

## REVIEW

# Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling

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## ABSTRACT

Evaporative heat dissipation is a key aspect of avian thermoregulation in hot environments. We quantified variation in avian thermoregulatory performance at high air temperatures ( $T_a$ ) using published data on body temperature ( $T_b$ ), evaporative water loss (EWL) and resting metabolic rate (RMR) measured under standardized conditions of very low humidity in 56 arid-zone species. Maximum  $T_b$  during acute heat exposure varied from  $42.5 \pm 1.3^\circ\text{C}$  in caprimulgids to  $44.5 \pm 0.5^\circ\text{C}$  in passerines. Among passerines, both maximum  $T_b$  and the difference between maximum and normothermic  $T_b$  decreased significantly with body mass ( $M_b$ ). Scaling exponents for minimum thermoneutral EWL and maximum EWL were 0.825 and 0.801, respectively, even though evaporative scope (ratio of maximum to minimum EWL) varied widely among species. Upper critical limits of thermoneutrality ( $T_{uc}$ ) varied by  $>20^\circ\text{C}$  and maximum RMR during acute heat exposure scaled to  $M_b^{0.75}$  in both the overall data set and among passerines. The slope of RMR at  $T_a > T_{uc}$  increased significantly with  $M_b$  but was substantially higher among passerines, which rely on panting, compared with columbids, in which cutaneous evaporation predominates. Our analysis supports recent arguments that interspecific within-taxon variation in heat tolerance is functionally linked to evaporative scope and maximum ratios of evaporative heat loss (EHL) to metabolic heat production (MHP). We provide predictive equations for most variables related to avian heat tolerance. Metabolic costs of heat dissipation pathways, rather than capacity to increase EWL above baseline levels, appear to represent the major constraint on the upper limits of avian heat tolerance.

**KEY WORDS:** Body temperature, Evaporative water loss, Gular flutter, Hyperthermia, Metabolic rate, Panting

## Introduction

The physiology of temperature regulation in wild birds has been of significant interest to comparative biologists for more than 175 years (reviewed by Kendeigh, 1944). The focus on thermoregulation in desert birds and the challenges that extreme heat and aridity impose on animal function largely began with a series of studies in the 1950s (Bartholomew and Dawson, 1953; Dawson, 1954, 1958). This classic early work recognized that animals were inseparable from their environments and that fitness and survival were contingent on the

integration of behavior, morphology and physiology (Kendeigh, 1934; Dawson, 1954). These studies also recognized that understanding thermoregulatory performance required the integration of energy and water balance. Dawson (1954), for example, examined the comparative biology of two species of towhees, one from wetter coastal California and the second from hotter, drier inland deserts, and found distinct differences between the two species in their metabolic and thermal responses to heat exposure and relative ability to offset metabolic and environmental heat loads via evaporative cooling.

Evaporative heat dissipation is vital for avian thermoregulation in hot environments where air temperature ( $T_a$ ) routinely exceeds normothermic body temperature ( $T_b$ ) (Fig. 1), as well as in cooler environments where heat generated as a by-product of activity may cause  $T_b$  to approach lethal limits (Calder and King, 1974; Nilsson and Nord, 2018). Because evaporation is the only process whereby heat can be lost when environmental temperature is higher than  $T_b$ , birds in hot environments face fundamental trade-offs between water conservation and avoiding lethal hyperthermia via evaporative cooling. In addition, trade-offs between thermoregulation and foraging may severely constrain birds' capacities to maintain body mass and successfully reproduce during hot weather (Conradie et al., 2019; Cunningham et al., 2013; du Plessis et al., 2012; van de Ven et al., 2020). Although sometimes overlooked in models of how heat dissipation may limit fitness (e.g. Nilsson and Nord, 2018; Speakman and Król, 2010; Speakman and Król, 2011), integrating the effects of evaporative heat loss and the effects on total water flux are essential for understanding the evolution of thermal physiology among animals living in hot, arid environments.

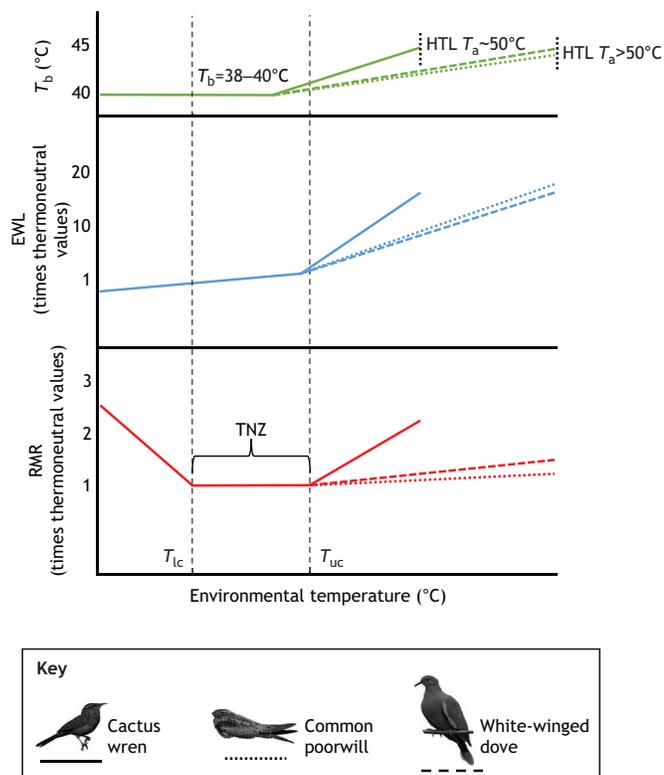
Our current understanding of physiological diversity and thermoregulatory patterns among birds exposed to heat lags behind other areas of avian thermal biology. Whereas large data sets have been compiled to examine the scaling of metabolic rates and evaporative water loss (EWL) at thermoneutral  $T_a$  (e.g. Lasiewski and Dawson, 1967; Londoño et al., 2015; Song and Beissinger, 2020; Williams, 1996), little is known about how avian evaporative cooling at high  $T_a$  and limits to heat tolerance scale with body mass ( $M_b$ ). In two of the few studies that have taken place, Calder and King (1974) reported that maximum  $\text{EWL} = 258.6 M_b^{0.80}$  (where EWL is in  $\text{mg min}^{-1}$  and  $M_b$  is in kg) among 12 species, and Weathers (1981) combined his data for six species spanning  $M_b$  of 12–126 g with those of earlier studies to show that the slope of mass-specific resting metabolic rate (RMR) above the upper critical limit of thermoneutrality ( $T_{uc}$ ) scales negatively with an exponent of approximately  $-0.65$ . More recently, literature data for 27 species were synthesized to model avian EWL at high  $T_a$  in the context of increasing water requirements associated with global heating (McKechnie and Wolf, 2010), and Song and Beissinger (2020) analysed the scaling of EWL at  $T_a = 40^\circ\text{C}$ , which these authors assumed to represent EWL at  $T_a$  above the thermoneutral zone. A related question that has also received relatively little attention concerns how scaling of EWL and RMR vary among groups

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**Fig. 1. Integration of processes related to avian thermoregulation in the heat across functionally diverse taxa.** We compared the responses of the cactus wren (Passeriformes), the common poorwill (Caprimulgiformes) and the white-winged dove (Columbiformes) from the deserts of southwestern North America to illustrate diversity in functional performance. As environmental temperatures approach/exceed body temperature ( $T_b$ ) – near the upper critical limit of thermoneutrality ( $T_{uc}$ ) – metabolic (red line) and environmental heat loads must be dissipated via evaporative water loss (blue line). Increasing heat loads also produce increases in  $T_b$  above normothermic levels (green line). Relative changes in  $T_b$ , evaporative water loss (EWL) and resting metabolic rates (RMR) with increases in environmental temperature are driven by the primary evaporative pathway (panting, gular flutter or cutaneous). In passerines (e.g. cactus wren), panting (continuous lines) is the primary pathway for evaporative heat dissipation and the large metabolic cost adds significantly to the total evaporative demand. In addition, passerines show a steep hyperthermic response and modest heat tolerance limits at air temperature ( $T_a$ )  $\sim$ 50°C when  $T_b$  approaches lethal values. In Columbiformes (e.g. white-winged dove), cutaneous evaporation (dashed lines) provides a very efficient evaporative mechanism with modest metabolic costs and hyperthermic responses, and heat tolerance limits may occur at  $T_a$  exceeding 60°C. Finally, in the Caprimulgiformes (e.g. common poorwill), evaporative water loss occurs primarily via gular flutter (dotted lines) and associated metabolic costs are minimal, allowing for a modest hyperthermic response and heat tolerance limit (HTL) which may also exceed  $T_a$ =60°C. It is important to note that thermoneutral RMR and EWL can vary substantially among taxa (Figs 3 and 6) and the patterns shown here illustrate fractional changes rather than absolute values.  $T_{lc}$ , lower critical limit of thermoneutrality; TNZ, thermoneutral zone.

differing in the relative importance of panting, gular flutter and cutaneous EWL for heat dissipation (Lasiewski and Seymour, 1972; Smit et al., 2018).

