

# Functional role of metabolic suppression in avian thermoregulation in the heat

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## ABSTRACT

Hypometabolism arising from active metabolic suppression occurs in several contexts among endotherms, particularly during heterothermic states such as torpor. However, observed  $Q_{10} \approx 1$  for avian resting metabolic rate within the thermoneutral zone, values far below the  $Q_{10} = 2-3$  expected on the basis of Arrhenius effects, suggests hypometabolism also plays a role in birds' thermoregulation at environmental temperatures approaching or exceeding normothermic body temperature ( $T_b$ ). We evaluated the occurrence of hypometabolism during heat exposure among birds by re-analysing literature data to quantify changes in  $T_b$  and resting metabolic rate (RMR) near the upper boundary of the thermoneutral zone, at air temperatures ( $T_{air}$ ) between the inflection above which  $T_b$  increases above normothermic levels ( $T_{b,inf}$ ) and the upper critical limit of thermoneutrality ( $T_{uc}$ ). Among the  $\sim 55\%$  of species in which  $T_{uc} - T_{b,inf} > 0$ ,  $Q_{10} < 2-3$  occurred in nine of 10 orders for which suitable data exist, indicating that hypometabolism during heat exposure is widespread across the avian phylogeny. Values of  $Q_{10} < 2-3$  were not restricted to small body mass, as previously proposed. Our findings support the idea that metabolic suppression reduces avian metabolic heat production and hence evaporative cooling requirements during heat exposure, with reductions of 20–30% in RMR in some species. Moreover, these findings add to evidence that hypometabolism is an important component of heat tolerance among endotherms such as birds and tropical arboreal mammals.

## 1. Introduction

Temperature has important and pervasive effects on the rates of biochemical reactions and overall metabolic rate (MR) via the Arrhenius effect, with a 10 °C increase in body temperature ( $T_b$ ) typically associated with a 2-3-fold increase in MR (Arrhenius, 1889; Christophersen, 1973). Arrhenius effects are quantified using the  $Q_{10}$  coefficient, the fractional change in rate associated with a 10 °C difference in  $T_b$  (Arrhenius, 1889; Christophersen, 1973). Although Arrhenius effects are best understood among ectotherms, in which the close coupling between environmental temperature ( $T_{env}$ ) and body temperature ( $T_b$ ) results in strong temperature-dependence of physiological and behavioural processes (Angilletta Jr., 2009; Christophersen, 1973; Huey et al., 2009), nevertheless,  $T_b$ -dependence of MR is also a feature of avian and mammalian thermoregulation (e.g., Geiser, 1988; Lyman et al., 1982; Lovegrove et al., 2014; Reher et al., 2018). During torpor and hibernation, for instance,  $Q_{10}$  for MR is often 2–3 when  $T_{env}$  is above the reduced  $T_b$  set point defended during heterothermy and animals are thermoconforming (Geiser 2004; Lyman et al., 1982; Lovegrove et al., 2014). Under these conditions, warmer  $T_{env}$  can result in increased MR, which may negatively affect the ability of hibernators, such as non-migratory

bats at temperate and boreal latitudes, to survive the winter using their stored fat reserves (e.g., Humphries et al., 2002).

Recent evidence suggests some endotherms use hypometabolism to avoid Arrhenius effects on MR when  $T_b$  is elevated during heat exposure (Lovegrove et al., 2014; Reher et al., 2018; Reher and Dausmann, 2021). Malagasy bats (*Macronycteris commersoni*), for instance, decreased MR during hyperthermic torpor on very hot days when skin temperature tracked  $T_{env}$ , even when  $T_b$  exceeded normothermic levels (Reher and Dausmann, 2021). Diurnal hyperthermic torpor was also observed in four nocturnal arboreal mammals, including tarsiers (*Tarsius syrichta*), leading Lovegrove et al. (2014) to posit that *T. syrichta* uses active metabolic suppression to avoid Arrhenius effects on MR during the heat of the day. Reductions in the magnitude of Arrhenius effects on metabolic heat production may confer benefits by avoiding or delaying lethal hyperthermia and dehydration (Levesque et al., 2018; Lovegrove et al., 2014; Weathers, 1981), potentially from increased heat storage capacity or the use of non-evaporative heat dissipation avenues (Dawson and Hudson, 1970; Gerson et al., 2019; Williams and Tieleman, 2005).

Although most evidence for a role of metabolic suppression in reducing Arrhenius effects on MR comes from tropical mammals, there is also some evidence for  $Q_{10} < 2-3$  in birds. Weathers (1981) reported

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$Q_{10} \approx 1$  in three of four species he investigated, in individuals whose  $T_b$  increased within their thermoneutral zone (TNZ) and before the onset of thermoregulatory behaviours such as panting and the accompanying approximately linear increases in resting metabolic rate (RMR) that occur at  $T_{air}$  above the upper critical limit of thermoneutrality ( $T_{uc}$ ). Lower-than-expected  $Q_{10}$  was also observed in budgerigars (*Melopsittacus undulatus*) (Weathers and Schoenbaechler, 1976). These authors reviewed the literature and noted that evidence for hypometabolism existed for 11 other bird species representing five orders (Weathers and Schoenbaechler, 1976), observations suggesting some birds employ active metabolic suppression during heat exposure to offset Arrhenius effects on MR.

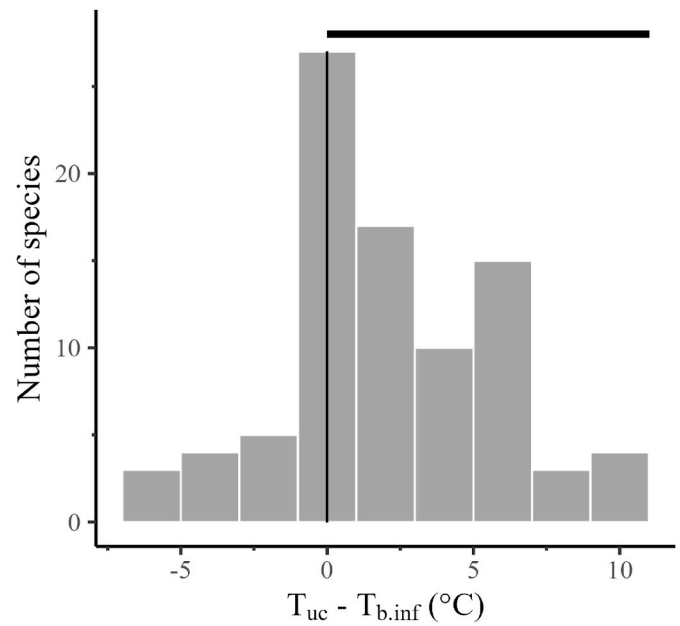
Despite Weathers' observations of avian  $Q_{10} < 2-3$  and the increasing evidence for a role of metabolic suppression during heterothermy among tropical mammals, no meta-analyses have been conducted to assess whether  $T_b$ -independence of MR at  $T_{env}$  approaching or exceeding normothermic  $T_b$  occurs across the avian phylogeny or whether it is limited to a subset of taxa. *A priori*, avoiding  $T_b$ -related increases in metabolic heat production within the TNZ may be expected to confer adaptive benefits by reducing water requirements for evaporative cooling as  $T_{env}$  approaches  $T_b$ . For this reason, we hypothesised that hypometabolism during heat exposure is widespread across the avian phylogeny and predicted that increases in  $T_b$  within the TNZ are associated lower-than-expected increases in RMR, evident as  $Q_{10}$  below the range of 2–3 associated with typical Arrhenius effects.

