

Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming

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Abstract

1. Characterizing heat tolerance is critical for predicting an organism's vulnerability to climate warming. Recent studies of ectotherms report that impacts of climate warming are expected to be greater in the tropics, where ectotherms tend to have lower heat tolerances and experience air temperatures closer to their heat tolerance limits than their temperate counterparts. However, similar comparisons of heat tolerance are largely lacking for endotherms, and it remains an open question whether climate warming will also disproportionately affect tropical endotherms.
2. To address this empirical gap, we measured thermoregulatory responses to acute heat stress in 81 bird species (23 temperate, 58 tropical), assembling the largest comparative dataset of endothermic heat tolerances to date.
3. After controlling for body mass and experimental chamber humidity, temperate species had significantly higher heat tolerance limits ($\Delta\text{HTL} = 2.2^\circ\text{C}$; 45.2 vs. 43.0°C) and upper critical temperatures ($\Delta\text{UCT} = 1.1^\circ\text{C}$; 38.7 vs. 37.6°C) on average than tropical species. Importantly, however, these differences do not appear to impact vulnerability to climate warming, as neither thermal safety margins [i.e. the difference between upper critical temperature (UCT) and maximum air temperature, T_{max}] nor warming tolerances [the difference between heat tolerance limit (HTL) and T_{max}] differed between temperate and tropical species. We also observed substantial variation in heat tolerance among avian orders, with pigeons and doves (Columbiformes) being among the most heat tolerant species in our dataset.
4. Overall, our results suggest that, from a physiological standpoint, tropical birds may not be systematically more susceptible to climate warming than temperate birds, contrasting previous studies of ectotherms. Furthermore, we show that certain avian clades may be more resilient to warming irrespective of local climate. However, because we only sampled at one temperate and one tropical site, we caution that replication from other habitats and localities are needed to evaluate the generality of our findings.

KEYWORDS

birds, climate warming, endotherms, heat tolerance limit, thermal safety margin, upper critical temperature, warming tolerance

1 | INTRODUCTION

Recent increases in global temperatures have had profound ecological and evolutionary implications for biodiversity and ecosystem integrity (Bellard et al., 2012; Bradshaw & Holzapfel, 2006; Parmesan, 2006; Walther et al., 2002). However, species are not equally vulnerable to climate warming. Instead, relative vulnerability is determined by a host of factors, including their present-day physiological thermal tolerance limits, the capacity for future evolutionary adaptation of those limits and aspects of their ecologies and life histories (i.e. behaviour, habitat specialization, etc.; reviewed in Williams et al., 2008). Understanding how these factors interact to dictate species' responses to climate warming is of primary importance in predicting and mitigating the impact of rising global temperatures (Huey et al., 2012; Somero, 2010).

Previous research in this area has focused largely on heat tolerance, a trait with clear implications for sensitivity to climate warming (Araújo et al., 2013; Deutsch et al., 2008). Although behavioural thermoregulation is an important first line of defense in mitigating the physiological impact of high temperatures (Kearney et al., 2009; Sunday et al., 2014), organisms must rely on heat tolerance when behavioural means are insufficient (Huey et al., 2012; Williams et al., 2008). A better understanding of geographic variation in heat tolerance is therefore critical for predicting where species will be most vulnerable to climate warming (Deutsch et al., 2008; Dillon et al., 2010; Huey et al., 2012; Somero, 2010).

While the absolute rate of climate warming increases with latitude (Dillon et al., 2010), its impacts are generally predicted to be greater in tropical regions, especially for ectotherms (Deutsch et al., 2008; Sunday et al., 2010, 2019). For example, tropical lizards, amphibians, arthropods and fish tend to have lower heat tolerance limits and have narrower thermal safety margins (i.e. are more likely to experience air temperatures that are closer to the limits of their heat tolerances) than their temperate counterparts (Deutsch et al., 2008; Diamond et al., 2012; Duarte et al., 2012; Huey et al., 2009, 2012; Vinagre et al., 2016). In contrast, similar comparative studies of geographic variation in heat tolerances are largely lacking for endotherms. Estimating heat tolerances of endotherms necessitates finding the limits of their thermoregulatory capabilities (characterized by uncontrolled hyperthermia and the inability to defend body temperature) in response to extreme heat (e.g. Gerson et al., 2019; reviewed in McKechnie & Wolf, 2019). These assays are logistically challenging and time-consuming (Lighton & Halsey, 2011; McKechnie & Wolf, 2019; Withers, 2001), which has hindered empirical estimation of endothermic heat tolerances until recently (see McKechnie & Wolf, 2019 for a review).

Due to the relative paucity of endothermic heat tolerance data, several meta-analyses (Araújo et al., 2013; Khaliq et al., 2014; Sunday et al., 2019) have instead used the upper critical temperature (UCT – the upper limit of the thermoneutral zone; Figure 1) as a proxy for assessing latitudinal variation in heat tolerance and susceptibility to climate warming. For example, Khaliq et al. (2014) concluded that tropical endotherms had narrower thermal safety margins (i.e. were currently experiencing maximum air temperatures closer to their

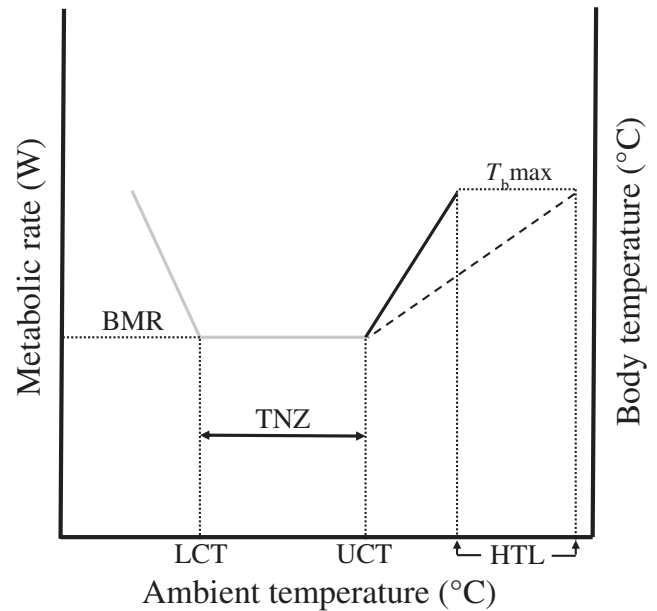


FIGURE 1 Schematic of an endothermic Scholander curve (adapted from Scholander et al., 1950). The thermoneutral zone (TNZ) is defined as the range of ambient temperatures at which temperature regulation is achieved without regulatory changes in metabolic heat production or evaporative heat loss (IUPS Thermal Commission, 2001). Within the TNZ, an endotherm is able to maintain a basal metabolic rate (BMR), the minimum metabolic cost of existence. However, at air temperatures below the lower critical temperature (LCT) or above the upper critical temperature (UCT), an endotherm must increase metabolic heat production to maintain internal temperature homeostasis. The solid and dashed black lines represent a high and low T_b slope (i.e. the slope of the relationship between body temperature and air temperature) respectively. Organisms with a high T_b slope (solid line) accumulate endogenous heat more rapidly, and may be expected to reach their heat tolerance limit (HTL) at a lower air temperature than organisms with a low T_b slope (dashed line)

UCTs) than their temperate counterparts and were therefore projected to be at greater risk from climate warming. However, some of these meta-analyses (e.g. Araújo et al., 2013; Khaliq et al., 2014), however, included UCT data that were either inaccurate or not suitable for inclusion due to a variety of methodological issues (McKechnie et al., 2017; Wolf et al., 2017). Therefore, the conclusions derived from these meta-analyses require re-examination. Furthermore, examination of the UCT alone does not fully characterize heat tolerance. At least two other traits—the rate of increase of endogenous heat load above the UCT (T_b slope) and the heat tolerance limit (HTL – the air temperature at which an endotherm loses the ability to regulate its body temperature)—must also be considered to more fully understand the limits of physiological function under heat stress in endotherms (Figure 1).