Comparative analyses of avian physiological responses to very high  $T_a$  are potentially confounded by methodological differences among studies. Early work on avian thermoregulation in the heat gave little hint of the effectiveness of evaporative cooling. Following work by Terroine and Trautmann (1927), Kendeigh (1939, 1944) and others, Dawson (1954) documented unexpectedly

modest heat tolerance, accompanied by pronounced increases in  $T_b$  and RMR at air temperatures above 35°C, in two species of towhees (Dawson, 1954). Based on observations that (a) in both towhee species RMR increased substantially 2.5- to 3-fold between  $T_a$ =35°C and  $T_a$ =42°C, and (b) none of the species investigated by that time was able to evaporatively dissipate more than 50% of metabolic heat production, Dawson (1954) concluded that ‘Panting thus appears to produce too much heat to be an efficient process for heat dissipation at high air temperatures’. One of the major factors responsible for Dawson reaching this conclusion appears to have been chamber humidity; relative humidities were 45–50% at  $T_a$ =42°C, conditions that probably severely impeded evaporative heat dissipation. Subsequent studies of evaporative cooling varied substantially in terms of chamber humidity (Coulombe, 1970; Dawson and Fisher, 1969; Schleucher, 1999; Tieleman et al., 2002; Weathers and Greene, 1998), a variable that exerts a strong influence on interactions between  $T_b$ , RMR and EWL at high  $T_a$  (Gerson et al., 2014; Lasiewski et al., 1966; van Dyk et al., 2019).

Recently, data on heat tolerance limits and maximum evaporative cooling capacity have become available for 56 bird species spanning a  $M_b$  range of 8–670 g and representing 14 orders (Table S1), all collected under similar conditions of high flow rates and consequently low chamber humidities (<1 kPa, equivalent to a relative humidity of 13.6% at  $T_a$ =40°C, and often considerably lower). These studies have focused on eliciting maximum rates of EWL and thereby determining upper thermoregulatory limits in terms of  $T_b$  and  $T_a$  tolerance. The species are all arid-zone birds from southwestern USA (14 species), arid Australia (nine species) or the Kalahari Desert and Nama Karoo regions of southern Africa (33 species). We use these data to (a) examine the scaling of variables related to avian heat tolerance and quantify variation associated with phylogenetically correlated traits such as the primary avenue of evaporative heat dissipation (panting, gular flutter or cutaneous evaporation), (b) identify correlations between functional traits and (c) quantify the potential error associated with using allometrically predicted values to model water requirements for evaporative cooling.

An improved understanding of the scaling of physiological variables related to evaporative cooling and heat tolerance, and the degree to which these traits are evolutionarily conserved across taxa, is directly relevant to modelling both acute, lethal and chronic, sublethal consequences of exposure to increasingly frequent and severe heat waves. Recent analyses have revealed that the arid-zone avifaunas of several of Earth’s major desert systems are likely to experience greatly increased risks of mortality during extreme heat events (Albright et al., 2017; Conradie et al., 2020). In addition, predictive equations for evaporative water requirements and energy demands during hot weather will be useful for modelling trade-offs between thermoregulation, foraging and nest provisioning (e.g. du Plessis et al., 2012; Sharpe et al., 2019; van de Ven et al., 2020) in species for which detailed physiological data are currently lacking.

## Data and analyses

We compiled data on avian resting metabolism, evaporative cooling,  $T_b$  and heat tolerance for one species of quail (Smith et al., 2015), five caprimulgids (O’Connor et al., 2017; Talbot et al., 2017), six columbids (McKechnie et al., 2016b; Smith et al., 2015), two owls (Talbot et al., 2018), two parrots (McWhorter et al., 2018), one sandgrouse (McKechnie et al., 2016a), one cuckoo and one roller (Smit et al., 2018) and 29 passerines (Czenze et al., 2020; Kemp and McKechnie, 2019; McKechnie et al., 2017; Smit et al., 2018; Smith et al., 2017; Whitfield et al., 2015) from recent

literature (Table S1). In addition, we included unpublished data for one species of each of the following: owl, sandgrouse, barbet, swift, mousebird, kestrel, thick-knee and passerine (Table S1).

In brief, all these data were collected using flow-through respirometry under conditions of low chamber humidity (dewpoints typically  $\sim 0^\circ\text{C}$ ) maintained using higher-than-typical flow rates (for details, see Whitfield et al., 2015). Birds were held in the dark and exposed to stepped profiles of increasing  $T_a$  in increments of  $2^\circ\text{C}$  when  $T_a > 40^\circ\text{C}$ , spending 10–30 min at each  $T_a$  value until stable  $T_b$ , EWL and RMR were reached. These conditions cannot be considered steady-state and the experimental protocol is analogous to the sliding cold exposure protocol used to elicit summit metabolism (Swanson et al., 1996). Steady-state measurements similar to those when quantifying parameters such as basal metabolic rate, where birds typically experience a single  $T_a$  value for 6–8 h, are not feasible when  $T_a$  is well above  $T_b$  and EWL may exceed  $5\% M_b \text{ h}^{-1}$ . Measurements ended when birds showed a loss of balance, lack of coordination or thermoregulatory failure, after which they were allowed to recover with *ad libitum* access to water and food before being released at their sites of capture. One study in which individuals were monitored for several weeks after release revealed no obvious adverse effects of the experimental protocol (Kemp and McKechnie, 2019).

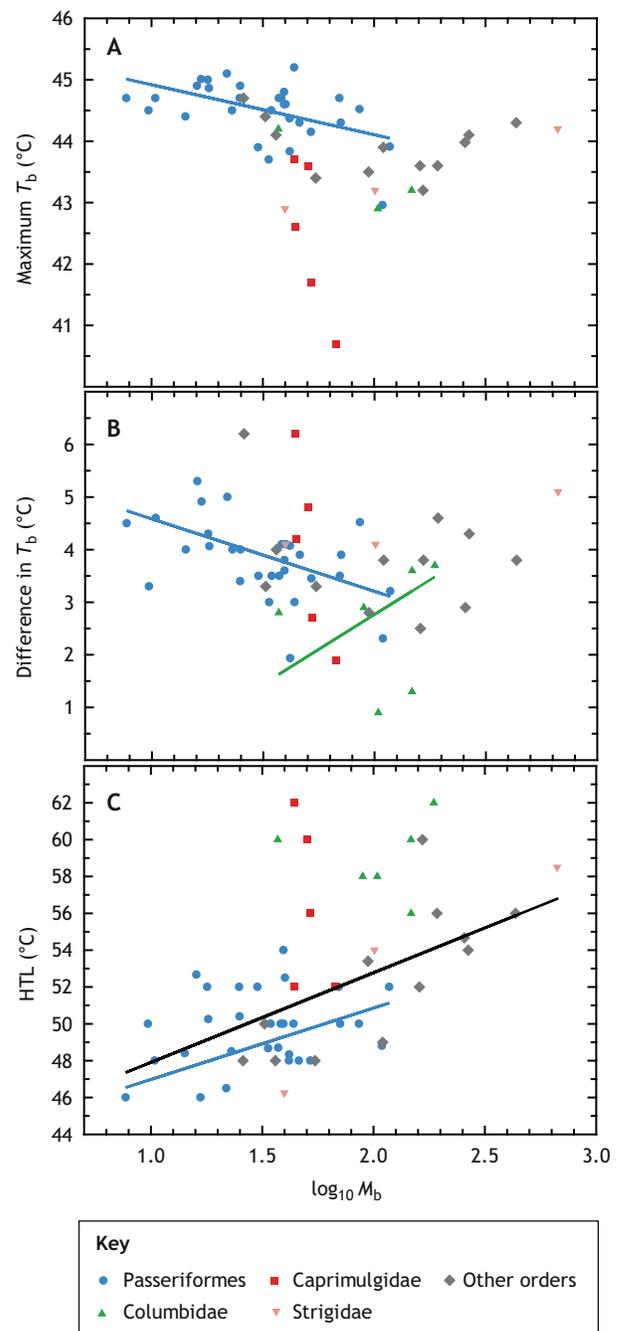
From each study we obtained minimum values for  $T_b$ , EWL and RMR at thermoneutrality (typically  $30\text{--}35^\circ\text{C}$ ), inflection  $T_a$  values above which each variable increased, the slopes of relationships at  $T_a$  above inflections and maximum values associated with thermal endpoints for calm birds, which were taken in all the studies as the heat tolerance limit (HTL), the  $T_a$  associated with loss of balance, coordination or rapid, uncontrolled increases in  $T_b$ , or sudden decreases in EWL or RMR (Whitfield et al., 2015). In these studies, the relationship between EWL and  $T_a$  was modelled using linear models at  $T_a$  above an inflection point. Although a number of authors have argued that the increase in EWL at high  $T_a$  is exponential rather than linear (e.g. Weathers, 1981, 1997), comparisons of the explanatory power of linear and polynomial models suggest little difference (Whitfield et al., 2015), and linear models greatly simplify comparisons among and within species.