## 2. Methods and materials

### 2.1. Data sources

Data from the literature and unpublished data sources (Appendix, Table S1) were compiled for 106 bird species ranging in body mass ( $M_b$ ) from ~7 g to ~700 g and representing 17 orders (Appendix, Table S1). The study sites for these species spanned various arid locations in South Africa, North America (USA), and Australia, as well as montane and coastal lowland areas in South Africa (multiple datasets exist for some species, for instance when conspecific populations were examined in >1 climatic region, yielding 115 datasets). Details of capture, holding conditions, and gas exchange measurements using flow-through respirometry with low chamber humidity (~1g H<sub>2</sub>O m<sup>-3</sup>; Freeman et al., 2020, 2022, 2024) are provided in each of the published studies (Appendix, Table S1), all of which followed the methodologies described by Whitfield et al. (2015) and Czenze et al. (2020), ensuring comparability for studies like the present one. In all these studies, intraperitoneally-injected passive integrated transponder (PIT) tags were used to measure core  $T_b$  during respirometry trials (e.g. Czenze et al., 2020; Freeman et al., 2020, 2022, 2024; Whitfield et al., 2015). Furthermore, for each species in these studies food was withheld prior to gas exchange for periods greater than the gut passage time predicted from body mass by Karasov (1990). We excluded published datasets not collected using comparable methodology, particularly the maintenance of low chamber humidity by using high flow rates. For each species/population, we re-analysed  $T_b$  and RMR measured between  $T_{air} = 25^\circ\text{C}-30^\circ\text{C}$  and the maximum  $T_{air}$  associated with thermal endpoints, as well as inflection  $T_{air}$  values for  $T_b$  ( $T_{b,inf}$ ) and RMR (i.e.,  $T_{uc}$ ).

Our primary data inclusion criterion for subsequent analyses was an increase in  $T_b$  within the TNZ (i.e.  $T_{uc} - T_{b,inf} > 0$ ), as for most species a  $Q_{10}$  value for MR cannot be estimated at  $T_{air} > T_{uc}$  because of the obscuring effects of MR increases associated with active heat dissipation processes such as panting (Weathers and Schoenbaechler, 1976; Weathers, 1981). We also included the following species lacking a discernible  $T_{uc}$ : Namaqua sandgrouse (*Pterocles namaqua*), Freckled nightjar (*Caprimulgus tristigma*) and Rufous-cheeked nightjar (*Caprimulgus rufigena*) (O'Connor et al., 2017; Czenze et al., 2021; Appendix, Table S1). Among species for which a  $T_{uc}$  was evident, values of  $T_{uc} - T_{b,inf}$  were normally distributed (Shapiro-Wilk normality test,  $p = 0.29$ ;



**Fig. 1.** Distribution of the difference between air temperature ( $T_{air}$ ) inflections for body temperature ( $T_b$ ) and resting metabolic rate ( $T_{b,inf}$  and  $T_{uc}$ , respectively) for the 90 avian species or populations which had identified  $T_{uc}$  and  $T_{b,inf}$ . Data sets for which  $T_{uc}$  and/or  $T_{b,inf}$  could not be identified were excluded from this analysis, as were outliers. The horizontal line above the histogram indicates data sets for which  $T_{uc} - T_{b,inf} > 0$  and therefore met the first data inclusion criterion for this study.

**Fig. 1.** Data sets for which  $T_{uc} - T_{b,inf} \leq 0$  were excluded from further analyses, as were those with sample sizes of  $\leq 6$  individuals.

### 2.2. $Q_{10}$ calculations and analyses

For each species in the remaining subset of studies (Table 1), relationships between  $T_{air}$ , RMR and  $T_b$  were evaluated using generalised linear mixed models (GLMMs) with individual included as a random factor, using the *nlme* package version 3.1–163 (Pinheiro et al., 2023) in R 4.3.1 (R Core Team, 2023) following Freeman et al. (2022). Values of  $T_{b,inf}$  and  $T_{uc}$  were estimated using the package *segmented* (Muggeo, 2008) and served as lower and upper bounds of the  $T_{air}$  range over which we estimated  $Q_{10}$ , unless  $T_{b,inf}$  was below the lower limit of thermoneutrality ( $T_{lc}$ ), in which case the  $T_{lc}$  was used as the lower bound, or if there was no discernible  $T_{uc}$ , in which case the highest  $T_{air}$  setpoint was used as the upper bound. Average RMR and  $T_b$  values were then calculated for these  $T_{air}$  values using the GLMMs using the slopes for RMR at  $T_{air} \leq T_{uc}$  and the  $T_b$  slope at  $T_{air} \geq T_{b,inf}$  for  $T_{air} \geq 28$ . This approach was necessary because  $T_{b,inf}$  and  $T_{uc}$  usually did not occur exactly at one of the experimental  $T_{air}$  setpoints and therefore GLMMs were used to have a standardised, repeatable method of calculating  $Q_{10}$  for each species, although in some cases our estimated  $Q_{10}$  may vary from those calculated using average RMR values at the nearest ( $\pm 1^\circ\text{C}$ )  $T_{air}$  setpoints (e.g., McKechnie et al., 2016a). The  $Q_{10}$  for each species was calculated using the standard equation describing the Arrhenius effect (Lovegrove et al., 2014; Snyder and Nestler, 1990; Withers, 1992):

$$Q_{10} = \left( \frac{R_2}{R_1} \right)^{10 / (T_2 - T_1)}$$

where  $R_1$  and  $R_2$  correspond to RMR (in Watts) at the  $T_{b,inf}$  and  $T_{uc}$ , respectively, and  $T_1$  and  $T_2$  correspond to  $T_b$  at each of these respective  $T_{air}$  values. For several species, the  $T_{b,inf}$  and  $T_{uc}$  occurred between experimental  $T_{air}$  setpoints and consequently, there were few (if any) RMR and  $T_b$  data between these inflection points. Therefore, to ensure