To begin to determine if there were systematic differences in heat tolerances between temperate and tropical endotherms, we measured thermoregulatory responses to acute heat stress in bird species from one temperate ($n = 23$) and one tropical ($n = 58$) sampling locality. In doing so, we also re-assessed the conclusion

of Khaliq et al. (2014) that climate warming will likely have greater impacts on tropical endotherms by estimating and comparing thermal safety margins of temperate and tropical species. Finally, recent studies of desert birds have implicated body size and phylogeny as important predictors of variation in avian heat tolerance. Specifically, heat tolerance limits of desert birds scale positively with body size (McKechnie, et al., 2017; Whitfield et al., 2015) and certain orders such as Caprimulgiformes and Columbiformes appear to have higher heat tolerance limits than others (McKechnie, et al., 2017; McKechnie et al., 2016; O'Connor et al., 2017; Smit et al., 2018). Therefore, we also used our dataset to explore how heat tolerance varied with body size and across avian orders in more mesic environments.

2 | MATERIALS AND METHODS

2.1 | Sampling localities

We conducted fieldwork in 2014 at one tropical (Gamboa, Republic of Panama – 09°07'N, 79°42'W) and one temperate (Aiken, South Carolina, United States – 33°32'N, 81°43'W) locality. We restricted sampling to the months of April–August (tropical wet season, temperate summer) for two reasons: (a) to control for the effects of seasonal variation in air temperature (T_a) on thermal physiology (Noakes et al., 2016; Pollock et al., 2019; Swanson, 2010), and (b) because species experience the highest air temperatures at both localities during this time period. Mean maximum air temperature during the sampling period was significantly higher at the temperate site (31.45°C) than the tropical site (29.05°C; $p < 0.001$; Figure S1). The range of water vapour pressures experienced during the sampling periods were broadly overlapping between the temperate (1.9–4.2 kPa) and tropical (2.6–4.8 kPa) study sites.

2.2 | Bird capture and housing protocols

We captured birds in mist-nets between 07:00–10:00 hr and banded them with uniquely numbered aluminum leg-bands to facilitate individual identification (Federal Bird Banding Permit #23942). We also determined sex when possible based on plumage dimorphism, and the presence of brood patches or cloacal protuberances. We immediately released individuals exhibiting external signs of being in reproductive condition. We then transported birds to a temperature-controlled lab held at 27°C (within the thermoneutral zone of all focal species; Pollock, 2016) and housed them in cloth-covered cages with water provided ad libitum for 1–3 hr.

2.3 | Quantifying thermoregulatory responses to acute heat stress

We measured thermoregulatory responses to acute heat stress in one focal individual at a time. Before beginning each heat stress

experiment, we weighed the focal individual using a digital scale (American Weigh Scales model AWS-201, 200 ± 0.01 g) and inserted a temperature-sensitive passive integrative transponder (PIT) tag (model Biothermo13: 13 mm \times 2.2 mm, Biomark, Inc.) into its cloaca. Cloacal temperature (hereafter T_b) is highly correlated with core body temperature and is commonly used as a proxy for core temperature (McCafferty et al., 2015). For small birds (e.g. <20 g), we measured cloacal diameter prior to insertion to ensure that individuals could accommodate the PIT tag. PIT tags were oriented with the temperature-sensitive end pointed inward and inserted fully into the cloaca using sterilized forceps. Because PIT tags were more peripheral to the core in larger birds and could therefore be expected to increasingly underestimate actual T_b , we ran a linear regression to test for a relationship between maximum T_b during the experiment and body mass (M_b). We found no relationship between the two variables ($p = 0.84$, $R^2 = 0.002$; Figure S2), indicating that PIT tags were not systematically underestimating core T_b in larger birds. We glued the small contour feathers around the cloaca together to impede the PIT tag from being expelled via defecation during the experiment. Nevertheless, a small percentage (5.9%; $n = 16$ birds) of focal birds defecated their PIT tags before experiments were completed—we discarded these individuals from subsequent analyses. All protocols were approved by the relevant Institutional Animal Care and Use Committees (IACUC # 12202, University of Illinois at Urbana-Champaign; #A2013 02-014-Y1-A0, University of Georgia; #2013-0101-2016, Smithsonian Tropical Research Institute) and we recorded no mortality as a result of PIT tag insertion. We calibrated PIT tags before experiments using a thermometer certified by the National Bureau of Standards, and determined that they were accurate across the range of experimental T_a to within $0.2 \pm 0.7^\circ\text{C}$ ($M \pm SD$). Following PIT tag insertion, the focal bird was placed in an airtight Plexiglas respirometry chamber inside a PTC-1 temperature cabinet (Sable Systems, Inc.) controlled by a Peltier device (Pelt-5, Sable Systems, Inc.). Throughout experiments, we regulated cabinet temperature and continuously monitored the chamber T_a using thermistor probes (model SEN-TH, Sable Systems, Inc., $\pm 0.2^\circ\text{C}$ accuracy). We used infrared cameras (model WCM-6LNV, Sabrent) to monitor bird behaviour and activity levels inside the chambers throughout the experiment. Because activity level can influence metabolic rate (Aschoff & Pohl, 1970) and confound the relationship between T_a and metabolic rate, we discarded data for focal birds that were frequently active inside the chamber or exhibited signs of stress behaviour (i.e. pecking the chamber, flight attempts).

We started each experiment at 30°C and allowed the focal individual to attain a stable, resting metabolic rate (RMR) and stable body temperature before beginning to increase the chamber T_a . Once the individual became normothermic (i.e. T_b between 38 and 42°C; Prinzinger et al., 1991) and was at rest ($M \pm SD = 23.2 \pm 18.1$ min; range = 18–119 min), we then began to increase chamber T_a in 3°C increments while measuring the focal bird's gas exchange. At each successive T_a , we held the individual for a minimum of 15 min (18 ± 5.3 min; range = 15–36 min) until we were able to obtain at least 5 min of stable gas traces at a given T_a . Once the individual had acclimated to a given

T_a , we continued to the next T_a , and repeated this process until the focal individual exhibited uncontrolled hyperthermia (see Section 2.5) or achieved a T_b of $\geq 45.5^\circ\text{C}$ (slightly below lethal T_b of $46\text{--}48^\circ\text{C}$ for birds; Arad & Marder, 1982; Brush, 1965; Dawson, 1954; Randall, 1943). We removed birds from the respirometry chambers immediately following onset of uncontrolled hyperthermia or alternatively, if they exhibited prolonged signs of distress behaviour (i.e. flight attempts, pecking the chamber walls, loss of coordination, etc.). Following heat stress experiments, we clipped the cloacal feathers with a small surgical scissors, at which point most individuals immediately defecated their PIT tags. A small subset of birds ($n = 19$) did not defecate their PIT tags, and we used a small forceps to manually remove PIT tags from these individuals. We then reweighed the focal individual, placed it in front of a fan and applied alcohol to its legs with a cotton ball to promote heat loss and provided water ad libitum to help restore water balance. Once birds had recovered and resumed normal behaviour ($\sim 30\text{--}60$ min), they were transported to the site of capture in cloth bags and released.

2.4 | Respirometry system and gas analysis

We used push-mode flow-through respirometry (Lighton & Halsey, 2011; Withers, 2001) to measure gas exchange of one individual at a time during the heat stress experiments. We pushed incurrent air (PP2 pump; Sable Systems, Inc.) through a column of Drierite to remove water and then pumped dried air into a mass-flow meter (Flowbar-8; Sable Systems, Inc.) that divided the air stream into two channels, each plumbed through Bevaline IV tubing (Cole-Parmer) to a separate respirometry chamber. One empty chamber (baseline) served as a reference to the animal chamber. During experiments, birds rested in the chamber on a perch made of wire mesh. The chamber inlet was situated on the lid of the chamber and the chamber outlet was on the side of the chamber opposite to the inlet to ensure that incurrent air flowed directly across the bird before exiting the chamber. Flow rates ($500\text{--}3,000$ ml/min) and chamber sizes (1.97 or 4.53 L) varied depending on the size of the focal species, with higher flow rates and larger chambers used for larger species. Excurrent air from one chamber at a time was subsampled manually at $100\text{--}150$ ml/min through barrel syringes, scrubbed of water vapour (Drierite) and analysed for $\%\text{CO}_2$ (FoxBox; Sable Systems, Inc.).