### Correlations between functional traits of passerines

A recent comparison of interspecific differences in thermal physiology between regularly drinking and non-drinking passerines from southern Africa revealed that HTL is correlated with evaporative scope, the ratio of maximum EWL to minimum EWL at thermoneutrality (Czenze et al., 2020). To test whether this correlation holds among passerines more broadly, we tested for significant relationships between evaporative scope and residual HTL (HTL scales significantly with  $M_b$ ; Fig. 2) and between the maximum ratio of evaporative heat loss (EHL) to metabolic heat production (MHP). To evaluate relationships between  $T_{uc}$  and increases in EWL above minimal levels and the onset of panting, we also fitted linear models to residual  $T_{uc}$  and inflection  $T_a$  for EWL, and residual  $T_{uc}$  and the  $T_a$  associated with the onset of panting. We restricted these analyses to the 30 passerines in our data set to avoid the potentially confounding effects of EHL via gular flutter or rapid cutaneous evaporation that predominates in several non-passerine orders.

### Potential error associated with use of allometrically predicted values

To quantify the potential error associated with predicting ecologically relevant parameters related to risk of lethal dehydration during extreme weather events on the basis of allometrically predicted rates of EWL rather than species-specific empirical data, we compared cumulative



**Fig. 2. Scaling of avian maximum body temperature and heat tolerance limits.** (A) Maximum body temperature ( $T_b$ ) during acute heat exposure decreases with increasing body mass ( $M_b$ , g) among passerines, with a best-fit model of  $T_b = -0.814 \log_{10} M_b + 45.734$ . (B) Difference between maximum  $T_b$  and normothermic daytime  $T_b$  under thermoneutral conditions ( $\Delta T_b$ ) scales negatively among passerines ( $\Delta T_b = -1.374 \log_{10} M_b + 5.956$ ) but positively among columbids ( $\Delta T_b = 2.646 \log_{10} M_b - 2.525$ ). (C) Heat tolerance limit (HTL, i.e. the maximum air temperature tolerated) scales positively among all species in our data set ( $\text{HTL} = 4.867 \log_{10} M_b + 43.040$ ) as well as within passerines ( $\text{HTL} = 3.873 \log_{10} M_b + 43.107$ ). All regressions are phylogenetically independent models generated using phylogenetic least squares regressions. See 'Data and analyses' section for details.

6 h water loss and time to lethal dehydration [cumulative EWL  $> 15\%$  of  $M_b$ , following Albright et al. (2017) and Conradie et al. (2020)] using both approaches. We modeled evaporative water requirements using a  $T_a$  profile corresponding to an extremely hot day with a  $T_a$

maximum of  $\sim 48^\circ\text{C}$  (data from <https://cals.arizona.edu/azmet/>), for each of 27/30 passerines in our data set. We excluded curve-billed thrasher (*Toxostoma curvirostre*) on account of an atypically high EWL inflection  $T_a$  (Smith et al., 2017) and white-browed sparrow-weaver (*Plocepasser mahali*) and sociable weaver (*Philetairus socius*) on account of EWL inflection  $T_a$  values not being reported in the original study (Whitfield et al., 2015). For each species, we modelled cumulative EWL during the 6 h period between 09:00 and 15:00 h using the actual slope of EWL against  $T_a$ , and then using the slope predicted from a regression model fitted to all passerine data in our data set. We took the actual and predicted survival times for each species as the period over which cumulative EWL remained  $\leq 15\%$   $M_b$ . We used linear regressions forced through the origin to model relationships between predicted and actual values, and calculated 95% prediction intervals for these models following Cooper and Withers (2006).

### Scaling analyses

To quantify relationships between physiological variables and  $M_b$  and to test for correlations between variables, we initially fitted linear regression models in R (<http://www.R-project.org/>). For variables that scaled significantly with  $M_b$ , we used the R package *ape* (Paradis and Schliep, 2018) to test for phylogenetic signal using the parameter  $\lambda$  (Freckleton et al., 2002). We used a consensus phylogenetic tree generated from 1000 trees downloaded from <http://www.birdtree.org> (Jetz et al., 2012) using the Hackett et al. (2008) phylogeny as a backbone. From these trees, a 50% majority-rule consensus tree was calculated using the consensus function in *ape*, as recommended by Rubolini et al. (2015). As significant phylogenetic signal was present for all variables examined, we present phylogenetically informed models based on phylogenetic least squares regressions using the 'gls' function in *ape*. All phylogenetic analyses were performed following Garamszegi (2014). Coefficients are presented with standard error of the mean (s.e.m.) and sample sizes ( $N$ ) refer to number of species.

### Body temperature and heat tolerance limits

The upper limits of  $T_b$  associated with the loss of balance or capacity for coordinated locomotion during acute heat exposure among arid-zone birds ranged from  $40.7^\circ\text{C}$  in freckled nightjars to  $45.2^\circ\text{C}$  in fork-tailed drongos, varying substantially among taxa (Table 1; Fig. 2). There was no overall effect of  $M_b$  on maximum  $T_b$ , but within passerines maximum  $T_b$  scaled significantly and negatively with  $\log_{10} M_b$  (coefficient =  $-0.814 \pm 0.276$ ,  $t = -3.045$ ,  $P = 0.005$ ,  $\lambda = 0.148$ ) (Fig. 2). The difference between normothermic and maximum  $T_b$  (i.e.  $\Delta T_b$ ) ranged from  $0.9^\circ\text{C}$  (mourning dove) to  $6.2^\circ\text{C}$  (Australian owl-nightjar and little swift) and did not scale significantly with  $M_b$  in the overall data set ( $t = -1.952$ ,  $P = 0.056$ ), but showed significant negative scaling within passerines (coefficient =  $-1.374 \pm 0.401$ ,  $t = -3.429$ ,  $P = 0.002$ ,  $\lambda = 0.46$ ). The slope of  $T_b$  as a function of high  $T_a$  varied  $\sim 14$ -fold from  $0.041$  to  $0.576^\circ\text{C } T_b$  per  $^\circ\text{C } T_a$  and was not significantly related to  $M_b$ .

Higher maximum  $T_b$  among passerines is consistent with the more pronounced use of facultative hyperthermia by songbirds compared with other orders (Gerson et al., 2019). A somewhat unexpected pattern to emerge from our analysis is that increases in  $T_b$  above normothermic levels are similar in magnitude in caprimulgids and passerines (Table 1); the fact that maximum  $T_b$  in the songbirds remains well above that of the nightjars reflects the nightjar's considerably lower mean normothermic  $T_b$  ( $38.5$  versus  $40.7^\circ\text{C}$ ). We also found passerine maximum  $T_b$  scaled negatively with  $M_b$  (Fig. 2) as a result of larger  $T_b$  increases in smaller species, with the expected maximum value for a 100 g songbird  $\sim 1^\circ\text{C}$  lower compared with a 10 g species.