**Table 1**

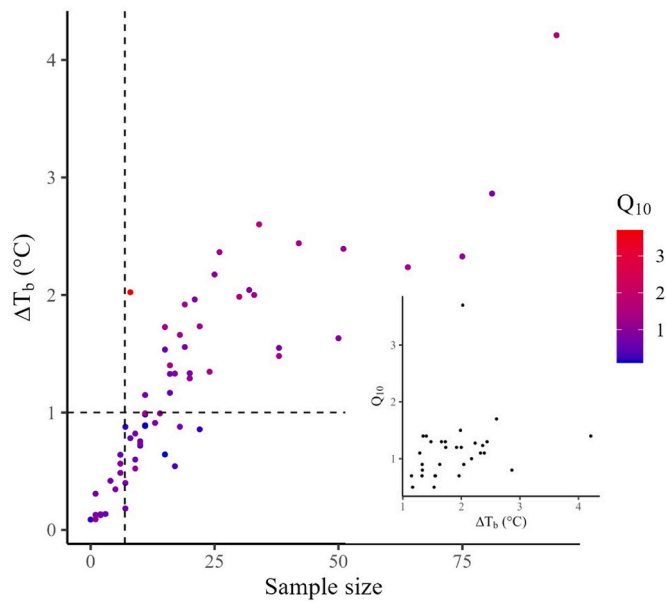
Q<sub>10</sub> values, change in body temperature ( $\Delta T_b$ ) and body mass ( $M_b$ ) of bird species in which  $T_b$  increased within the thermoneutral zone (TNZ). The magnitude of change in  $T_b$  ( $>1$  °C) and the number of data points ( $n \geq 7$ ) for resting metabolic rate (RMR) within this range were used as additional criteria for subsequent phylogenetic analyses. Species included in the final analyses are indicated in bold font.

Species	Order	Climate	Location	$M_b$ (g)	Q <sub>10</sub>	$\Delta T_b$ (°C)	n	Ref
<i>Apus affinis</i>	Apodiformes	Lowland	South Africa	25.9	0.8	0.3	5	5
<i>Apus caffer</i>	Apodiformes	Montane	South Africa	27.3	0.8	0.4	7	5
<i>Bycanistes bucinator</i>	Bucerotiformes	Lowland	South Africa	702.7	1.1	0.1	1	1
<b><i>Tockus leucomelas</i></b>	<b>Bucerotiformes</b>	<b>Arid</b>	<b>South Africa</b>	<b>219.6</b>	<b>1.2</b>	<b>2.0</b>	<b>33</b>	<b>17</b>
<i>Aegotheles cristatus</i>	Caprimulgiformes	Arid	Australia	44	1.4	1.4	16	15
<i>Caprimulgus rufigena</i>	Caprimulgiformes	Arid	South Africa	52.2	1.3	2.2	64	12
<i>Caprimulgus tristigma</i>	Caprimulgiformes	Arid	South Africa	67.3	1.1	2.3	75	12
<i>Chordeiles acutipennis</i>	Caprimulgiformes	Arid	South Africa	50.6	1.3	1.7	18	15
<i>Phalaenoptilus nuttallii</i>	Caprimulgiformes	Arid	North America	44.3	1.3	1.5	38	15
<i>Burhinus capensis</i>	Charadriiformes	Arid	South Africa	434.3	0.9	1.6	50	3
<i>Colius colius</i>	Coliiformes	Arid	South Africa	36.2	0.1	0.9	11	7
<i>Oena capensis</i>	Columbiformes	Arid	South Africa	37.1	1.1	2.4	51	9
<i>Streptopelia capicola</i>	Columbiformes	Arid	South Africa	147.5	1.4	1.3	24	9
<i>Coracias caudatus</i>	Coraciiformes	Arid	South Africa	94.5	0.7	1.5	38	13
<i>Halcyon albiventris</i>	Coraciiformes	Lowland	South Africa	62.1	0.6	0.8	10	5
<i>Merops persicus</i>	Coraciiformes	Lowland	South Africa	46.3	0.1	1.0	11	5
<i>Cuculus gularis</i>	Cuculiformes	Arid	South Africa	110	3.7	2.0	8	13
<i>Acanthagenys rufogularis</i>	Passeriformes	Arid	Australia	41.7	1.3	1.7	15	10
<i>Andropadus importunus</i>	Passeriformes	Lowland	South Africa	30.6	1.1	0.5	9	5
<i>Calandrella cinerea</i>	Passeriformes	Montane	South Africa	25.5	1.3	2.4	42	5
<i>Calendulauda africanoides</i>	Passeriformes	Arid	South Africa	23	0.7	0.1	2	2
<i>Campicoloides bifasciatus</i>	Passeriformes	Montane	South Africa	34.8	0.2	0.9	7	5
<i>Certhilauda albescens</i>	Passeriformes	Arid	South Africa	28.2	0.5	0.1	3	6
<i>Certhilauda subcoronata</i>	Passeriformes	Arid	South Africa	40	0.8	1.3	20	2
<i>Chersomanes albofasciata</i>	Passeriformes	Montane	South Africa	28	0.9	2.0	32	5
<i>Chersomanes albofasciata</i>	Passeriformes	Arid	South Africa	25	0.5	1.2	16	2
<i>Cossypha natalensis</i>	Passeriformes	Lowland	South Africa	29.6	1.5	2.0	30	5
<i>Cracticus torquatus</i>	Passeriformes	Arid	Australia	86	1.2	1.9	19	10
<i>Emberiza capensis</i>	Passeriformes	Arid	South Africa	19.7	0.8	0.5	6	6
<i>Emberiza impetuani</i>	Passeriformes	Arid	South Africa	14.2	0.5	1.5	15	5
<i>Eremopterix verticalis</i>	Passeriformes	Arid	South Africa	16	0.8	0.9	13	2
<i>Euplectes capensis</i>	Passeriformes	Arid	South Africa	30.6	0.7	1.3	16	6
<i>Euplectes orix</i>	Passeriformes	Lowland	South Africa	16.8	0.9	0.7	10	5
<i>Hypargos margaritatus</i>	Passeriformes	Lowland	South Africa	12.5	0.5	0.8	8	6
<i>Laniarius atrococcineus</i>	Passeriformes	Arid	South Africa	46.2	0.6	0.8	9	2
<i>Lanius collaris</i>	Passeriformes	Arid	South Africa	37.3	0.1	0.6	15	2
<i>Lanius collaris</i>	Passeriformes	Lowland	South Africa	40.6	0.3	0.7	10	5
<i>Lanius collaris</i>	Passeriformes	Montane	South Africa	39.7	0.3	0.5	17	5
<b><i>Myrmecocichla formicivora</i></b>	<b>Passeriformes</b>	<b>Montane</b>	<b>South Africa</b>	<b>48.3</b>	<b>1</b>	<b>2.2</b>	<b>25</b>	<b>5</b>
<i>Petrochelidon spilodera</i>	Passeriformes	Montane	South Africa	21	0.2	0.9	22	5
<i>Ploceus ocularis</i>	Passeriformes	Lowland	South Africa	26.1	1.3	1.0	11	5
<i>Ploceus subaureus</i>	Passeriformes	Lowland	South Africa	28.5	1	0.6	6	5
<b><i>Ploceus velatus</i></b>	<b>Passeriformes</b>	<b>Montane</b>	<b>South Africa</b>	<b>28.9</b>	<b>0.7</b>	<b>1.1</b>	<b>11</b>	<b>5</b>
<i>Pomatostomus ruficeps</i>	Passeriformes	Arid	Australia	52	0.8	0.1	2	10
<i>Prinia maculosa</i>	Passeriformes	Arid	South Africa	7.4	0.5	0.6	6	6
<i>Prinia subflava</i>	Passeriformes	Lowland	South Africa	9.1	0.2	0.1	0	5
<i>Pycnonotus tricolor</i>	Passeriformes	Lowland	South Africa	36.8	0.7	0.4	4	5
<b><i>Pycnonotus tricolor</i></b>	<b>Passeriformes</b>	<b>Montane</b>	<b>South Africa</b>	<b>40.2</b>	<b>1.2</b>	<b>1.7</b>	<b>22</b>	<b>5</b>
<b><i>Quelea quelea</i></b>	<b>Passeriformes</b>	<b>Montane</b>	<b>South Africa</b>	<b>17.9</b>	<b>0.8</b>	<b>2.9</b>	<b>81</b>	<b>4</b>
<i>Serinus albogularis</i>	Passeriformes	Arid	South Africa	22.1	1.1	1.0	14	6
<b><i>Spermestes cucullata</i></b>	<b>Passeriformes</b>	<b>Lowland</b>	<b>South Africa</b>	<b>9.1</b>	<b>0.7</b>	<b>1.6</b>	<b>19</b>	<b>5</b>
<i>Spizocorys starki</i>	Passeriformes	Arid	South Africa	17.9	0.7	0.9	18	2
<i>Spreo bicolor</i>	Passeriformes	Montane	South Africa	99.3	0.8	0.1	1	5
<i>Telophorus zeylonus</i>	Passeriformes	Montane	South Africa	66.8	0.5	0.9	11	5
<b><i>Toxostoma curvirostre</i></b>	<b>Passeriformes</b>	<b>Arid</b>	<b>North America</b>	<b>70.6</b>	<b>1.1</b>	<b>1.3</b>	<b>20</b>	<b>14</b>
<i>Zosterops pallidus</i>	Passeriformes	Arid	South Africa	7.7	0.6	0.6	9	2
<b><i>Zosterops pallidus</i></b>	<b>Passeriformes</b>	<b>Arid</b>	<b>South Africa</b>	<b>9.6</b>	<b>0.7</b>	<b>2.0</b>	<b>21</b>	<b>6</b>
<i>Zosterops virens</i>	Passeriformes	Lowland	South Africa	11	0.7	0.3	1	5
<i>Tricholaema leucomelas</i>	Piciformes	Arid	South Africa	34.2	0.6	0.2	7	8
<b><i>Psophodesma varius</i></b>	<b>Psittaciformes</b>	<b>Arid</b>	<b>Australia</b>	<b>54.6</b>	<b>0.9</b>	<b>1.3</b>	<b>17</b>	<b>11</b>
<i>Pterocles burchelli</i>	Pterocliiformes	Arid	South Africa	192.9	1.2	2.4	26	8
<b><i>Pterocles namaqua</i></b>	<b>Pterocliiformes</b>	<b>Arid</b>	<b>South Africa</b>	<b>165.8</b>	<b>1.4</b>	<b>4.2</b>	<b>94</b>	<b>12</b>
<b><i>Megascops kennicottii</i></b>	<b>Strigiformes</b>	<b>Arid</b>	<b>North America</b>	<b>101</b>	<b>1.7</b>	<b>2.6</b>	<b>34</b>	<b>16</b>