Humidity has been shown to influence the thermoregulatory responses of birds to high temperatures (Gerson et al., 2014; McKechnie & Wolf, 2019; Powers, 1992), so we progressively increased flow rates throughout experiments to maintain chamber humidity below 25% (i.e. the relative humidity at 40°C above which evaporative cooling capacity is substantially inhibited; McKechnie & Wolf, 2019). However, at higher air temperatures, water vapour pressure increases. As a result, relative humidities exceeded 25% in 30.3% ($n = 77$) of our experiments, although we were able to maintain chamber humidity below 30% RH in all cases. The maximum water vapour pressure recorded during all experiments (3.7 kPa) was well within the range of water vapour pressures experienced by birds at both the temperate ($1.9\text{--}4.2$ kPa) and tropical ($2.6\text{--}4.8$ kPa) study sites, indicating that experimental

humidities were ecologically relevant. Nevertheless, to account for the impact of humidity on metrics of heat tolerance, we included maximum experimental water vapour pressure as a covariate in our analysis (see Section 2.8 section below).

During each experiment, we recorded T_b at 10-s intervals using a PIT tag reader (HPRPlus Reader, Biomark, Inc.) and the program Bioterm (Biomark, Inc.) and flow rate, T_a , and $\%\text{CO}_2$ in each chamber at 1-s intervals using the program Expedata (Sable Systems, Inc.). We used a Catmull-Rom spline correction to correct for drift and then converted $\%\text{CO}_2$ to $\dot{V}\text{CO}_2$ (rate of CO_2 production, measured in ml CO_2/min) using equation (10.5) from Lighton (2008) and assuming an RQ of 0.85 (Gessaman & Nagy, 1988).

2.5 | Characterizing heat tolerances

2.5.1 | Upper critical temperature (UCT)

As defined by McNab (2002), the UCT is the upper limit of the thermoneutral zone, above which an endotherm must rely on evaporative cooling to maintain temperature homeostasis (Figure 1). To estimate the UCT of focal individuals, we obtained 3-min averages of $\dot{V}\text{CO}_2$ and corresponding T_a for each individual throughout the experiment, generating a series of paired T_a and $\dot{V}\text{CO}_2$ measurements. We then identified inflection points in the relationship between T_a and $\dot{V}\text{CO}_2$ using piecewise linear regression (R package SEGMENTED; Muggeo, 2008).

2.5.2 | Slope of the relationship between T_b and T_a (T_b slope)

Above the UCT, birds rely on evaporative cooling to maintain a stable internal T_b and reduce heat load (McNab, 2002). To estimate the accumulation of internal heat load during heat stress experiments, previous studies have used a metric termed the 'coefficient of heat strain' (HS_{coeff}), defined as the slope of the relationship between metabolic heat production and T_a (Weathers, 1981, 1997; Whitfield et al., 2015). One potential problem with the HS_{coeff} is that birds exhibit substantial variation in their ability to dissipate heat (Dawson, 1982), and therefore increases in metabolic heat production do not necessarily translate directly into increases in heat load. To control for interspecific variation in evaporative heat loss capacity, we instead opted to use T_b slope—the slope of the relationship between T_b and T_a , because we were interested in quantifying the accumulation of internal body heat in relation to increasing air temperature.

2.5.3 | Heat tolerance limit (HTL)

We defined HTL as the T_a at which onset of hyperthermia (i.e. loss of T_b regulation) occurred (McKechnie & Wolf, 2019; Whitfield et al., 2015). Hyperthermia can result from physiological limitation

of heat dissipation rates or acute dehydration (Albright et al., 2017). We deemed birds to have reached HTL if they (a) exhibited signs of distress associated with hyperthermia such as loss of coordination (Whitfield et al., 2015) or (b) exhibited rapid increases in T_b of $\geq 0.5^\circ\text{C}/\text{min}$ over a 3-min interval consistent with uncontrolled hyperthermia (McKechnie & Wolf, 2019).

In combination, UCT, T_b slope, and HTL allow for a thorough characterization of heat tolerance in endotherms. The UCT represents the temperature at which endotherms begin to require evaporative heat loss to maintain temperature homeostasis, yet it is not a direct measure of how quickly endotherms accumulate heat (i.e. T_b slope) or how resistant they are to acute heat stress (i.e. HTL). In principle, T_b slope should also be functionally linked to HTL—organisms with higher T_b slope should accumulate heat faster and reach HTL at lower temperatures than organisms with low T_b slope (Figure 1).

2.6 | Indices of vulnerability to climate warming

We estimated vulnerability to climate warming using two indices related to local maximum air temperature (T_{max})—thermal safety margins and warming tolerances. We defined thermal safety margin (TSM) as the difference between T_{max} at each respective sampling locality and the species' mean UCT ($\text{UCT}-T_{\text{max}}$; following Khaliq et al., 2014). We adopted warming tolerance (WT) from the ectotherm literature (Duarte et al., 2012) and defined it as the difference between local T_{max} and the species mean HTL ($\text{HTL}-T_{\text{max}}$). T_{max} data were derived from weather stations [National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information's (NCEI) Climate Data Online (<https://www.ncdc.noaa.gov/cdo-web/>)]. Weather station data were available for 98% of dates within the sampling period at each locality (range = 94%–100%). Although these data were derived from weather stations located as close as possible (≤ 10 miles) to each respective sampling locality, we acknowledge that they only approximate the thermal conditions experienced by birds, and do not account for microclimatic variation present within the sampling locality (e.g. Walsberg, 1993). We averaged daily maximum

temperatures across the sampling period to estimate T_{max} at each sampling locality. We chose to take the average of the daily T_{max} across the sampling period during which the species were measured to account for the fact that most physiological traits are flexible and vary depending on the environmental conditions to which the organism is recently exposed (Piersma & Drent, 2003; Piersma & van Gils, 2010).

2.7 | Controlling for phylogeny

To control for the influence of phylogeny on heat tolerances, we derived a phylogeny of the focal taxa (Figure S3) by pruning the maximum likelihood avian phylogenetic tree of Burleigh et al. (2015) with the 'drop.tip' function in the R package APE (Paradis et al., 2004) to include all focal species ($n = 81$). We chose the Burleigh et al. (2015) phylogenetic tree because it contained nearly all (96.3%) of our focal taxa and has similar topology compared to other commonly used avian phylogenetic trees (e.g. Hackett et al., 2008; Prum et al., 2015).

Because three of our focal species (*Cyphorhinus phaeocephalus*, *Malacoptila panamensis*, *Melanerpes rubricapillus*) were not included in the Burleigh et al. (2015) phylogeny, we substituted three congeneric species (*Cyphorhinus arada*, *Malacoptila semicincta*, *Melanerpes aurifrons*, respectively) to approximate their position in the tree. We then used this phylogeny to conduct phylogenetic generalized least squares regression (PGLS). To determine which branch-length transformation to use, we first compared a Brownian motion model of trait evolution (Grafen, 1989) to an Ornstein-Uhlenbeck model (stabilizing selection; Martins & Hansen, 1997) using Akaike's information criterion (AIC). The Brownian motion model had lower AIC scores, and so we retained this model of trait evolution for further phylogenetic analyses.

We estimated Pagel's λ (Pagel, 1999) in the residual error of each regression model while simultaneously estimating regression parameters (Revell, 2010), and then scaled regression models using the estimates of λ . We detected phylogenetic signal in the residuals of all physiological traits (Table 1) and therefore we only present results from PGLS regressions (following Freckleton, 2009).