The upper limits to  $T_b$  among arid-zone species we report here were associated with loss of balance and coordinated locomotor function. They are thus broadly consistent with criteria for critical thermal maxima (Lutterschmidt and Hutchison, 1997), although they should be viewed as conservative estimates of maximum values that avoid lethal consequences (McKechnie and Wolf, 2019). Maximum  $T_b$  values among these arid-zone species are lower than the known range of avian lethal  $T_b$ ,  $46$ – $48^\circ\text{C}$  (Arad and Marder, 1982; Dawson, 1954; Randall, 1943). A few authors have reported tolerance of  $T_b$  approaching  $46^\circ\text{C}$  (Dmi'el and Tel-Tzur, 1985),  $47^\circ\text{C}$  (Weathers, 1997) or even  $48$ – $49^\circ\text{C}$  (Freeman et al., 2020) in passerines without any apparent adverse effects, but arid-zone species generally appear not to attain such high values.

Heat tolerance limits (i.e. the  $T_a$  associated with compromised locomotor ability or thermoregulatory failure) varied by  $16^\circ\text{C}$  from  $46$  to  $62^\circ\text{C}$  (Table 1), with significant positive scaling in the overall data set (coefficient =  $4.867 \pm 1.038$ ,  $t = 4.687$ ,  $P < 0.001$ ,  $\lambda = 1.04$ ; Fig. 2). HTL also scaled significantly within passerines (coefficient =  $3.873 \pm 1.118$ ,  $t = 3.463$ ,  $P = 0.002$ ,  $\lambda = 0.88$ ; Fig. 2). The HTL values we analyse here represent the maximum  $T_a$  values that birds endured for short periods. In addition to confirming that HTLs are consistently much higher in caprimulgids and columbids compared with songbirds, our analysis reveals that HTL scales positively with  $M_b$  in both the overall data set and within passerines. This finding is surprising as, *a priori*, the higher surface area to volume ratios of smaller species might be expected to permit more rapid heat dissipation and hence tolerance of higher environmental temperatures. One possibility is that this pattern arises from the non-steady-state nature of the stepped profile of progressively higher  $T_a$  used in all the studies included here and the greater thermal inertia of larger birds. However, the fact that the largest species for which data are available, a 434 g thick-knee and 668 g owl, had  $\Delta T_b$  and maximum  $T_b$  values similar to those of much smaller species (Fig. 2) argues against the possibility of these scaling patterns representing an experimental artefact.

The evolutionarily conserved differences in HTL among taxa are, we suspect, functionally related to broad ecological differences. For instance, the high HTLs of several nightjars are consistent with these nocturnal birds sometimes spending the entire diurnal period

**Table 1. Summary of normothermic and hyperthermic body temperature ( $T_b$ ), the difference between normothermic and hyperthermic values ( $\Delta T_b$ ) and heat tolerance limit among passerines, columbids, caprimulgids and other orders**

Taxon	Normothermic $T_b$ ( $^\circ\text{C}$ )	Maximum $T_b$ ( $^\circ\text{C}$ )	$\Delta T_b$ ( $^\circ\text{C}$ )	Heat tolerance limit ( $^\circ\text{C}$ )
Passerines	$40.7 \pm 0.6$	$44.5 \pm 0.5$	$3.8 \pm 0.7$	$49.7 \pm 2.0$ (46–54)
Columbids	$40.9 \pm 0.4$	$43.4 \pm 1.0$	$2.5 \pm 1.2$	$59.0 \pm 2.1$ (56–62)
Caprimulgids	$38.5 \pm 0.6$	$42.5 \pm 1.3$	$4.0 \pm 1.7$	$56.4 \pm 4.6$ (52–62)
Other	$39.9 \pm 0.9$	$43.8 \pm 0.5$	$3.9 \pm 0.5$	$52.5 \pm 4.2$ (46–60)

Heat tolerance limit is the maximum air temperature ( $T_a$ ) tolerated during acute heat exposure. See main text for details. Values are presented as means  $\pm$  s.d. with ranges in parentheses.

on the ground exposed to intense solar radiation and operative temperatures 10–15°C above  $T_b$ , particularly when breeding (Grant, 1982; O'Connor et al., 2018). The even higher average HTL of doves and pigeons, reflecting their capacity to rapidly dissipate heat cutaneously at little metabolic cost (Calder and Schmidt-Nielsen, 1966; Webster and Bernstein, 1987), is consistent with the ground-foraging habits of granivorous species, their ability to depress  $T_b$  to cool their eggs during incubation (Russell, 1969; Walsberg and Voss-Roberts, 1983) and their strong dependence on surface water (Fisher et al., 1972; Willoughby and Cade, 1967).

Our analysis of thermoregulatory traits among passerines confirms the correlation between evaporative scope and HTL recently reported for 17 southern African species by Czenze et al. (2020) is also apparent in a data set spanning two other arid regions, Australia and North America. The weaker but nevertheless significant relationship between maximum EHL/MHP and HTL further suggests that the comparative efficiency of evaporative cooling processes is also a determinant of the highest environmental temperatures songbirds can tolerate (Fig. 3).

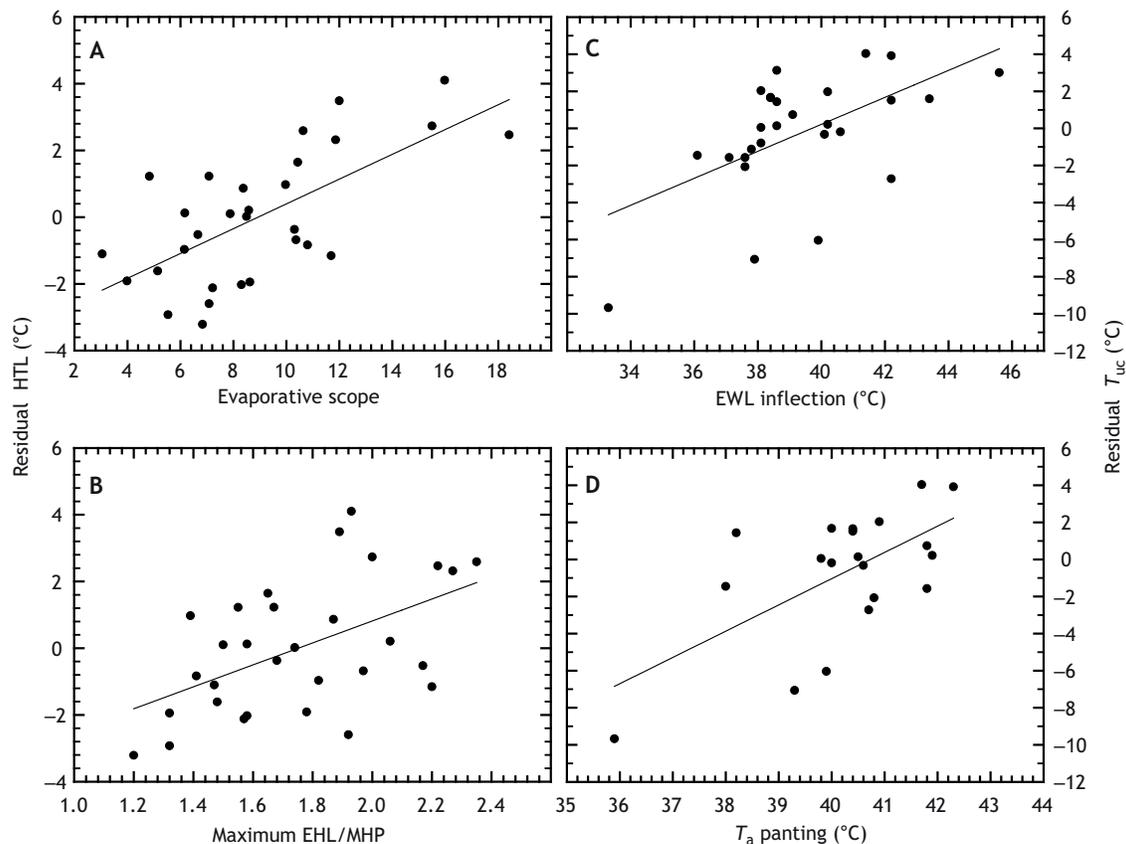
### Evaporative water loss

Minimum EWL at thermoneutral  $T_a$  scaled positively with  $\log_{10} M_b$  (Fig. 4; coefficient=0.825±0.061,  $t=13.423$ ,  $P<0.001$ ,  $\lambda=0.46$ ). Significant scaling was also evident for passerines (coefficient=0.808±0.102,  $t=7.872$ ,  $P<0.001$ ,  $\lambda=0.58$ ) and columbids