Sources: (1) Coulson et al., unpubl; (2) Czenze et al. (2020); (3) Czenze et al. (2021); (4) Freeman et al. (2020); (5) Freeman et al. (2022); (6) Freeman et al. (2024); (7) Freeman et al., unpubl; (8) McKechnie et al. (2016a); (9) McKechnie et al. (2016b); (10) McKechnie et al. (2017); (11) McWhorter et al. (2018); (12) O'Connor et al. (2017); (13) Smit et al. (2018); (14) Smith et al., 2017; (15) Talbot et al. (2017); (16) Talbot et al. (2018); (17) van Jaarsveld et al. (2021).

confidence in the Q<sub>10</sub> values we excluded species with  $\leq 6$  data points between  $T_{uc}$  and  $T_{b,inf}$  or for which  $T_b$  changed by  $< 1$  °C (Fig. 2). The Q<sub>10</sub> data included in the final data set were then mapped onto an avian maximum likelihood tree constructed using phylogenies from [www.bir](http://www.bir)

[tree.org](http://tree.org) (Jetz et al., 2012) using the Hackett backbone (Hackett et al., 2008) following Freeman et al. (2022), using *Mesquite* (Maddison and Maddison, 2014).



**Fig. 2.** Relationship between change in  $T_b$  ( $^{\circ}\text{C}$ ) and the number of data points. Inclusion criterion for  $Q_{10}$  values based on the sample size ( $n \geq 7$ , horizontal dashed line) of data points within the range over which  $Q_{10}$  was calculated and the change in  $T_b$  ( $\Delta T_b \geq 1$ , vertical dashed line). Each species'  $Q_{10}$  is indicated by colour, with higher values indicated in red and low values shown in blue. The inset graph shows the nonsignificant relationship ( $p = 0.17$ ) between the calculated  $Q_{10}$  and change in  $T_b$  for  $\Delta T_b \geq 1$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**3. Results**