TABLE 1 Phylogenetic generalized least squares regression model outputs for upper critical temperature (UCT), slope of the relationship between air temperature and body temperature (T_b slope), heat tolerance limit (HTL) thermal safety margin (TSM) and warming tolerance (WT). Main effects for all models included sampling locality (temperate vs. tropical), body mass (M_b), and maximum water vapour pressure measured during the experiment (WVP). $M \pm SD$ for tropical and temperate species for each trait is shown, as well as the phylogenetic signal (λ) and p -value of each main effect. Bold font indicates a significant p -value ($\alpha = 0.05$)

Model	$M \pm SD$ ($^\circ\text{C}$)		λ	$p(\text{locality})$	$p(M_b)$	$p(\text{WVP})$
	Tropical	Temperate				
HTL ~ locality + M_b + WVP	43.0 \pm 1.6	45.2 \pm 2.0	0.48	<0.0001	0.74	<0.0001
UCT ~ locality + M_b + WVP	37.6 \pm 1.5	38.7 \pm 1.8	0.41	0.01	0.26	0.001
T_b slope ~ locality + M_b + WVP	0.55 \pm 0.27	0.48 \pm 0.29	0.50	0.39	0.60	0.15
TSM ~ locality + M_b + WVP	8.6 \pm 1.5	8.3 \pm 1.8	0.41	0.18	0.26	0.001
WT ~ locality + M_b + WVP	14.0 \pm 1.6	14.8 \pm 2.0	0.48	0.12	0.74	<0.0001

2.8 | Statistical analysis

We used the ‘pgls’ function in the R package CAPER (Orme et al., 2012) to run all PGLS regressions. To test for differences in heat tolerances between tropical and temperate species, we constructed multivariate additive linear models for each of the three metrics of heat tolerance (UCT, T_b slope, and HTL) with sampling locality (tropical vs. temperate), body mass (M_b) and experimental water vapour pressure (WVP) as main effects. We included M_b due to its well-known allometric relationship with physiological traits such as basal metabolic rate (McKechnie & Wolf, 2004) and HTL (McKechnie, et al., 2017; Whitfield et al., 2015). To test for differences in sensitivity to climate warming between tropical and temperate species, we conducted analogous regressions for TM and WT. To explore phylogenetic variation in heat tolerances and sensitivity to climate warming among avian orders, we ran ordinary least squares (OLS) regressions with order as the predictor variable for all three heat tolerance metrics and the two metrics of sensitivity to climate warming.

In total, we measured thermoregulatory responses to acute heat stress in 254 individuals representing 81 species (23 temperate, 58 tropical; Table S1) from 26 families (21 tropical, 15 temperate; 10 families shared by both study sites) and five orders (Columbiformes, Coraciiformes, Passeriformes, Piciformes, Psittaciformes). Because we had small sample sizes ($n < 3$ individuals) for nearly half (39/81) of our focal species, we conducted analyses in two ways: (a) on the entire complement of focal species and (b) on 42 focal species (17 temperate, 25 tropical) that had sample size of $n \geq 3$ individuals (following recommendations for minimal sample sizes for physiological analyses in McKechnie & Wolf, 2004). We found qualitatively similar results between analyses for all traits (Table S2), and therefore we

report results from the analysis of the entire complement of focal species.

3 | RESULTS

Multivariate models including experimental water vapour pressure (WVP) and body mass (M_b) revealed a significant effect of WVP on two of three metrics of heat tolerance (i.e. UCT, UTL) and both indices of sensitivity to climate warming (i.e. TSM, WT; Table 1), whereas M_b did not have a significant effect on any of the three traits or either warming index (Table 1). Specifically, WVP was positively correlated with all four traits—species that experienced higher maximum WVP during experiments tended to have higher UCTs and UTLs and broader TSMs and WTs (Figure S4). However, maximum WVP did not differ between temperate and tropical species ($p = 0.11$, Figure S5), indicating that experimental humidities were comparable between study sites.

After controlling for the effects of body mass and WVP, we found significant differences in some heat tolerance metrics between temperate and tropical bird species. Temperate species had higher heat tolerance limits (HTL - $\bar{x} = 2.2^\circ\text{C}$ higher; Table 1; Figure 2A) and upper critical temperatures (UCT - $\bar{x} = 1.1^\circ\text{C}$ higher; Table 1; Figure 2B) than tropical species. In contrast, T_b slope did not differ between temperate and tropical species (Table 1; Figure 2C). We also found substantial variation in heat tolerance metrics within each locality (Figure 2), but tropical species exhibited less variation than temperate species with respect to all three traits [HTL ($CV_{\text{trop}} = 3.8$; $CV_{\text{temp}} = 4.5$), UCT ($CV_{\text{trop}} = 3.9$; $CV_{\text{temp}} = 4.8$) and T_b slope ($CV_{\text{trop}} = 49.4$; $CV_{\text{temp}} = 59.8$)].

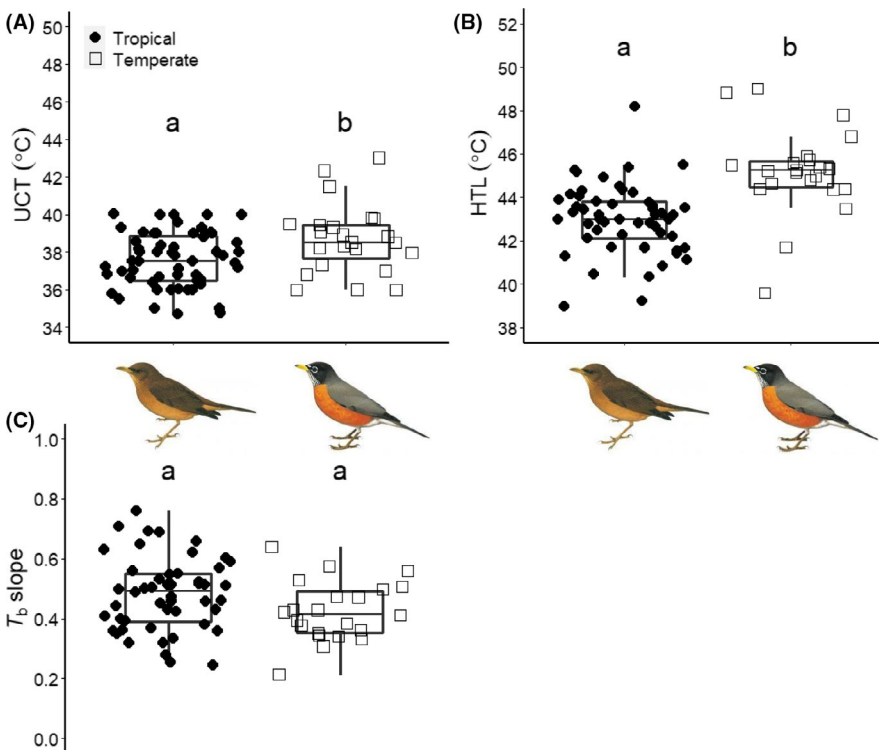


FIGURE 2 Box plots of (A) upper critical temperature (UCT), (B) heat tolerance limit (HTL), and (C) T_b slope of tropical (black circles, $n = 58$) and temperate (white squares, $n = 23$) bird species. Letters above box plots denote significant differences ($\alpha = 0.05$) between sampling localities as derived from PGLS regressions. Temperate species had significantly higher UCTs and HTLs than tropical species, whereas T_b slope did not differ between temperate and tropical species. Exemplar species are Clay-coloured Thrush *Turdus grayi* (tropical) and American Robin *Turdus migratorius* (temperate)

Despite the differences in some metrics of heat tolerance between temperate and tropical birds, we found little evidence of systematic differences in sensitivity to climate warming. Thermal safety margins (TSM) did not differ significantly ($p = 0.18$) between tropical ($\bar{x} = 8.6 \pm 1.5^\circ\text{C}$) and temperate species ($\bar{x} = 8.3 \pm 1.9^\circ\text{C}$; Table 1; Figure 3A). Similarly, warming tolerances (WT) did not differ significantly ($p = 0.12$) between tropical ($14.0 \pm 1.6^\circ\text{C}$) and temperate species (14.8 ± 2.0 ; Table 1; Figure 3B).

