve, South Africa, over a range of air temperatures (29–43 °C). (a) Evaporative water loss (EWL; mg h^{-1}), (b) resting metabolic rate (RMR; W), (c) body temperature ($^\circ\text{C}$), and (d) efficiency (calculated from EWL/RMR), each with predicted best fit trendlines and 95% confidence intervals

Table 2: Model coefficients summary table for models explaining evaporative water loss (mg h^{-1}) as a function of age (Age1 = adult), body mass (M_b), air temperature (T_{air}), and the interaction of air temperature and age (indicated by $T_{\text{air}} \cdot \text{Age1}$). Included are Full Model (all predictor variables), Null Model (with no predictor variables), Best Model (for selection process see the text), and parsimonious models (models created using predictor variables with significant effects in Best Model). For evaporative water loss the Best Model was the same as the Full Model. P -values lower than 0.05 are highlighted in bold. ΔAICc refers to the difference in AICc from the Best/Full Model

	AICc	Factor	Estimate	SE	t-value	χ^2	df	p-value
Full Model	976.30	Intercept	-2 544.18	920.41	-2.76			
		Age1	131.53	684.02	0.19	5.45	65	<0.05
		M_b	19.94	14.72	1.35	1.84	65	0.196
		T_{air}	70.25	16.51	0.25	57.57	65	<0.01
		$T_{\text{air}} \cdot \text{Age}$	-12.54	18.87	-0.66	0.44	65	0.506
Null Model	1 044.79 ($\Delta 68.49$)	Intercept	746.71	65.78	11.35			
Age	1 032.36 ($\Delta 56.06$)	Intercept	906.10	107.40	8.43			
		Age	-236.00	130.40	-1.81	3.28	67	0.070
T_{air}	1 001.76 ($\Delta 25.46$)	Intercept	-1 414.08	293.25	-4.82			
		T_{air}	60.45	7.96	7.60	57.7	67	<0.01

Resting metabolic rate was significantly higher for juveniles compared with that of adults (pooled average: adults = 1.11 ± 0.46 W, juveniles = 1.79 ± 0.82 W; $\chi^2_{65} = 8.03$, $p = 0.005$), increased significantly with increasing air temperature for both adults and juveniles ($\chi^2_{66} = 12.96$, $p < 0.001$), and increased at a significantly greater rate for juveniles compared with adults (adult slope = 0.03 ± 0.01 W °C⁻¹; juvenile slope = 0.10 ± 0.04 W °C⁻¹; $\chi^2_{65} = 5.77$, $p < 0.05$; Figure 1b, Table 3).

Body temperature was significantly higher for juveniles compared with adults (adults = 41.26 ± 1.05 °C, juveniles = 41.74 ± 1.18 °C; $\chi^2_{66} = 4.36$, $p = 0.037$) and increased significantly for both juveniles and adults at increasing air temperature ($\chi^2_{66} = 49.42$, $p < 0.001$; Figure 1c, Table 4).

The only factor included in the best model for evaporative cooling efficiency was air temperature, with efficiency increasing significantly for both juveniles and adults

at increasing air temperature ($\chi^2_{65} = 69.21$, $p < 0.001$; Figure 1d, Table 5).

Juvenile Cape Rockjumpers exhibited no difference in efficiency compared with adults, but had higher evaporative water loss, resting metabolic rate and body temperature. In addition, while age was not included in the best model for cooling efficiency, juvenile resting metabolic rate increased at a significantly greater rate in juveniles compared with that of adults in the full model, and perhaps explains why cooling efficiency increased at a significantly lower rate for juveniles compared with adults in the full model (adult slope = 0.03 ± 0.00 MHP/EHL °C⁻¹; juvenile slope = 0.01 ± 0.00 MHP/EHL °C⁻¹; $\chi^2_{65} = 9.12$, $p < 0.01$). Our sample size of juvenile Cape Rockjumpers was small and restricted to one breeding season, and therefore limits us from drawing firm conclusions concerning the development of thermoregulatory mechanisms in dealing with

Table 3: Model coefficient summary table for models explaining resting metabolic rate (Watts) as a function of age (age1 = adult), body mass (M_b), air temperature (T_{air}), and the interaction of air temperature*age ($T_{air}:age1$). Included are the Full Model (all predictor variables), Null Model (with no predictor variables), Best Model (for selection process see in text), and parsimonious models (models created using predictor variables with significant effects in Best Model). P -values lower than 0.05 are highlighted in bold. Δ AICc refers to the difference in AICc from the Best Model

	AICc	Factor	Estimate	SE	t-value	χ^2	df	p-value
Full Model	129.94 (Δ 8.74)	Intercept	-3.20	1.73	-1.85			
		T_{air}	0.10	0.03	3.93	14.35	65	<0.01
		Age1	1.72	1.09	1.59	8.42	65	<0.01
		M_b	0.03	0.03	0.97	0.95	65	0.331
		$T_{air}:Age1$	-0.07	0.03	-2.40	5.77	65	<0.05
Null Model	127.17 (Δ 5.97)	Intercept	1.35	0.14	9.40			
Best Model	121.20	Intercept	0.16	0.51	0.31			
		Age1	-0.74	0.26	-2.83	8.03	66	<0.01
		T_{air}	0.05	0.01	3.60	12.96	66	<0.01
T_{air}	124.75 (Δ 3.55)	Intercept	-0.33	0.49	-0.66			
		T_{air}	0.05	0.01	3.58	12.82	67	<0.01
Age	123.70 (Δ 2.55)	Intercept	1.82	0.21	8.88			
		Age	-0.71	0.25	-2.81	7.92	67	<0.01