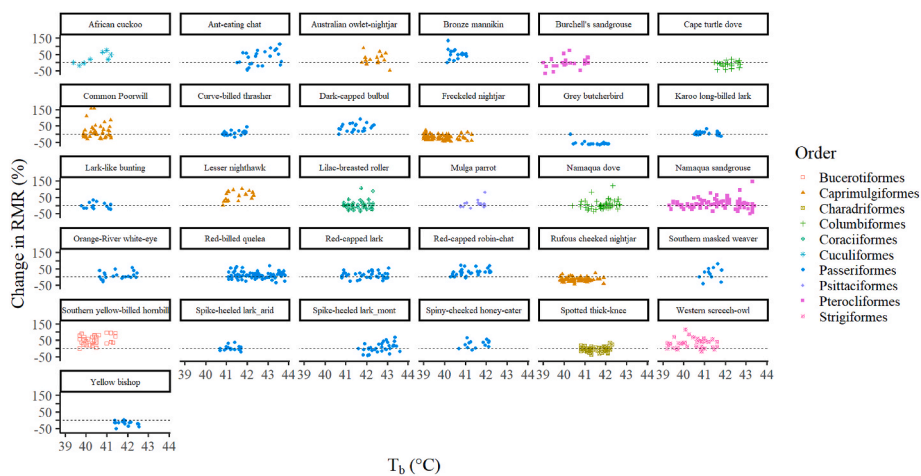
Values of  $T_{uc} - T_{b,inf}$  among species for which a clear  $T_{uc}$  exists ranged from  $-7^{\circ}\text{C}$  to  $11^{\circ}\text{C}$  (Fig. 1) with the Namaqua dove (*Oena capensis*) as an outlier at  $17.7^{\circ}\text{C}$ , whereas for the sandgrouse and two caprimulgids without a  $T_{uc}$  the corresponding range was  $19.6^{\circ}\text{C}$ – $32^{\circ}\text{C}$ . Of the 106 species for which data were available, 58 species representing 13 orders met the criterion of  $T_{uc} - T_{b,inf} > 0$  (for three of which data were available for populations in  $>1$  climatic region; Table 1; Fig. 2). Of these 58 species, 30 (with one, *Chersomanes albofasciata*, occurring in both arid and montane regions), also met our second data inclusion criterion

(Table 1; Figs. 2–4). Among these 30 species, representing 10 orders with  $M_b$  ranging from  $\sim 9$  to  $\sim 430\text{g}$ ,  $Q_{10}$  ranged from 0.5 to 3.8, with  $Q_{10} < 1$  in species including bronze mannikin (*Spermestes cucullata*) and Cape turtle dove (*Streptopelia capicola*) and  $Q_{10} = 1$ – $2$  in species including Namaqua sandgrouse (*Pterocles namaqua*), spotted thick-knee (*Burhinus capensis*) and Western screech owl (*Megascops kennicottii*). In only one species, African cuckoo (*Cuculus gularis*), was  $Q_{10} > 2$  ( $Q_{10} = 3.7$ , Fig. 4). When *C. gularis* was excluded, the mean  $\pm$  SD  $Q_{10}$  for all included species was  $1.02 \pm 0.32$ . The proportional change in RMR between the  $T_{b,inf}$  and  $T_{uc}$  ranged from  $\sim -50$ – $150\%$  (Fig. 3) indicating that RMR decreased for some species (i.e.,  $Q_{10} < 1$ ), but increased on others ( $Q_{10} > 1$ ). However, variation in  $Q_{10}$  did not show any obvious phylogenetic pattern (Fig. 4), with a wide range of values in some orders, including passerines ( $Q_{10} = 0.5$ – $1.5$ ). We found that  $Q_{10}$  values were not significantly related to body mass ( $p = 0.38$ ) or change in  $T_b$  ( $p = 0.17$ ).

**4. Discussion**

Our analyses support the hypothesis that metabolic suppression and reduced Arrhenius effects are a general feature of avian thermoregulation in the heat, with smaller-than-expected increases in RMR with increasing  $T_b$  within the TNZ evident in species representing nine orders. These findings confirm earlier observations by Weathers (1981) and Weathers and Schoenbaechler (1976), but also argue against these authors' conclusion that  $T_b$ -independent thermoneutral RMR is confined to species with  $M_b < 150\text{g}$ ; the four species in our dataset with  $M_b > 150\text{g}$  showed  $Q_{10}$  between 0.9 and 1.4. The phylogenetic diversity of species in which metabolic suppression occurs during heat exposure raises the possibility of this being a pleisiomorphic trait among birds.

Our results also support the notion that hypometabolism during heat exposure reduces the amount of metabolic heat produced and hence heat dissipation requirements (Weathers and Schoenbaechler, 1976). In red-billed queleas (*Quelea quelea*,  $Q_{10} = 0.8$ ), for example, the observed RMR of  $0.44\text{W}$  at  $T_{air} = 43.8^{\circ}\text{C}$  is 72% of the  $0.61\text{W}$  expected if  $Q_{10} = 2.5$ . Similarly, the RMR =  $1.06\text{W}$  of Namaqua sandgrouse (*Pterocles namaqua*,  $Q_{10} = 1.4$ ) at  $T_{air} = 60^{\circ}\text{C}$  is equivalent to 79% of the RMR =  $1.34\text{W}$  expected if  $Q_{10} = 2.5$ . Avoiding increases in metabolic heat production with increasing  $T_b$  has significant implications for birds' water economy by decreasing evaporative cooling requirements (Weathers, 1981; Weathers and Schoenbaechler, 1976). These savings are greatest for species that lack a  $T_{uc}$ ; in *P. namaqua* and *C. rufigena*,  $Q_{10} = 2.5$  for RMR would result in rates of EWL equivalent to 21 and 11%



**Fig. 3.** Relative change in resting metabolic rates (RMR) as body temperature ( $T_b$ ) increases for each of the 30 species which had a  $T_b$  inflection below their upper critical temperature of thermoneutrality ( $T_{uc}$ ) and seven or more weathers data points within this range of air temperatures. Each species' order is indicated by colour and shape of the data points. Data are included for two populations of spike-heeled lark, one inhabiting a desert habitat ("\_arid") and the other montane grasslands ("\_mont"). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

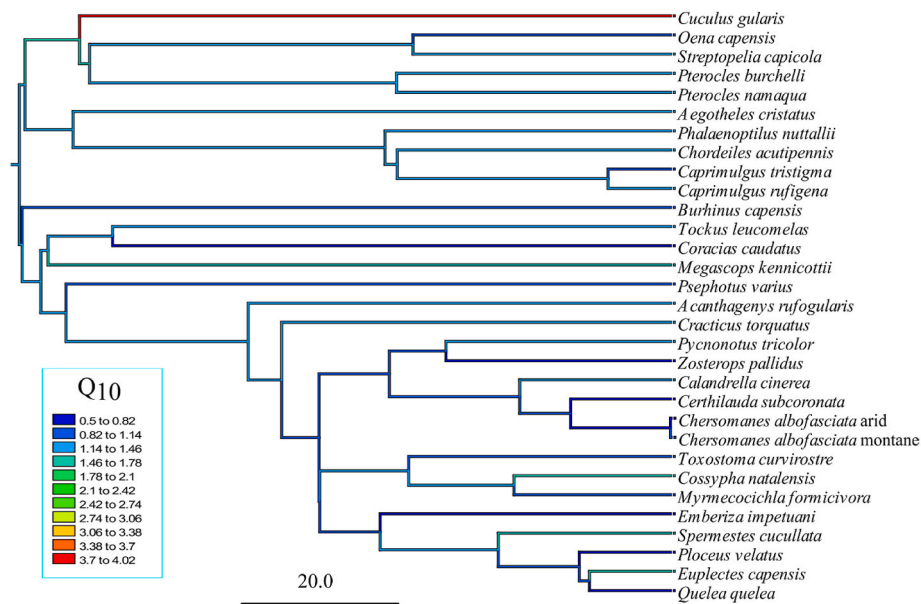


Fig. 4. The phylogenetic tree of the 30 analysed species, pruned from the maximum-likelihood phylogeny (Hackett et al., 2008). Line colour indicates the  $Q_{10}$  value of the species, with red indicating the highest  $Q_{10}$  values ( $\geq 3.7$ ) and dark blue the lowest (0.5 – 0.84). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