Heat tolerance metrics varied substantially among species and orders. Across all species, HTL ranged from 39 to 49°C ($\bar{x} = 43.6^\circ\text{C}$), UCT ranged from 35 to 43°C ($\bar{x} = 37.9^\circ\text{C}$) and T_b slope ranged from 0.21 to 1.78 ($\bar{x} = 0.53$; Table S1). Doves and pigeons (order Columbiformes) had significantly higher UCT, HTL, TSM, and WT compared to all other orders, which did not differ from one another (Figure 4A,B,D). Coraciiformes had significantly higher T_b slope compared to all other orders, which did not differ from one another (Figure S6).

4 | DISCUSSION

We found significant differences in heat tolerance metrics between temperate and tropical birds. After controlling for body mass and experimental humidity, temperate species had higher HTL ($\sim 2.2^\circ\text{C}$ – the air temperature at which hyperthermia occurred) and UCT ($\sim 1.1^\circ\text{C}$ – the air temperature above which endotherms must actively thermoregulate via evaporative cooling), although T_b slope (the rate of accumulation of endogenous heat load above the UCT) did not differ between temperate and tropical species (Figure 2). Thus, on average, temperate birds tolerated higher air temperatures than tropical birds. Even so, estimates of sensitivity to climate warming (i.e., thermal safety margin and warming tolerance) did not differ between temperate and tropical species. Thus, tropical birds may not be systematically more susceptible to climate warming than temperate birds, in contrast to previous studies of ectotherms. However, because we only sampled at one temperate and one tropical site, we

FIGURE 3 Box plots of (A) thermal safety margin (TSM) and (B) warming tolerance (WT) of tropical (black circles, $n = 58$) and temperate (white squares, $n = 23$) bird species. Letters above box plots denote significant differences ($\alpha = 0.05$) between sampling localities as derived from PGLS regressions. Neither TSM nor WT differed between temperate and tropical species. Exemplar species are Clay-coloured Thrush *Turdus grayi* (tropical) and American Robin *Turdus migratorius* (temperate)

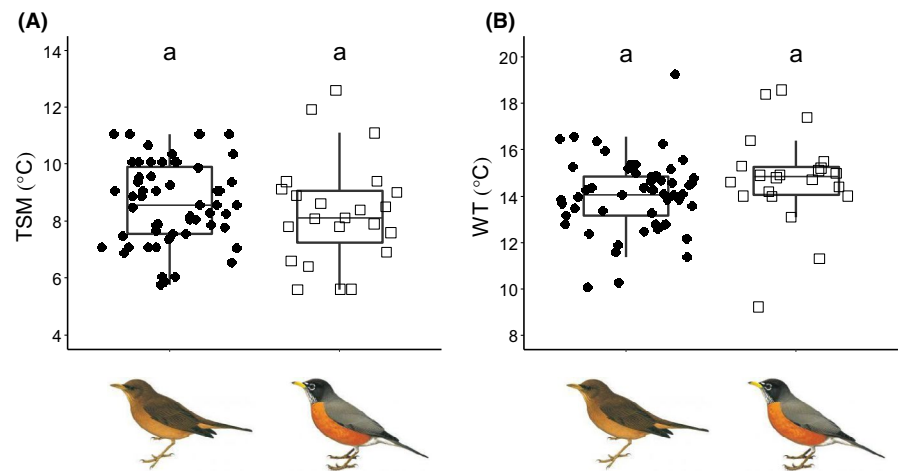
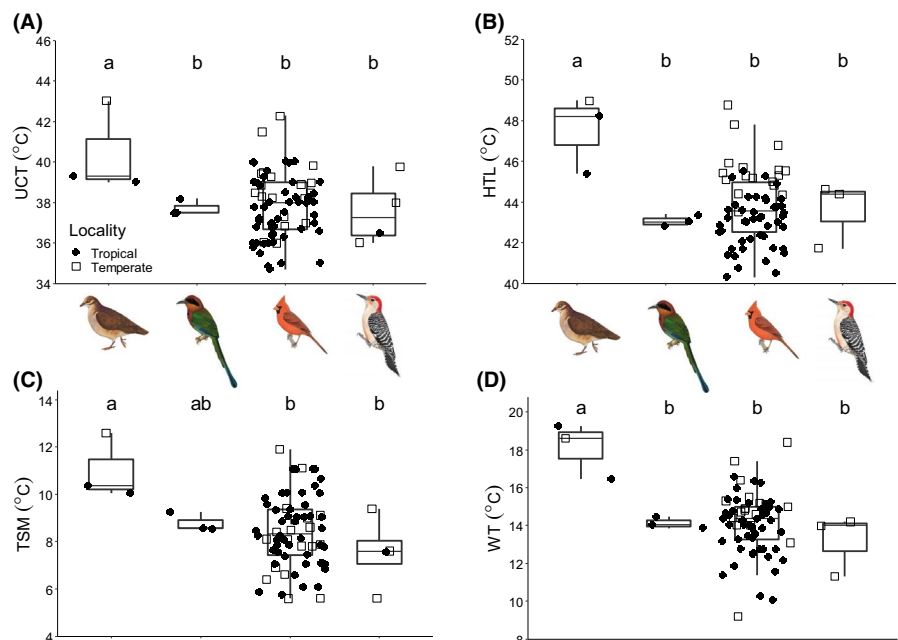


FIGURE 4 Box plots of (A) upper critical temperature (UCT), (B) heat tolerance limit (HTL), (C) thermal safety margin (TSM) and (D) warming tolerance (WT) of the four avian orders with $n \geq 3$ species, including Columbiformes ($n = 3$), Coraciiformes ($n = 3$), Passeriformes ($n = 71$), and Piciformes ($n = 4$). Black circles denote tropical focal species and white squares denote temperate focal species. Letters denote significant differences ($\alpha = 0.05$) between parameter estimates derived from PGLS regressions. Exemplar species from left to right: Ruddy Quail-dove, *Geotrygon montana* (Columbidae: Columbiformes); Rufous Motmot *Baryphthengus martii* (Momotidae: Coraciiformes); Northern Cardinal *Cardinalis cardinalis* (Cardinalidae: Passeriformes); Red-bellied Woodpecker *Melanerpes carolinus* (Picidae: Piciformes)



caution that replication from other habitats and localities are needed to evaluate the generality of our findings.

There was a substantial degree of overlap in the distributions for all three heat tolerance metrics between temperate and tropical bird species (Figure 2), in contrast to the clear latitudinal differences in heat tolerance that have been described in ectotherms (Deutsch et al., 2008; Sunday et al., 2010, 2019). As a result, tropical and temperate bird species had equally large thermal safety margins (i.e. the difference between maximum air temperature and the species' upper critical temperature) in our dataset, in contrast to conclusions derived from previous meta-analyses. For example, Khaliq et al. (2014) reported that tropical endotherms had narrower thermal safety margins than temperate counterparts, and a greater projected degree of thermal mismatch (i.e. probability of experiencing air temperatures that exceed UCT) across their geographic distributions. This discrepancy may be due to data quality issues in Khaliq et al. (2014), which has recently been criticized for including inaccurate or spurious UCT data (Wolf et al., 2017), and highlights the importance of standardized data collection in broad-scale macrophysiological inference (Chown & Gaston, 2016; Gaston et al., 2009).