Table 4: Model coefficient summary table for models explaining body temperature (°C) as a function of age (age1 = adult), body mass (M_b), air temperature (T_{air}), and the interaction of air temperature*age ($T_{air}:age1$). Included are the Full Model (all predictor variables), Null Model (with no predictor variables), Best Model 1 (for selection process see in text), and parsimonious models (models created using predictor variables with significant effects in Best Model). P -values lower than 0.05 are highlighted in bold. Δ AICc refers to the difference in AICc from the Best Model 1

	AICc	Factor	Estimate	SE	t-value	χ^2	df	p-value
Full Model	206.87 (Δ 10.78)	Intercept	38.13	1.82	19.50			
		T_{air}	0.10	0.03	7.04	50.52	65	<0.01
		Age1	-4.22	0.30	-1.96	4.10	65	<0.05
		M_b	0.00	0.03	0.01	0.00	65	0.973
		$T_{air}:Age1$	0.10	0.06	1.73	2.99	65	0.084
Null Model	223.32 (Δ 27.23)	Intercept	41.41	0.13	313.20			
Best Model 1	196.09	Intercept	35.43	0.93	38.20			
		Age1	-0.59	0.28	-2.09	4.36	66	<0.05
		T_{air}	0.18	0.03	7.03	49.42	66	<0.01
T_{air}	197.15 (Δ 1.06)	Intercept	35.09	0.92	38.06			
		T_{air}	0.18	0.03	6.95	48.27	67	<0.01
Age	223.42 (Δ 27.33)	Intercept	41.74	0.23	179.40			
		Age1	-0.48	0.28	-1.70	2.88	67	0.090

Table 5: Model coefficients summary table for models explaining evaporative cooling efficiency as a function of age (Age1 = adult), body mass (M_b), air temperature (T_{air}), and the interaction of air temperature*age ($T_{air}:age1$). Included are the Full Model (all predictor variables), Null Model (with no predictor variables), and Best Model (for selection process see in text). P -values lower than 0.05 are highlighted in bold. $\Delta AICc$ refers to the difference in AICc from the Best Model

	AICc	Factor	Estimate	SE	t -value	χ^2	df	p -value
Full Model	-92.08 ($\Delta 17.02$)	Intercept	-0.13	0.28	0.46			
		T_{air}	0.01	0.01	1.67	79.46	65	<0.01
		Age1	-0.57	0.21	-2.73	1.33	65	0.249
		M_b	0.00	0.00	-0.40	0.16	65	0.692
		$T_{air}:Age1$	0.02	0.01	3.02	9.12	65	<0.01
Null Model	-77.06 ($\Delta 34.67$)	Intercept	0.38	0.02	20.02			
Best Model	-111.73	Intercept	-0.41	0.10	-4.23			
		T_{air}	0.02	0.00	8.32	69.21	67	<0.01

heat. Yet, to the best of our knowledge, our study is one of the first to compare avian physiological responses at high temperatures between juveniles and adults. The lack of significant difference in efficiency between adult and juvenile individuals seems to suggest Cape Rockjumper fledglings show similar abilities to dissipate metabolic heat evaporatively. However, the overall water and energy demands, and thus thermoregulatory cost, were higher in the juvenile Cape Rockjumpers during our study. A higher resting metabolic rate may elevate food demands, and further increase the demands for evaporative cooling. These elevated energy and water demands provide a possible physiological explanation for observations made by Weathers and Sullivan (1989) reporting increased foraging requirements in young compared with adult Yellow-eyed Juncos under hot conditions.

We observed adults begin panting at $T_{air} = 35.83 \pm 1.19$ °C in summer, while juvenile birds all panted immediately after being put in the chamber at $T_{air} \approx 30$ °C. The higher resting metabolic rate we found in juveniles compared with adults (Figure 1b) suggests that juveniles have higher total heat dissipation requirements (from a higher metabolic heat load), and this alone could be responsible for the immediacy of juveniles' panting, which consequently contributes to the elevated rates of evaporative water loss in juveniles (Figure 1a). Panting at these relatively low temperatures, combined with higher rates of evaporative water loss, implies young birds will face increased water requirements compared with adults under warm conditions.

While Rising and Hudson (1974) found no difference in metabolic responses of young Black-capped Chickadees *Poecile atricapillus* compared with adults at temperatures of <30 °C, a comparative study of metabolic rates at 39 °C in nestlings from 59 species by Ton and Martin (2016) found strong positive correlations between body mass, metabolic rate and growth rates. However, neither of these studies directly compared results of juvenile birds with adult birds across a temperature gradient. An important avenue for further study is whether juvenile birds are at greater risk of mismatches between energy and water demands and supply during hot weather, compared with adults. Cape Rockjumper population declines may be partially due to survival rates of juvenile individuals in instances of heat waves or drought, especially as the majority of

breeding occurs during spring, with juveniles fledging at the hottest and driest part of the year. For example, on a day with 8 h of 30 °C air temperature juveniles would lose an average of 12% body mass (based on our recorded rate of 753.2 ± 202.55 mg h⁻¹ evaporative water loss at 30 °C and an average body mass of 50 g) compared with 8% body mass for adults (based on our recorded rate of 526.5 ± 266.5 mg h⁻¹ evaporative water loss at 30 °C and an average body mass of 52.5 g).


In summary, our results indicate the costs of physiological thermoregulation may vary with age, similar to what has been found in behavioural studies (Weathers and Sullivan 1989), where young birds appear to be more sensitive to higher temperatures than adults. The implications of how age-related variation in behavioural and thermoregulatory responses at high temperatures may affect population persistence under hotter climate conditions is yet unknown and would be an important avenue for future studies.

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ORCID

Krista Oswald  <https://orcid.org/0000-0001-8745-4432>

Alan Lee  <https://orcid.org/0000-0002-5858-9351>

Ben Smit  <https://orcid.org/0000-0003-4160-8242>

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