higher, respectively, compared to observed EWL at the highest  $T_{air}$  these species reached (Czenze et al., 2021; O'Connor et al., 2017), assuming unchanged ratios of evaporative heat loss to metabolic heat production. The physiological significance of lower-than-expected avian  $Q_{10}$  in terms of water balance was dismissed by Tieleman and Williams (1999). However, their arguments in this regard do not stand up to close scrutiny, as they were modelled closely on those of Snyder and Nestler (1990) and Heldmaier and Ruf (1992) against the use of  $Q_{10}$  values for inferring mechanisms involved in entry into hibernation or torpor, making their applicability to thermoregulation during heat exposure questionable. In reality, avoiding Arrhenius effects on metabolic heat production can equate to significant water savings.

In addition to confirming that reduced Arrhenius effects occur widely among birds, our analysis reveals unexpected interspecific variation in  $Q_{10}$  values. Among ectotherms, variation in  $Q_{10}$  for MR is thought to vary with body size (Barlow 1961; Hölker, 2006; Rao and Bullock, 1954, but see also Scholander et al., 1953). Additionally, variation in ectotherm  $Q_{10}$  has been attributed to acclimatisation to  $T_{env}$  or climate adaptation (DeLiberto et al., 2022; Rao and Bullock, 1954; Addo-Bediako et al., 2002; Nielsen et al., 1999). Sources of variation in the  $Q_{10}$  of MR within the TNZ in endotherms has received far less attention. Our findings here do not support the argument of Weathers and Schoenbaechler (1976) that  $Q_{10}$  values vary with body mass. The possibility of climate adaptation in endotherm  $Q_{10}$  remains to be investigated, but would require a larger data set spanning a wider range of latitudes and habitats than included in our present analysis.

Our data confirm metabolic suppression during heat exposure is widespread across the avian phylogeny, however, too few data are currently available to convincingly test hypotheses concerning adaptive variation in this trait. For instance, in tropical and subtropical lowland habitats characterized by high humidity, where birds have evolved pronounced hyperthermia tolerance (Weathers 1981; Freeman et al., 2022), avoiding Arrhenius effects on metabolic heat production may significantly benefit heat balance during hot weather. One constraint on the availability of suitable data concerns the fact that studies we reviewed for this analysis focussed more strongly on thermoregulation at  $T_{air} > T_b$  than on relationships between  $T_b$  and RMR within the TNZ; whereas increments of 2 °C in experimental  $T_{air}$  were used at  $T_{air} > 40$  °C, larger increments of 4 °C below  $T_{air} = 40$  °C hindered our ability

to accurately estimate  $Q_{10}$  within the TNZ (e.g., Czenze et al., 2020; Whitfield et al., 2015, Table 1, Appendix, Table S1). We recommend future studies exploring Arrhenius effects on avian metabolic rates in the TNZ involve physiological measurements over smaller increments in experimental  $T_{air}$ .

Metabolic heat production associated with heat dissipation pathways, particularly panting, is the primary constraint on the avian capacity to avoid lethal hyperthermia during extreme heat exposure when  $T_{env}$  exceeds  $T_b$  (McKechnie et al., 2021). Avoidance of Arrhenius effects on RMR, similar to those we have demonstrated here within the TNZ, are also likely to confer adaptive benefits at  $T_{env} > T_{uc}$ , even during bouts of activity. However, estimating  $Q_{10}$  for RMR under these conditions is challenging, as doing so requires that increases in overall MR be partitioned into those reflecting increasing  $T_b$  versus those associated with panting or other evaporative cooling pathways. Partitioning increases in RMR in this way may be possible when bouts of panting are intermittent and rates of gas exchange are measured in respirometry systems with rapid equilibrium times (Lasiewski et al., 1966) achieved by combining a small chamber with rapid flow rates (see, for example, the short-term fluctuations in  $CO_2$  production and EWL in Figure 5D of W.A. Talbot et al., 2017).

The evidence we present here for widespread avian hypometabolism during heat exposure confirms that metabolic suppression plays a role in heat tolerance among both birds (Weathers and Schoenbaechler 1976; Weathers 1981) and mammals (Lovegrove et al., 2014; Reher et al., 2018). It also supports arguments that the capacity for hypometabolism is a plesiomorphic trait among both classes (Lovegrove et al., 2014). Although, many unanswered questions about the role of avian hypometabolism during heat exposure remain. First, why do species vary in terms of whether  $T_b$  starts increasing within the TNZ, or only from the  $T_{uc}$  upwards? The lack of a bimodal distribution in  $T_{uc} - T_{b,inf}$  (Fig. 1) suggests a physiological continuum rather than discrete responses. Second, how does the functional role of hypometabolism vary with biotic and abiotic variables? For instance, is there stronger selection for active metabolic suppression in species that forage in exposed microsites and experience higher  $T_{env}$  than species foraging in shaded locations? An additional consideration would be including a wider array of phylogenetically diverse species with an increased range of body masses. Such an approach may increase our understanding around the relationship

between functional traits and hypometabolism. Finally, all the data we included in our analyses here were collected under conditions of low humidity. However, reductions in metabolic production and evaporative cooling requirements are, *a priori*, expected to confer benefits both in terms of water conservation in arid environments as well as hyperthermia avoidance in humid environments where evaporative heat dissipation is impeded, making humidity a variable of interest for future research on avian hypometabolism during heat exposure.

### Data availability

The data included in this analysis are available at <https://data.mendeley.com/datasets/7283n2png5/1>.

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### CRediT authorship contribution statement

**Jochen J. Voges:** Writing – original draft, Formal analysis, Data curation. **Marc T. Freeman:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Blair O. Wolf:** Writing – review & editing, Supervision. **Andrew E. McKechnie:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2024.103924>.