We found substantial variation in heat tolerances within and among avian orders, consistent with previous studies of desert birds (e.g. McKechnie, et al., 2017). For example, within the order Passeriformes, we found that HTL spanned a range of almost 10°C (~39–49°C). Importantly, pigeons and doves (order Columbiformes) had significantly higher HTLs compared to other orders, recapitulating evidence of the superior heat tolerances of Columbiform birds relative to other avian clades (Marder & Arieli, 1988; Marder & Gavrieli-Levin, 1987; McKechnie et al., 2016; Smith et al., 2015). Correspondingly, Columbiformes had higher thermal safety margins and warming tolerances relative to other orders, indicating that they may be better able to cope with rising global temperatures relative to other avian orders such as Passeriformes (Albright et al., 2017). Interspecific variation in heat tolerance has been linked to the mechanism of evaporative cooling—Columbiforms rely largely on cutaneous evaporative water loss to dissipate heat at high environmental temperatures, which is much more effective than the respiratory evaporative water loss commonly employed by other avian lineages (McKechnie et al., 2016). Interestingly, the HTLs that we estimated for Columbiforms at our study sites ranged from ~45 to 49°C, similar to the HTLs of desert passerines (Smith et al., 2017; Whitfield et al., 2015) and far below the HTLs of desert Columbiforms (>60°C; McKechnie et al., 2016; Smith et al., 2015). The large differences in HTL of mesic and desert Columbiforms further reinforce the findings that heat tolerances can vary greatly within orders (McKechnie, et al., 2017), although it remains unclear whether acclimatization or local adaptation is driving these differences.

High chamber humidities (e.g. >25% relative humidity at 40°C; McKechnie & Wolf, 2019) can impede evaporative cooling and result in lower estimates of heat tolerance metrics such as UCT and HTL (Gerson et al., 2014; McKechnie & Wolf, 2019). Therefore, because relative humidity exceeded 25% in approximately 30% of our experiments, we included maximum experimental water vapour pressure

as a covariate in our analysis. We found that WVP was positively correlated with UCT and UTL—species with higher UCTs and UTLs had higher chamber humidities (Figure S4), likely because air can absorb more moisture at higher temperatures. Thus, our estimates of UCT and UTL may be slight underestimates of these metrics relative to their actual values under drier conditions that allow for maximal evaporative cooling potential. Nevertheless, the maximum WVP of any individual bird during heat stress experiments (3.7 kPa) was well within the range of WVPs experienced by species in the wild at both the temperate (1.9–4.2 kPa) and tropical (2.6–4.8 kPa) study sites, indicating the ecological relevance of the experimental conditions. Furthermore, maximum WVP did not differ between temperate and tropical species, indicating that experimental humidities were comparable and validating direct comparisons of heat tolerance metrics between species at each sampling locality. Future studies that estimate heat tolerances across a broader range of humidities will be necessary to quantify the impact of humidity on metrics of heat tolerance.

Because we only sampled birds at one tropical and one temperate site characterized by differing temperature regimes (Figure S1), it is impossible to discern whether the observed patterns of heat tolerance are due to acclimatization history or genetically based trait differences. For example, temperate species may have higher heat tolerances simply due to mean daily T_{\max} being ~1.5°C higher at the temperate sampling locality (Figure S1). Furthermore, differences in humidity regimes between the two sampling localities could also be interacting with temperature to influence estimates of heat tolerance metrics. Future studies that collect heat tolerance data across a broader geographic extent (e.g. Gerson et al., 2019) and/or estimate the capacity for phenotypic flexibility with controlled acclimation or common garden experiments (sensu Wikelski et al., 2003) will be necessary to contextualize the patterns we report here.

4.1 | Implications for climate warming

Our estimates of thermal safety margins suggest that both temperate and tropical bird species are currently often experiencing air temperatures that are well below their UCTs. In fact, even a projected 2°C increase in global mean T_a and increases in mean maximum T_a of 3–4°C by 2050 (IPCC, 2018) would not exceed the thermal safety margins of any bird species we measured. Furthermore, warming tolerances did not differ between temperate and tropical species, and virtually all species had warming tolerances in excess of 10°C. Our results are again in contrast to Khaliq et al. (2014), who found that 15% of bird species they sampled were currently already experiencing temperatures beyond their thermal safety margins and thus, already experiencing physiological impacts of climate warming. While our findings suggest that birds from mesic habitats may be more buffered from rising temperatures than previously suggested, it is important to consider maximum T_a as a distribution rather than a mean value. Extreme heat waves are increasing in frequency and intensity with climate change (Russo et al., 2014) and are projected

to cause catastrophic mortality in birds inhabiting arid environments world-wide (Albright et al., 2017; Conradie et al., 2020; McKechnie & Wolf, 2010). Extreme heat waves could similarly impact mesic bird populations by (a) exceeding their warming tolerance and resulting in direct mortality (e.g. Bourne et al., 2020; Van de Ven et al., 2020) or (b) exceeding their thermal safety margins and resulting in sublethal fitness impacts such as reduced activity and body condition (du Plessis et al., 2012) or impaired social interactions (Rat et al., 2020). Thus, future modelling scenarios should take these factors into consideration when attempting to predict the complex impacts of climate warming on bird populations. Nevertheless, the conclusion that tropical birds are systematically more vulnerable to climate warming than their temperate counterparts, as has been suggested repeatedly in the literature (Jetz et al., 2007; Khaliq et al., 2014; La Sorte & Jetz, 2010; Şekercioğlu et al., 2012), may need to be re-assessed.

Although our results are an important first step towards understanding the impacts of climate warming on endotherms, there are several factors that may influence physiological responses of birds to high air temperatures and should be considered in future analyses. First, we did not measure thermoregulatory responses to operative temperatures (*sensu* Bakken, 1976), which incorporate humidity and solar radiation and can often far exceed air temperatures (Walsberg, 1993; Wolf & Walsberg, 1996). Operative temperatures that exceed birds' thermal safety margins could still have sublethal impacts on energy expenditure and resource allocation that impact fitness (Du Plessis et al., 2012; Van de Ven et al., 2019). Second, periodic temperature extremes or climatic events such as heat waves may result in air temperatures that exceed birds' thermal safety margins and may exert strong selective pressures on bird populations (McKechnie & Wolf, 2010). The threat of acute heat stress may be particularly strong for desert bird species, which are regularly exposed to extremely high T_a and have far greater HTL (i.e. $<60^{\circ}\text{C}$) than those of the mesic species described in our analysis (McKechnie et al., 2016; Smith et al., 2015; Whitfield et al., 2015). Indeed, desert species are already projected to be much more vulnerable to climate warming (Albright et al., 2017; Conradie et al., 2020; McKechnie & Wolf, 2010). Future studies that estimate heat tolerances of species from different biomes and take into account the influence of other environmental factors (e.g. humidity, solar radiation, wind, etc.) on thermoregulation will be necessary to evaluate the generality of the conclusions derived from this analysis. Similar studies in mammals are also needed to determine the applicability of these conclusions for endotherms in general (McKechnie & Wolf, 2019). Incorporating heat tolerances into mechanistic niche models (Kearney & Porter, 2009) and accounting for acclimatization capacity (Somero, 2010) will add much greater precision to estimates of the biological impacts of climate warming (e.g. Buckley et al., 2011).

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AUTHORS' CONTRIBUTIONS

H.S.P., J.D.B. and Z.A.C. conceived and designed the research; H.S.P. collected and analysed the data; H.S.P., J.D.B. and Z.A.C. wrote and edited the paper.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.c2fqz6166> (Pollock et al., 2020).