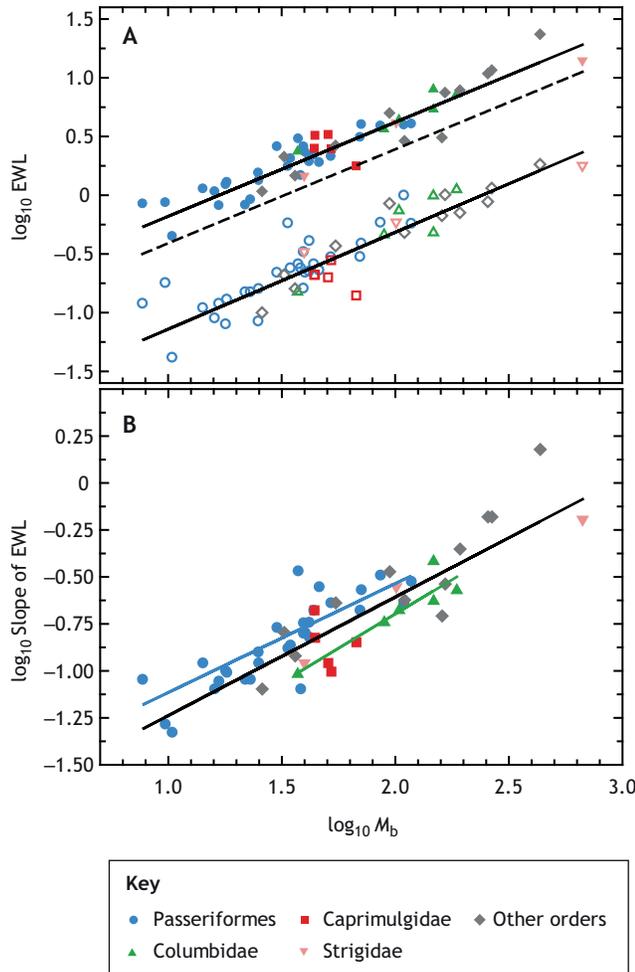
(coefficient=1.108±0.255,  $t=4.349$ ,  $P=0.012$ ,  $\lambda=0.77$ ). Overall scaling of maximum EWL involved a very similar exponent (Fig. 4; coefficient=0.801±0.033,  $t=24.004$ ,  $P<0.001$ ,  $\lambda=-0.12$ ). Maximum EWL of passerines had a shallower slope (coefficient=0.708±0.058,  $t=11.916$ ,  $P<0.001$ ,  $\lambda=-0.20$ ), as did that of doves (coefficient=0.740±0.134,  $t=5.537$ ,  $P=0.005$ ,  $\lambda=-0.12$ ) (Fig. 4). Both maximum EWL and minimum EWL expressed as percentages of  $M_b$  decreased with increasing  $M_b$  (Fig. 5).

Inflection  $T_a$  values above which EWL increased varied by >10°C, with values for most species between 36 and 43°C. These inflection  $T_a$  values did not scale significantly with  $M_b$ . The slope of increasing EWL above these inflection points was strongly dependent on  $M_b$  in the overall data set (coefficient=0.631±0.051,  $t=12.426$ ,  $P<0.001$ ,  $\lambda=0.76$ ), with significant effects of  $M_b$  for passerines (coefficient=0.580±0.075,  $t=7.770$ ,  $P<0.001$ ,  $\lambda=0.54$ ) and columbids (coefficient=0.730±0.163,  $t=4.466$ ,  $P=0.011$ ,  $\lambda=0.44$ ). Evaporative scope varied widely, from 3.1 in pyrrhuloxias to 18.4 in sociable weavers (*P. socius*), with considerable overlap among taxa (Fig. 6).

The remarkably similar scaling of thermoneutral EWL and maximum EWL during acute heat exposure (exponents of 0.825 and 0.801, respectively; Fig. 4) occurs despite large differences in evaporative scope among and within taxa (Fig. 6). Minimum EWL predicted from a regression fitted to our data is considerably higher (75% for a 10 g species, 108% for a 100 g species) than values predicted for desert birds by Williams (1996). This difference, we suspect, reflects



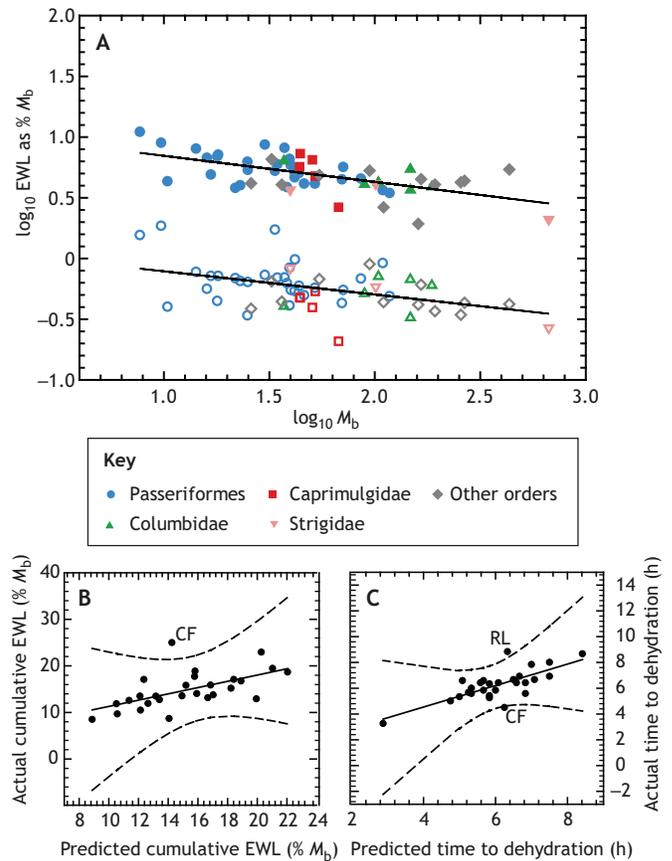
**Fig. 3.** Among passerines, several variables related to heat tolerance were correlated in a manner suggestive of functional links. Both evaporative scope [i.e. maximum evaporative water loss (EWL)/minimum thermoneutral EWL; A] and maximum evaporative heat loss/metabolic heat production (B) significantly predicted residual heat tolerance limit ( $HTL_{resid}$ ) calculated from a linear regression of HTL versus body mass ( $M_b$ ). Some correlations were weaker than expected: residual upper critical limit of thermoneutrality ( $T_{uc}$ ) was only weakly correlated with the inflection air temperature ( $T_a$ ) above which EWL rapidly increased above thermoneutral levels (C) and the  $T_a$  value associated with the onset of panting (D). Continuous lines indicate significant phylogenetically informed linear model (see text for coefficients).



**Fig. 4. Scaling of avian evaporative water loss.** (A) Minimum thermoneutral evaporative water loss ( $EWL_{min}$ ,  $g\ h^{-1}$ ; open symbols) and maximum evaporative water loss ( $EWL_{max}$ ,  $g\ h^{-1}$ ; filled symbols) during acute heat exposure increase with body mass. The continuous lines are phylogenetically independent regression models describing the relationship with body mass ( $M_b$ , g):  $\log_{10}EWL_{min}=0.825\log_{10}M_b-1.966$  and  $\log_{10}EWL_{max}=0.801\log_{10}M_b-0.981$ . Additional significant scaling relationships which for clarity have not been plotted are for  $EWL_{min}$  in passerines ( $\log_{10}EWL_{min}=0.808\log_{10}M_b-1.893$ ) and columbids ( $\log_{10}EWL_{min}=1.108\log_{10}M_b-2.507$ ) and  $EWL_{max}$  in passerines ( $\log_{10}EWL_{max}=0.701\log_{10}M_b-0.813$ ) and columbids ( $\log_{10}EWL_{max}=0.740\log_{10}M_b-0.819$ ). The dashed line is the scaling relationship for avian  $EWL_{max}$  reported by Calder and King (1974). (B) Slope of increases in avian evaporative water loss ( $EWL$ ,  $g\ h^{-1}\ ^\circ C^{-1}$ ) at high air temperatures scales positively with  $M_b$ , with a best-fit phylogenetically independent regression of  $\log_{10}slope=0.631\log_{10}M_b-1.869$  (continuous black line). For passerines,  $\log_{10}slope=0.580\log_{10}M_b-1.695$  (blue line) and for columbids,  $\log_{10}slope=0.730\log_{10}M_b-2.157$  (green line).

several factors. First, data included in the present analysis were typically active-phase measurements at  $T_a \approx 35^\circ C$ , compared with the combination of active- and rest-phase measurements at  $T_a \approx 25^\circ C$  analysed by Williams (1996). Second, although Williams (1996) excluded measurements from studies involving low flow rates and hence elevated chamber humidities, a cursory examination of his sources suggests that, in general, humidity was often well above the very low levels characteristic of the present data set.