### References

- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2002. Metabolic cold adaptation in insects: a large-scale perspective. *Funct. Ecol.* 16, 332–338.
- Angilletta Jr., M.J., 2009. Thermal acclimation. In: *Thermal Adaptation: A Theoretical and Empirical Synthesis*, pp. 126–156.
- Arrhenius, S., 1889. Über die Reaktionsgeschwindigkeit bei der Inversion von Rohrzucker durch Säuren. *Z. Phys. Chem.* 4.
- Barlow, G.W., 1961. Intra- and interspecific differences in rate of oxygen consumption in gobiid fishes of the genus *Gillichthys*. *Biol. Bull.* 121, 209–229. <https://www.jstor.org/stable/1539427>.
- Christophersen, J., 1973. Basic aspects of temperature action on microorganisms. In: Precht, H., Christophersen, J., Hensel, H., Larcher, W. (Eds.), *Temperature and Life*. Springer-Verlag Berlin Heidelberg, pp. 3–86.
- Czenze, Z.J., Kemp, R., Jaarsveld, B., Freeman, M.T., Smit, B., Wolf, B.O., McKechnie, A. E., 2020. Regularly drinking desert birds have greater evaporative cooling capacity and higher heat tolerance limits than non-drinking species. *Funct. Ecol.* 34, 1589–1600. <https://doi.org/10.1111/1365-2435.13573>.
- Czenze, Z.J., Kemp, R., Jaarsveld, B., Freeman, M.T., Smit, B., Wolf, B.O., McKechnie, A. E., 2020. Regularly drinking desert birds have greater evaporative cooling capacity

- and higher heat tolerance limits than non-drinking species. *Funct. Ecol.* 34, 1589–1600.
- Czenze, Z.J., Freeman, M.T., Kemp, R., van Jaarsveld, B., Wolf, B.O., McKechnie, A.E., 2021. Efficient evaporative cooling and pronounced heat tolerance in an eagle-owl, a thick-knee and a sandgrouse. *Front. Ecol. Evol.* 9, 799302 <https://doi.org/10.3389/fevo.2021.799302>.
- Czenze, Z.J., Freeman, M.T., Kemp, R., van Jaarsveld, B., Wolf, B.O., McKechnie, A.E., 2021. Efficient evaporative cooling and pronounced heat tolerance in an eagle-owl, a thick-knee and a sandgrouse. *Front. Ecol. Evol.* 9, 799302.
- Dawson, W.R., Hudson, J.W., 1970. *Birds*. In: Whittow, G.C. (Ed.), *Comparative Physiology of Thermoregulation Vol.1, Comparative Physiology of Thermoregulation*. Academic Press, New York, pp. 256–277.
- DeLiberto, A.M., Drown, M.K., Ehrlich, M.A., Oleksiak, M.F., Crawford, D.L., 2022. Feeling the heat: variation in thermal sensitivity within and among populations. *J. Exp. Biol.* 225, jeb244831 <https://doi.org/10.1242/jeb.244831>.
- Freeman, M.T., Czenze, Z.J., Schoeman, K., McKechnie, A.E., 2020. Extreme hyperthermia tolerance in the world's most abundant wild bird. *Sci. Rep.* 10, 13098 <https://doi.org/10.1038/s41598-020-69997-7>.
- Freeman, M.T., Czenze, Z.J., Schoeman, K., McKechnie, A.E., 2020. Extreme hyperthermia tolerance in the world's most abundant wild bird. *Sci. Rep.* 10, 13098.
- Freeman, M.T., Czenze, Z.J., Schoeman, K., McKechnie, A.E., 2022. Adaptive variation in the upper limits of avian body temperature. *Proc. Natl. Acad. Sci. USA* 119, 2116645119. <https://doi.org/10.1073/pnas>.
- Freeman, M.T., Czenze, Z.J., Schoeman, K., McKechnie, A.E., 2022. Adaptive variation in the upper limits of avian body temperature. *Proc. Natl. Acad. Sci. USA* 119, 2116645119.
- Freeman, M.T., Coulson, B., Short, J.C., Ngcamphalala, C.A., Makola, M.O., McKechnie, A.E., 2024. Evolution of avian heat tolerance: the role of atmospheric humidity. *Ecology* e4279. <https://doi.org/10.1002/ecy.4279>.
- Freeman, M.T., Coulson, B., Short, C.J., Ngcamphalala, C.A., Makola, M.O., McKechnie, A.E., 2024. Evolution of avian heat tolerance: the role of atmospheric humidity. *Ecology* e4279. <https://doi.org/10.1002/ecy.4279>.
- Geiser, F., 1988. Reduction of metabolism during hibernation and daily torpor in mammals and birds: temperature effect or physiological inhibition? *J. Comp. Physiol. B* 158, 25–37.
- Geiser, F., 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* 66, 239–274.
- Gerson, A.R., McKechnie, A.E., Smit, B., Whitfield, M.C., Smith, E.K., Talbot, W.A., McWhorter, T.J., Wolf, B.O., 2019. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. *Funct. Ecol.* 33, 597–607. <https://doi.org/10.1111/1365-2435.13274>.
- Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 320, 1763–1768. <https://doi.org/10.1126/science.1157704>.
- Heldmaier, G., Ruf, T., 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. *J. Comp. Physiol. B* 162, 696–706. <https://doi.org/10.1007/BF00301619>.
- Hölker, F., 2006. Effects of body size and temperature on metabolism of bream compared to sympatric roach. *Anim. Biol.* Leiden 56, 23–37.
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H.J.Á., Garland, T., 2009. Why tropical forest lizards are vulnerable to climate warming. *Proc. Royal Soc. B* 276, 1939–1948. <https://doi.org/10.1098/rspb.2008.1957>.
- Humphries, M.M., Thomas, D.W., Speakman, J.R., 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418, 313–316. <https://doi.org/10.1038/nature00903>.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K., Mooers, A.O., 2012. The global diversity of birds in space and time. *Nature* 491, 444–448. <https://doi.org/10.1038/nature11631>.
- Karasov, W.H., 1990. Digestion in birds: chemical and physiological determinants and implications. In: Morrison, M.L., Ralph, C.J., Verner, J., Jeh, J.R. (Eds.), *Studies in Avian Biology*. Cooper Ornithological Society, Los Angeles, CA, pp. 391–415.
- Lasiewski, R.C., Acosta, A.L., Bernstein, M.H., 1966. Evaporative water loss in birds - I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *J. Comp. Biochem. Physiol.* 19, 445–457.
- Levesque, D.L., Tuen, A.A., Lovegrove, B.G., 2018. Staying hot to fight the heat-high body temperatures accompany a diurnal endothermic lifestyle in the tropics. *J. Comp. Physiol. B* 188, 707–716. <https://doi.org/10.1007/s00360-018-1160-7>.
- Lovegrove, B.G., Canale, C., Levesque, D., Fluch, G., Řeháková-Petrů, M., Ruf, T., 2014. Are tropical small mammals physiologically vulnerable to Arrhenius effects and climate change? *Physiol. Biochem. Zool.* 87, 30–45. <https://doi.org/10.1086/673313>.
- Lyman, C.P., Willis, J.S., Malan, A., Wang, L.C.H., 1982. Hibernation and torpor in mammals and birds. Academic Press, New York.
- Maddison, D.R., Maddison, W.P., 2014. Chromaseq: A Mesquite Package for Analyzing Sequence Chromatograms.
- McKechnie, A.E., Smit, B., Whitfield, M.C., Noakes, M.J., Talbot, W.A., Garcia, M., Gerson, A.R., Wolf, B.O., 2016a. Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*). *J. Exp. Biol.* 219, 2137–2144. <https://doi.org/10.1242/jeb.146563>.
- McKechnie, A.E., Whitfield, M.C., Smit, B., Gerson, A.R., Smith, E.K., Talbot, W.A., McWhorter, T.J., Wolf, B.O., 2016b. Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *J. Exp. Biol.* 219, 2145–2155. <https://doi.org/10.1242/jeb.138776>.