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REFERENCES

- Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences of the United States of America*, 114, 2283–2288. <https://doi.org/10.1073/pnas.1613625114>
- Arad, Z., & Marder, J. (1982). Strain differences in heat resistance to acute heat stress between the bedouin desert fowl, the white leg-horn and their crossbreeds. *Comparative Biochemistry and Physiology Part A: Physiology*, 72, 191–193. [https://doi.org/10.1016/0300-9629\(82\)90031-7](https://doi.org/10.1016/0300-9629(82)90031-7)
- Araújo, M. B., Ferri-Yañez, F., Bozinovic, F., Marquet, P. A., Valladares, F., & Chown, S. L. (2013). Heat freezes niche evolution. *Ecology Letters*, 16, 1206–1219. <https://doi.org/10.1111/ele.12155>

- Aschoff, J., & Pohl, H. (1970). Der ruheumsatz von vögeln als funktion der tageszeit und der körpergröße. *Journal of Ornithology*, 111, 38–47.
- Bakken, G. S. (1976). A heat transfer analysis of animals: Unifying concepts and the application of metabolism chamber data to field ecology. *Journal of Theoretical Biology*, 60, 337–384. [https://doi.org/10.1016/0022-5193\(76\)90063-1](https://doi.org/10.1016/0022-5193(76)90063-1)
- Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377. <https://doi.org/10.1111/j.1461-0248.2011.01736.x>
- Bourne, A. R., Cunningham, S. J., Spottiswoode, C. N., & Ridley, A. R. (2020). High temperatures drive offspring mortality in a cooperatively breeding bird. *bioRxiv*. doi: 10.1101/2020.05.31.126862.
- Bradshaw, W. E., & Holzapfel, C. M. (2006). Evolutionary response to rapid climate change. *Science*, 312, 1477–1478.
- Brush, A. H. (1965). Energetics, temperature regulation and circulation in resting, active and defeathered California quail, *Lophortyx californicus*. *Comparative Biochemistry and Physiology*, 15, 399–421. [https://doi.org/10.1016/0010-406X\(65\)90141-6](https://doi.org/10.1016/0010-406X(65)90141-6)
- Buckley, L. B., Waaser, S. A., MacLean, H. J., & Fox, R. (2011). Does including physiology improve species distribution model predictions of responses to recent climate change? *Ecology*, 92, 2214–2221. <https://doi.org/10.1890/11-0066.1>
- Burleigh, J. G., Kimball, R. T., & Braun, E. L. (2015). Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution*, 84, 53–63. <https://doi.org/10.1016/j.ympev.2014.12.003>
- Chown, S. L., & Gaston, K. J. (2016). Macrophysiology—progress and prospects. *Functional Ecology*, 30, 330–344. <https://doi.org/10.1111/1365-2435.12510>
- Conradie, S. R., Woodborne, S. M., Wolf, B. O., Pessato, A., Mariette, M. M., & McKechnie, A. E. (2020). Avian mortality risk during heat waves will increase greatly in arid Australia during the 21st century. *Conservation Physiology*, 8, coaa048. <https://doi.org/10.1093/conphys/coaa048>
- Dawson, W. R. (1954). Temperature regulation and water requirements of the brown and Abert towhees, *Pipilo fuscus* and *Pipilo aberti*. In W. H. Furgason, A. M. Bullock, & A. M. Schechtman (Eds.), *University of California Publications in Zoology*, 59 (pp. 81–124). University of California Press.
- Dawson, W. R. (1982). Evaporative losses of water by birds. *Comparative Biochemistry and Physiology A*, 71, 495–509. [https://doi.org/10.1016/0300-9629\(82\)90198-0](https://doi.org/10.1016/0300-9629(82)90198-0)
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E., & Dunn, R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, 18, 448–456. <https://doi.org/10.1111/j.1365-2486.2011.02542.x>
- Dillon, M. E., Wang, G., & Huey, R. B. (2010). Global metabolic impacts of recent climate warming. *Nature*, 467, 704–706. <https://doi.org/10.1038/nature09407>
- Du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., & Ridley, A. R. (2012). The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, 18, 3063–3070. <https://doi.org/10.1111/j.1365-2486.2012.02778.x>
- Duarte, H., Tejedo, M., Katzenberger, M., Marangoni, F., Baldo, D., Beltrán, J. F., Martí, D. A., Richter-Boix, A., & Gonzalez-Voyer, A. (2012). Can amphibians take the heat? Vulnerability to climate warming in subtropical and temperate larval amphibian communities. *Global Change Biology*, 18, 412–421. <https://doi.org/10.1111/j.1365-2486.2011.02518.x>
- Freckleton, R. P. (2009). The seven deadly sins of comparative analysis. *Journal of Evolutionary Biology*, 22, 1367–1375. <https://doi.org/10.1111/j.1420-9101.2009.01757.x>
- Gaston, K. J., Chown, S. L., Calosi, P., Bernardo, J., Bilton, D. T., Clarke, A., Clusella-Trullas, S., Ghalambor, C. K., Konarzewski, M., Peck, L. S., Porter, W. P., Pörtner, H. O., Rezende, E. L., Schulte, P. M., Spicer, J. I., Stillman, J. H., Terblanche, J. S., & van Kleunen, M. (2009). Macrophysiology: A conceptual reunification. *American Naturalist*, 174, 595–612. <https://doi.org/10.1086/605982>
- 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. *Functional Ecology*, 33, 597–607. <https://doi.org/10.1111/1365-2435.13274>
- Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology*, 87, 782–795. <https://doi.org/10.1086/678956>
- Gessaman, J. A., & Nagy, K. A. (1988). Energy metabolism: Errors in gas-exchange conversion factors. *Physiological Zoology*, 61, 507–513. <https://doi.org/10.1086/physzool.61.6.30156159>
- Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 326, 119–157.
- 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>
- 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. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1939–1948. <https://doi.org/10.1098/rspb.2008.1957>
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 1665–1679.
- Intergovernmental Panel on Climate Change. (2018). *Global warming of 1.5°C: An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. Geneva, Switzerland: World Meteorological Organization.
- IUPS Thermal Commission. (2001). Glossary of terms for thermal physiology. *Japanese Journal of Physiology*, 51, 245–280.
- Jetz, W., Wilcove, D. S., & Dobson, A. P. (2007). Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, 5, e157. <https://doi.org/10.1371/journal.pbio.0050157>
- Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: Combining physiological and spatial data to predict species' ranges. *Ecology Letters*, 12, 334–350. <https://doi.org/10.1111/j.1461-0248.2008.01277.x>
- Kearney, M., Shine, R., & Porter, W. P. (2009). The potential for behavioural thermoregulation to buffer 'cold-blooded' animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 3835–3840. <https://doi.org/10.1073/pnas.0808913106>
- Khalig, I., Hof, C., Prinzing, R., Böhning-Gaese, K., & Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20141097.