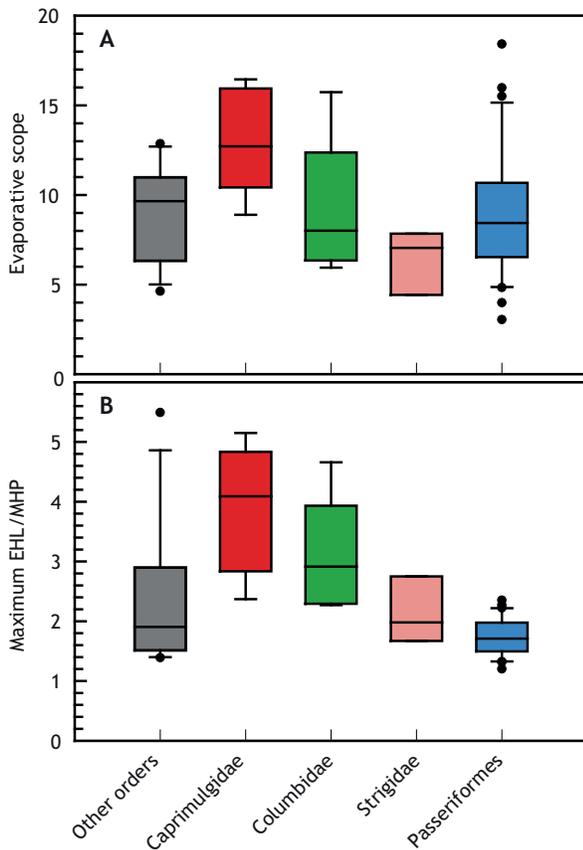
Calder and King (1974) presented an analysis of maximum EWL in 12 species ranging in  $M_b$  from 11 g zebra finches to 88 kg ostriches. The scaling exponent these authors reported (0.80) is identical to ours, but the intercept of our equation is 70% higher



**Fig. 5. Scaling of evaporative water loss as a percentage of body mass.** (A) Rates of evaporative water loss ( $EWL$ ,  $\% M_b\ h^{-1}$ ) during acute heat exposure expressed as percentage body mass ( $M_b$ ) decrease with increasing  $M_b$ . The relationship between maximum EWL ( $EWL_{max}$ ; filled symbols) and  $M_b$  (g) is described by the conventional model  $\log_{10}EWL_{max}=-0.215\log_{10}M_b+1.061$ , and the corresponding model for minimum EWL ( $EWL_{min}$ ; open symbols) is  $\log_{10}EWL_{min}=-0.191\log_{10}M_b+0.086$ . For passerines, estimates of water requirements for evaporative cooling (B) and time to lethal dehydration (C) based on allometrically predicted slopes for EWL as a function of air temperature (see Fig. 4) can differ substantially from values calculated from species-specific empirical data. (B) Cumulative EWL estimated for a 6 h period on a very hot day (see text for details) expressed as a percentage of  $M_b$ . (C) Time taken to reach a lethal dehydration limit of 15% of  $M_b$ . Of the 27 passerines species modelled here, common fiscals (*Lanius collaris*; indicated as 'CF') and red larks (*Calendulauda burra*; 'RL') fell outside 95% prediction intervals (dashed lines). The continuous line in each panel represents a linear regression forced through the origin.

(Fig. 4). The negative scaling of maximum EWL expressed as a percentage of  $M_b$  (Fig. 5), such that a 5 g bird loses the equivalent of  $7.6\% M_b\ h^{-1}$  compared with  $3.0\% M_b\ h^{-1}$  in a 500 g bird, is the physiological basis for smaller species being more vulnerable to lethal dehydration during extreme heat events compared with larger species (Albright et al., 2017; McKechnie and Wolf, 2010). Our analysis of EWL slope at high  $T_a$  supports the findings of Song and Beissinger (2020), but also reveals taxonomic variation whereby EWL increases more rapidly in passerines compared with similarly sized columbids (Fig. 4), reflecting the lower efficiency of panting compared with predominantly cutaneous evaporation. For a given incremental increase in  $T_a$ , a greater increase in EWL is necessary in songbirds to dissipate environmental heat loads and the additional metabolic heat generated by panting.

Evaporative scope broadly overlaps across taxa, with both the highest and lowest values in our data set occurring in passerines (Fig. 6), a taxon



**Fig. 6. Phylogenetic variation in avian evaporative cooling capacity.**

(A) Evaporative scope during acute heat exposure (ratio of maximum to minimum evaporative water loss) and (B) maximum ratio of evaporative heat loss to metabolic heat production (EHL/MHP) vary substantially among avian taxa. Data included in the box-and-whisker plots are 30 songbirds (Passeriformes), three owls (Strigiformes), six doves and pigeons (Columbiformes), four nightjars and one owl-nightjar (Caprimulgiformes) and 12 pooled representatives of ten other orders: Pterocliiformes, Cuculiformes, Coraciiformes, Apodiiformes, Piciformes, Coliiformes, Falconiformes, Charadriiformes, Galliformes and Psittaciformes.

that lacks gular flutter or major cutaneous contributions to evaporative cooling (Dawson, 1982; Wolf and Walsberg, 1996). This high degree of overlap suggests that the primary avenue of evaporation *per se* (i.e. panting, gular flutter or cutaneous evaporation) is not the major determinant of the maximum rate of EWL a bird can achieve. The only group whose average evaporative scope is noticeably higher than those of other taxa is the caprimulgids (Fig. 6), in which gular flutter predominates (Cowles and Dawson, 1951; Dawson and Fisher, 1969; Talbot et al., 2017), but this probably reflects the disproportionately large gapes of nightjars. The broad similarities in evaporative scope across taxa varying in the primary avenue of evaporative heat dissipation contrast markedly with taxonomic variation in maximum EHL/MHP (Fig. 6) and HTL (Fig. 2), revealing that the relative metabolic costs of heat dissipation pathways are the primary determinant of upper limits to evaporative cooling capacity and heat tolerance.

Recent studies predict large increases in the risks of lethal dehydration during hot weather for birds inhabiting the deserts of southwest North America and arid Australia when the cumulative evaporative cooling requirements of resting birds in shaded microsites exceed lethal dehydration limits (Albright et al., 2017; Conradie et al., 2020). Our comparison of cumulative EWL and associated survival times based on species-specific empirical data with those estimated

using allometrically predicted values suggests that predicted values are often suitable for estimating water requirements of species for which neither empirical data nor detailed biophysical models (e.g. Kearney et al., 2016) are available. In a few cases, however, species deviate substantially from these predicted values. For example, using allometrically predicted values (Fig. 5) resulted in a substantial underestimate of cumulative water losses and an over-estimate of survival time by common fiscals and an under-estimate of survival time in the red lark (*Calendulauda burra*), a threatened species restricted to a small area in southern Africa (Dean and Ryan, 2005).