- McKechnie, A.E., Gerson, A.R., McWhorter, T.J., Smith, E.K., Talbot, W.A., Wolf, B.O., 2017. Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *J. Exp. Biol.* 220, 2436–2444. <https://doi.org/10.1242/jeb.155507>.
- McKechnie, A.E., Gerson, A.R., Wolf, B.O., 2021. Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *J. Exp. Biol.* 224, jeb229211.
- McWhorter, T.J., Gerson, A.R., Talbot, W.A., Smith, E.K., McKechnie, A.E., Wolf, B.O., 2018. Avian thermoregulation in the heat: evaporative cooling capacity and thermal tolerance in two Australian parrots. *J. Exp. Biol.* 221 <https://doi.org/10.1242/jeb.168930>.
- McWhorter, T.J., Gerson, A.R., Talbot, W.A., Smith, E.K., McKechnie, A.E., Wolf, B.O., 2018. Avian thermoregulation in the heat: evaporative cooling capacity and thermal tolerance in two Australian parrots. *J. Exp. Biol.* 221.
- Muggeo, V.M.R., 2008. Segmented: an R package to fit regression models with broken-line relationships. *R. News* 8, 20–25.
- Nielsen, M.G., Elmes, G.W., Kipyatkov, V.F., 1999. Respiratory  $Q_{10}$  varies between populations of two species of *Myrmica* ants according to the latitude of their sites. *J. Insect Physiol.* 45, 559–564.
- O'Connor, R.S., Wolf, B.O., Brigham, R.M., McKechnie, A.E., 2017. Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J. Comp. Physiol. B* 187, 477–491. <https://doi.org/10.1007/s00360-016-1047-4>.
- O'Connor, R.S., Wolf, B.O., Brigham, R.M., McKechnie, A.E., 2017. Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 187, 477–491.
- Pinheiro, J., Bates, D., R Core Team, 2023. Nlme: linear and nonlinear mixed effects models. R package version 3, 1–163. <https://CRAN.R-project.org/package=nlme>.
- Rao, K.P., Bullock, T.H., 1954.  $Q_{10}$  as a function of size and habitat temperature in poikilotherms. *Am. Nat.* 88, 33–44.
- Reher, S., Dausmann, K.H., 2021. Tropical bats counter heat by combining torpor with adaptive hyperthermia. *Proc. Royal Soc. B* 288. <https://doi.org/10.1098/rspb.2020.2059>.
- Reher, S., Ehlers, J., Rabarison, H., Dausmann, K.H., 2018. Short and hyperthermic torpor responses in the Malagasy bat *Macronycteris commersoni* reveal a broader hypometabolic scope in heterotherms. *J. Comp. Physiol. B* 188, 1015–1027. <https://doi.org/10.1007/s00360-018-1171-4>.
- Scholander, P.F., Flagg, W., Walters, V., Irving, L., 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.* 26, 67–92.
- Smit, B., Whitfield, M.C., Talbot, W.A., Gerson, A.R., McKechnie, A.E., Wolf, B.O., 2018. Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance. *J. Exp. Biol.* 221 <https://doi.org/10.1242/jeb.174870>.
- Smith, E.K., O'Neill, J.J., Gerson, A.R., McKechnie, A.E., Wolf, B.O., 2017. Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert songbirds. *J. Exp. Biol.* 220, 3290–3300. <https://doi.org/10.1242/jeb.161141>.
- Snyder, G.K., Nestler, J.R., 1990. Relationships between body temperature, thermal conductance,  $Q_{10}$  and energy metabolism during daily torpor and hibernation in rodents. *J. Comp. Physiol. B* 159, 667–675.
- Talbot, W.A., McWhorter, T.J., Gerson, A.R., McKechnie, A.E., Wolf, B.O., 2017. Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone Caprimulgiformes from two continents. *J. Exp. Biol.* 220, 3488–3498. <https://doi.org/10.1242/jeb.161653>.
- Talbot, W.A., McWhorter, T.J., Gerson, A.R., McKechnie, A.E., Wolf, B.O., 2017. Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone Caprimulgiformes from two continents. *J. Exp. Biol.* 220, 3488–3498.
- Talbot, W.A., Gerson, A.R., Smith, E.K., McKechnie, A.E., Wolf, B.O., 2018. Avian thermoregulation in the heat: metabolism, evaporative cooling and gular flutter in two small owls. *J. Exp. Biol.* jeb171108. <https://doi.org/10.1242/jeb.171108>.
- Talbot, W.A., Gerson, A.R., Smith, E.K., McKechnie, A.E., Wolf, B.O., 2018. Avian thermoregulation in the heat: metabolism, evaporative cooling and gular flutter in two small owls. *J. Exp. Biol.* 221, jeb171108.
- Tieleman, B.I., Williams, J.B., 1999. The role of hyperthermia in the water economy of desert birds. *Physiol. Biochem. Zool.* 72, 87–100. <https://doi.org/10.1086/316640>.
- van Jaarsveld, B., Bennett, N.C., Czenze, Z.J., Kemp, R., Vande Ven, T.M.F.N., Cunningham, S.J., McKechnie, A.E., 2021. How hornbills handle heat: sex-specific thermoregulation in the southern yellow-billed hornbill. *J. Exp. Biol.* 224 <https://doi.org/10.1242/jeb.232777>.
- Weathers, W.W., 1981. Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiol. Zool.* 54, 345–361.
- Weathers, W.W., Schoenbaechler, D.C., 1976. Regulation of body temperature in the Budherygah, *Melopsittacus undulatus*. *Aust. J. Zool.* 24, 39–47.
- Whitfield, M.C., Smit, B., McKechnie, A.E., Wolf, B.O., 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* 218, 1705–1714. <https://doi.org/10.1242/jeb.121749>.
- Whitfield, M.C., Smit, B., McKechnie, A.E., Wolf, B.O., 2015. Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* 218, 1705–1714.
- Williams, J.B., Tieleman, B.I., 2005. Physiological adaptation in desert birds. *Bioscience* 55, 416–425.
- Withers, P.C., 1992. *Comparative Animal Physiology*. International. Saunders College Publishing, New York.