- La Sorte, F. A., & Jetz, W. (2010). Avian distributions under climate change: Towards improved projections. *Journal of Experimental Biology*, 213, 862–869. <https://doi.org/10.1242/jeb.038356>
- Lighton, J. R. B. (2008). *Measuring metabolic rates: A manual for scientists*. Oxford, UK: Oxford University Press.
- Lighton, J. R. B., & Halsey, L. G. (2011). Flow-through respirometry applied to chamber systems: Pros and cons, hints and tips. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 158, 265–275. <https://doi.org/10.1016/j.cbpa.2010.11.026>
- Marder, J., & Arieli, Y. (1988). Heat balance of acclimated pigeons (*Columba livia*) exposed to temperatures up to 60°C Ta. *Comparative Biochemistry and Physiology Part A: Physiology*, 91, 165–170. [https://doi.org/10.1016/0300-9629\(88\)91610-6](https://doi.org/10.1016/0300-9629(88)91610-6)
- Marder, J., & Gavrieli-Levin, I. (1987). The heat-acclimated pigeon: An ideal physiological model for a desert bird. *Journal of Applied Physiology*, 62, 952–958. <https://doi.org/10.1152/jap.1987.62.3.952>
- Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149, 646–667. <https://doi.org/10.1086/286013>
- McCafferty, D. J., Gallon, S., & Nord, A. (2015). Challenges of measuring body temperatures of free-ranging birds and mammals. *Animal Biotelemetry*, 3, 33. <https://doi.org/10.1186/s40317-015-0075-2>
- McKechnie, A. E., Coe, B. H., Gerson, A. R., & Wolf, B. O. (2017). Data quality problems undermine analyses of endotherm upper critical temperatures. *Journal of Biogeography*, 44, 2424–2426. <https://doi.org/10.1111/jbi.12941>
- 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. *Journal of Experimental Biology*, 220, 2436–2444. <https://doi.org/10.1242/jeb.155507>
- McKechnie, A. E., Whitfield, M. C., Smit, B., Gerson, A. R., Smith, E. K., Talbot, W. A., Garcia, M., Gerson, A. R., & Wolf, B. O. (2016). Avian thermoregulation in the heat: Efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *Journal of Experimental Biology*, 219, 2145–2155. <https://doi.org/10.1242/jeb.138776>
- McKechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6, 253–256.
- McKechnie, A. E., & Wolf, B. O. (2004). The allometry of avian basal metabolic rate: Good predictions need good data. *Physiological and Biochemical Zoology*, 77, 502–521. <https://doi.org/10.1086/383511>
- McKechnie, A. E., & Wolf, B. O. (2019). The physiology of heat tolerance in small endotherms. *Physiology*, 34, 302–313. <https://doi.org/10.1152/physiol.00011.2019>
- McNab, B. K. (2002). *The physiological ecology of vertebrates: A view from energetics*. Ithaca, NY: Comstock Publishing Associates.
- Muggeo, V. M. (2008). Segmented: An R package to fit regression models with broken-line relationships. *R News*, 8, 20–25.
- Noakes, M. J., Wolf, B. O., & McKechnie, A. E. (2016). Seasonal and geographical variation in heat tolerance and evaporative cooling capacity in a passerine bird. *Journal of Experimental Biology*, 219, 859–869. <https://doi.org/10.1242/jeb.132001>
- 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. *Journal of Comparative Physiology B*, 187, 477–491. <https://doi.org/10.1007/s00360-016-1047-4>
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2012). Caper: Comparative analyses of phylogenetics and evolution in R. *R Package Version 0.5*, 2, 458.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401, 877–884. <https://doi.org/10.1038/44766>
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290. <https://doi.org/10.1093/bioinformatics/btg412>
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics*, 37, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, 18, 228–233. [https://doi.org/10.1016/S0169-5347\(03\)00036-3](https://doi.org/10.1016/S0169-5347(03)00036-3)
- Piersma, T., & van Gils, J. A. (2010). *The flexible phenotype: A body-centred integration of ecology, physiology, and behaviour*. Oxford University Press.
- Pollock, H. S. (2016). *The influence of spatiotemporal variation in ambient temperature on the ecology and physiology of birds* (PhD thesis). University of Illinois at Urbana-Champaign.
- Pollock, H. S., Brawn, J. D., Agin, T. J., & Cheviron, Z. A. (2019). Differences between temperate and tropical birds in seasonal acclimatization of thermoregulatory traits. *Journal of Avian Biology*, 50, 1–11. <https://doi.org/10.1111/jav.02067>
- Pollock, H. S., Brawn, J. D., & Cheviron, Z. A. (2020). Data from: Heat tolerances of temperate and tropical birds and their implications for susceptibility to climate warming. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.c2fqz6166>
- Powers, D. R. (1992). Effect of temperature and humidity on evaporative water loss in Anna's hummingbird (*Calypte anna*). *Journal of Comparative Physiology B*, 162, 74–84. <https://doi.org/10.1007/BF00257939>
- Prinzinger, R., Preßmar, A., & Schleucher, E. (1991). Body temperature in birds. *Comparative Biochemistry and Physiology Part A: Physiology*, 99, 499–506. [https://doi.org/10.1016/0300-9629\(91\)90122-S](https://doi.org/10.1016/0300-9629(91)90122-S)
- Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573. <https://doi.org/10.1038/nature15697>
- Randall, W. C. (1943). Factors influencing the temperature regulation of birds. *American Journal of Physiology*, 139, 56–63. <https://doi.org/10.1152/ajplegacy.1943.139.1.56>
- Rat, M., Mathe-Hubert, H., McKechnie, A. E., Sueur, C., & Cunningham, S. J. (2020). Extreme and variable environmental temperatures are linked to reduction of social network cohesiveness in a highly social passerine. *Oikos*. <https://doi.org/10.1111/oik.07463>
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1, 319–329. <https://doi.org/10.1111/j.2041-210X.2010.00044.x>
- Russo, S., Dosio, A., Graversen, R. G., Sillmann, J., Carrao, H., Dunbar, M. B., Singleton, A., Montagno, P., Barbola, P., & Vogt, J. V. (2014). Magnitude of extreme heat waves in present climate and their projection in a warming world. *Journal of Geophysical Research: Atmospheres*, 119, 12–500. <https://doi.org/10.1002/2014JD022098>
- Scholander, P. F., Hock, R., Walters, V., Johnson, F., & Irving, L. (1950). Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin*, 99, 237–258. <https://doi.org/10.2307/1538741>
- Şekercioğlu, Ç. H., Primack, R. B., & Wormworth, J. (2012). The effects of climate change on tropical birds. *Biological Conservation*, 148, 1–18. <https://doi.org/10.1016/j.biocon.2011.10.019>
- 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. *Journal of Experimental Biology*, 221, 1–10. <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. *Journal of Experimental Biology*, 220, 3290–3300. <https://doi.org/10.1242/jeb.161141>

- Smith, E. K., O'Neill, J., Gerson, A. R., & Wolf, B. O. (2015). Avian thermoregulation in the heat: Resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *Journal of Experimental Biology*, 218, 3636–3646. <https://doi.org/10.1242/jeb.128645>
- Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, 213, 912–920. <https://doi.org/10.1242/jeb.037473>
- Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2010). Global analysis of thermal tolerance and latitude in ectotherms. *Proceedings of the Royal Society B: Biological Sciences*, 278, 1823–1830.
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5610–5615. <https://doi.org/10.1073/pnas.1316145111>
- Sunday, J., Bennett, J. M., Calosi, P., Clusella-Trullas, S., Gravel, S., Hargreaves, A. L., Leiva, F. P., Verberk, W. C., Olalla-Tárraga, M. A., & Morales-Castilla, I. (2019). Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20190036.
- Swanson, D. L. (2010). Seasonal metabolic variation in birds: Functional and mechanistic correlates. In C. F. Thompson (Ed.), *Current ornithology* (Vol. 17, pp. 75–129). Springer Publishing Inc.
- Van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool: Behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, 191, 205–215. <https://doi.org/10.1007/s00442-019-04486-x>
- Van de Ven, T. M. F. N., McKechnie, A. E., Er, S., & Cunningham, S. J. (2020). High temperatures are associated with substantial reductions in breeding success and offspring quality in an arid-zone bird. *Oecologia*, 193, 225–235. <https://doi.org/10.1007/s00442-020-04644-6>
- Vinagre, C., Leal, I., Mendonça, V., Madeira, D., Narciso, L., Diniz, M. S., & Flores, A. A. (2016). Vulnerability to climate warming and acclimation capacity of tropical and temperate coastal organisms. *Ecological Indicators*, 62, 317–327. <https://doi.org/10.1016/j.ecolind.2015.11.010>
- Walsberg, G. E. (1993). Thermal consequences of diurnal microhabitat selection in a small bird. *Ornis Scandinavica*, 24, 174–182. <https://doi.org/10.2307/3676733>
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., Fromentin, J. M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395. <https://doi.org/10.1038/416389a>
- Weathers, W. W. (1981). Physiological thermoregulation in heat-stressed birds: Consequences of body size. *Physiological Zoology*, 54, 345–361. <https://doi.org/10.1086/physzool.54.3.30159949>
- Weathers, W. W. (1997). Energetics and thermoregulation by small passerines of the humid, lowland tropics. *The Auk*, 114, 341–353. <https://doi.org/10.2307/4089237>
- 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. *Journal of Experimental Biology*, 218, 1705–1714. <https://doi.org/10.1242/jeb.121749>
- Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A., & Gwinner, E. (2003). Slow pace of life in tropical sedentary birds: A common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society of London B: Biological Sciences*, 270, 2383–2388.
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A., & Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biology*, 6, e325. <https://doi.org/10.1371/journal.pbio.0060325>
- Withers, P. C. (2001). Design, calibration and calculation for flow-through respirometry systems. *Australian Journal of Zoology*, 49, 445–461. <https://doi.org/10.1071/ZO00057>
- Wolf, B. O., Coe, B. H., Gerson, A. R., & McKechnie, A. E. (2017). Comment on an analysis of endotherm thermal tolerances: Systematic errors in data compilation undermine its credibility. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162523.
- Wolf, B. O., & Walsberg, G. E. (1996). Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology*, 77, 2228–2236. <https://doi.org/10.2307/2265716>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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