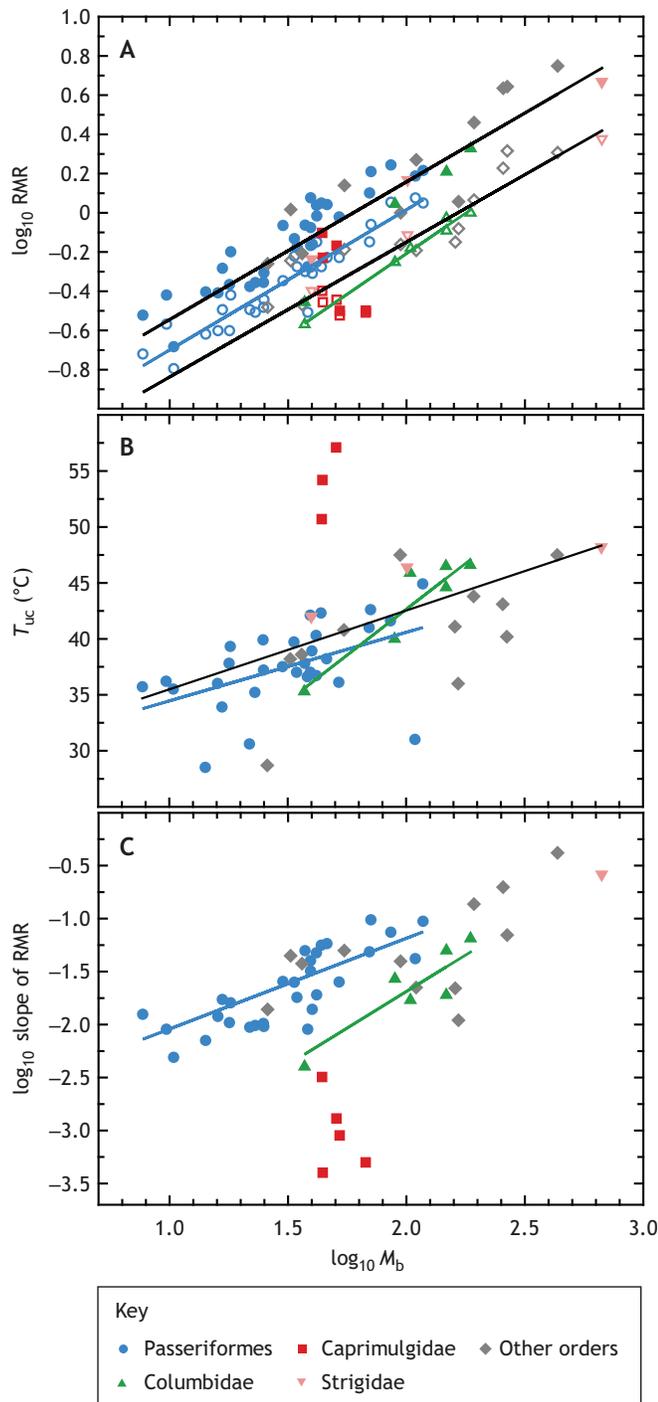
### Resting metabolic rate

Minimum RMR at thermoneutral  $T_a$  scaled positively and significantly with  $M_b$  (Fig. 7; coefficient=0.688±0.032,  $t=21.775$ ,  $P<0.001$ ,  $\lambda=0.98$ ) in the overall data set, as well as within passerines (coefficient=0.715±0.043,  $t=16.496$ ,  $P<0.001$ ,  $\lambda=0.77$ ) and columbids (coefficient=0.827±0.046,  $t=18.062$ ,  $P<0.001$ ,  $\lambda=1.12$ ). Maximum RMR at high  $T_a$  scaled positively with  $M_b$  (Fig. 7, coefficient=0.748±0.052,  $t=14.275$ ,  $P<0.001$ ,  $\lambda=0.92$ ). Maximum RMR also scaled significantly with  $M_b$  in passerines (coefficient=0.738±0.055,  $t=13.34$ ,  $P<0.001$ ,  $\lambda=0.63$ ) and columbids (coefficient=0.788±0.000,  $t=309,704.05$ ,  $P<0.001$ ,  $\lambda=1.98$ ).

Minimum daytime RMRs for passerines were 30–50% higher than values predicted from the overall data set, qualitatively consistent with the ~12% significantly higher basal metabolic rates of passerines compared with non-passerines (Londoño et al., 2015). Maximum RMR shows much greater variability around the phylogenetically independent regression line (Fig. 7). It is striking, for instance, that the maximum RMR values of several caprimulgids were below the minimum RMR of most species. The maximum RMR of 0.317 W in the 67 g freckled nightjar is equivalent to just 19.6% of the maximum RMR of the 71 g curve-billed thrasher, reflecting the extremely high efficiency of gular flutter in caprimulgids compared with panting in passerines.

Inflection  $T_a$  values for RMR, which we interpret as  $T_{uc}$ , varied widely from ~29°C in lark-like buntings (*Emberiza impetuani*) to ~48°C in spotted eagle-owls (*Bubo africanus*; Fig. 7). In addition, significant inflections in RMR were evident only at  $T_a>50^\circ\text{C}$  in three species of caprimulgids.  $T_{uc}$  scaled positively and significantly with  $M_b$  (Fig. 7; coefficient=7.045±1.638,  $t=4.300$ ,  $P<0.001$ ) and although there were differences in slope among orders, there was low phylogenetic signal ( $\lambda=0.99$ ). In passerines,  $T_{uc}$  scaled significantly and positively with  $M_b$  (coefficient=6.130±2.078,  $t=2.952$ ,  $P=0.006$ ,  $\lambda=0.34$ ), and the same was true for columbids (coefficient=16.405±3.200,  $t=5.127$ ,  $P=0.007$ ,  $\lambda=1.33$ ).

The positive scaling of  $T_{uc}$  among passerines and columbids (Fig. 6) supports Weathers' (1981) observation that the interval between  $T_{uc}$  and the  $T_a$  at which  $T_a=T_b$  decreases with increasing  $M_b$ . Our analysis also offers an opportunity to evaluate recent suggestions that the  $T_{uc}$  of endotherms provides an index of upper thermal tolerance appropriate for global-scale analyses of climate change vulnerability (Araújo et al., 2013; Khaliq et al., 2015, 2014). Even after excluding caprimulgids, which have exceptionally shallow slopes of RMR against  $T_a$  and discernible inflections only at  $T_a\geq 50^\circ\text{C}$ , there remains interspecific variation in  $T_{uc}$  of ~20°C (Fig. 7). The magnitude of this variation among species occupying similar climates and similar latitudes, together with the marked differences among taxa in evaporative cooling efficiency at  $T_a>T_{uc}$ , argues against the notion that  $T_{uc}$  is a meaningful proxy for avian upper thermal tolerance limits (Khaliq et al., 2014, 2015, 2017). Moreover, ~40% of species in our data set have  $T_{uc}>40^\circ\text{C}$ . This fraction is far greater than that shown in fig. 1 of Khaliq et al. (2014),



**Fig. 7. Scaling of avian resting metabolic rates.** (A) Thermoneutral resting metabolic rate ( $RMR_{min}$ , W; open symbols) and maximum resting metabolic rate ( $RMR_{max}$ ; filled symbols) during acute heat exposure increase with increasing body mass ( $M_b$ , g). The black continuous lines are phylogenetically independent regressions:  $\log_{10}RMR_{min}=0.688\log_{10}M_b-1.525$  and  $\log_{10}RMR_{max}=0.748\log_{10}M_b-1.400$ . Also shown are regressions for  $RMR_{min}$  in passerines (blue line,  $\log_{10}RMR_{min}=0.715\log_{10}M_b-1.414$ ) and columbids (green line,  $\log_{10}RMR_{min}=0.827\log_{10}M_b-1.862$ ). The  $RMR_{max}$  of passerines was also significantly related to  $M_b$  ( $\log_{10}RMR_{max}=0.749\log_{10}M_b-1.273$ ), although this line is not shown. (B) Upper critical limit of thermoneutrality ( $T_{uc}$ ) was significantly related to  $M_b$  in the overall data set (black line,  $T_{uc}=7.045\log_{10}M_b+28.442$ ) as well as among passerines (blue line,  $T_{uc}=6.130\log_{10}M_b+28.328$ ) and columbids (green line,  $T_{uc}=16.405\log_{10}M_b+9.824$ ). (C) Slope of RMR at air temperature above  $T_{uc}$  ( $W\ ^\circ C^{-1}$ ) was positively related to  $M_b$  (g) in passerines (blue line,  $\log_{10}\text{slope}=0.856\log_{10}M_b-2.897$ ) and columbids (green line,  $\log_{10}\text{slope}=1.379\log_{10}M_b-4.4460$ ).

reflecting the inclusion by these authors of a large number of data from studies where RMR was not measured over a wide enough range of  $T_a$  to reliably estimate  $T_{uc}$  (Wolf et al., 2017), as well as the combination of active- and rest-phase values included in the former study. Our analysis also reveals that  $T_a=40^\circ C$  often does not fall above avian  $T_{uc}$ , as recently assumed by Song and Beissinger (2020).

One of the clearest patterns of evolutionarily conserved variation to emerge from our analysis concerns the slope of RMR at  $T_a>T_{uc}$ . Models fitted to slopes of RMR as a function of  $T_a>T_{uc}$  revealed significant variation in intercepts, indicating that separate scaling relationships are needed for different taxa (Fig. 7). RMR slope scaled significantly and positively with  $M_b$  in passerines (coefficient= $0.856\pm 1.121$ ,  $t=7.070$ ,  $P<0.001$ ,  $\lambda=0.78$ ) and columbids (coefficient= $1.379\pm 0.324$ ,  $t=4.255$ ,  $P=0.013$ ,  $\lambda=1.62$ ). Slopes are five to 10 times higher in passerines compared with columbids, with virtually no increase in RMR above a  $T_{uc}$  in several caprimulgids. In a comparative analysis of thermoregulation in 19 passerines and seven non-passerines, Weathers (1981) found that the slope of mass-specific RMR at high  $T_a$  (in  $mW\ g^{-1}\ h^{-1}\ ^\circ C^{-1}$ ), which he designated the coefficient of heat strain, scaled to  $12.5M_b^{-0.65}$ . Fitting a conventional regression to mass-specific slopes for the passerines in our data set revealed significant negative scaling to  $M_b^{-0.36}$ , with predicted slopes 2.4- to 4.7-fold higher over the  $M_b$  range of 10–100 g compared with those predicted by Weathers' equation. We suspect one reason for these marked differences concerns the ranges of  $T_a$  over which RMR was measured: Weathers' (1981) data for six species involved maximum  $T_a$  values between 42 and 44.5°C, with similar  $T_a$  ranges in many of the published studies from which he obtained data. Consequently, few of the slopes included by Weathers (1981) are based on conditions where birds were maintaining  $T_b<T_a$ .

Maximum EHL/MHP varied from 1.20 in yellow-plumed honeyeaters (*Lichenostomus ornatus*) to 5.49 in Namaqua sandgrouse (*Pterocles namaqua*). Considerable among-taxa variation was evident, with values for caprimulgids and columbids consistently and substantially higher than those for passerines (Fig. 6). The range of maximum EHL/MHP values for other orders (1.39–5.49) exceeded the combined range for passerines, owls, nightjars and doves (1.20–5.15; Fig. 5).

### Functional aspects of passerine heat tolerance

Among the passerines in our data set, residual HTL was significantly correlated with both evaporative scope (coefficient= $0.352\pm 0.077$ ,  $t=4.592$ ,  $P\leq 0.001$ ,  $\lambda=0.487$ ) and maximum EHL/MHP (coefficient= $2.976\pm 1.026$ ,  $t=2.901$ ,  $P=0.007$ ,  $\lambda=0.361$ ; Fig. 3). The  $T_{uc}$  occurred at  $T_a$  values  $3.2\pm 3.6^\circ C$  lower ( $N=20$ , range 10.8°C lower to 3.2°C higher) than the onset of panting, and  $1.9\pm 3.2^\circ C$  ( $N=27$ , range 9.4°C lower to 3.5°C higher) lower than the inflection  $T_a$  above which EWL increased above baseline levels. Both  $T_a$  associated with the onset of panting (coefficient= $0.903\pm 0.377$ ,  $t=2.396$ ,  $P=0.028$ ,  $\lambda=1.066$ ) and EWL inflection  $T_a$  (coefficient= $0.795\pm 0.203$ ,  $t=3.923$ ,  $P<0.001$ ,  $\lambda=0.648$ ) were significantly correlated with residual  $T_{uc}$  (Fig. 3).

### Potential error associated with use of allometrically predicted values

Comparisons of cumulative EWL over a 6 h period on an extremely hot day estimated using actual EWL slopes and predicted slopes for passerines (Fig. 4) revealed that actual and predicted values were typically similar, but in a few instances differed substantially (Fig. 5). Predicted cumulative EWL values for the 27 species we evaluated were all within the 95% prediction intervals, with the exception of common fiscal (*Lanius collaris*) for which the actual

value was equivalent to 175% of that estimated using an allometrically predicted slope (Fig. 5). For estimated survival times before cumulative EWL exceeds 15%  $M_b$ , predicted versus actual values fell within the 95% prediction intervals except for common fiscal (actual=72% of predicted) and red lark (*C. burra*; actual=140% of predicted) (Fig. 5).

### Conclusions and emerging questions

Our analysis of thermoregulation during acute heat exposure among 56 arid-zone birds reveals several novel scaling patterns, including the positive scaling of HTL, and confirms scaling patterns identified previously for variables such as maximum EWL (Calder and King, 1974), slope of EWL (Song and Beissinger, 2020) and slope of RMR (Weathers, 1981). However, the present study also reveals large differences among orders in these variables, particularly the slope of RMR. Moreover, because the studies from which we obtained data involved methods designed to elicit the upper limits of heat tolerance and evaporative cooling, this review confirms the presence of consistent taxonomic differences in HTL and maximum EHL/MHP. Caprimulgids and columbids emerge as the most heat-resistant taxa, although there is evidence for similarly pronounced heat tolerance in representatives of some other non-passerine taxa. The broad overlap among taxa in terms of evaporative scope, but a lack of such overlap in the scaling of the slope of RMR and the large differences in maximum EHL/MHP reveals that, on a broad scale, upper limits to avian heat tolerance are constrained by the metabolic costs of heat dissipation mechanisms to a much greater extent than by limitations on the capacity to increase EWL above baseline levels.

These patterns of scaling and phylogenetic variation among physiological variables related to evaporative cooling and heat tolerance have several implications for modelling physiological aspects of avian responses to climate change. First, they reiterate the size dependence of cumulative EWL and hence survival time on extremely hot days, with smaller species reaching dehydration tolerance limits sooner than larger species (McKechnie and Wolf, 2010). The relationship between heat tolerance limits (i.e. maximum  $T_a$  tolerated during acute heat exposure) and  $M_b$ , among passerines in particular, also suggests that smaller species are more vulnerable to lethal hyperthermia during extreme heat events. In addition to these general scaling effects, our analysis of evolutionarily conserved variation suggests that lethal effects of extreme heat will vary across taxa. Passerines, on account of the relatively low efficiency of panting, may be expected to be disproportionately affected during heat-related mortality events, a prediction supported by the prominence of passerines and parrots (which also lack gular flutter or pronounced cutaneous evaporation) in historical accounts of mortality among Australian species (e.g. Finlayson, 1932; McGilp, 1932; see also Conradie et al., 2020). Taxa such as columbids and caprimulgids are better able to tolerate extreme  $T_a$  during such events, particularly if water is available. Even in the absence of drinking, however, estimated survival times are substantially longer for columbids and caprimulgids compared with comparatively sized passerines.

One important limitation of our analysis is that it focuses solely on arid-zone birds, and involves data collected at low humidities. Avian evaporative cooling in more mesic habitats may be severely constrained by higher humidity levels, particularly in humid tropical lowlands (Weathers, 1986, 1997). Relatively few studies have investigated interactions between evaporative cooling and experimentally manipulated humidity (Gerson et al., 2014; Powers, 1992; van Dyk et al., 2019) and much remains to be explored in this area. Similarly, few data are available on limits to evaporative cooling and heat tolerance along non-desert species or how these traits vary

across broad biomes (Milne et al., 2015). It is also noteworthy that there are a small number of reports of maximum avian  $T_b$  being substantially higher than the range for arid-zone species. Weathers (1997) documented tolerance of  $T_b=47^\circ\text{C}$  in a passerine from Panama's lowlands and argued that tolerance of such a high  $T_b$  may evolve in response to the constraints imposed by high humidity on evaporative cooling. Tolerance of even more extreme hyperthermia has recently been documented in an African ploceid passerine, the red-billed quelea (*Quelea quelea*), with maximum  $T_b$  averaging  $48.0^\circ\text{C}$  and individual values of up to  $49.1^\circ\text{C}$  (Freeman et al., 2020). Data from species across a range of habitats are needed to identify global patterns in limits to avian evaporative cooling and inform models of species' sensitivity (Williams et al., 2008) to climate change.

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### Competing interests

The authors declare no competing or financial interests.

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### Supplementary information

Supplementary information available online at <https://jeb.biologists.org/lookup/doi/10.1242/jeb.229211.supplemental>

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