The functional significance of facultative hyperthermia varies with body size and phylogeny in birds

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Abstract

1. Facultative hyperthermia, the elevation of body temperature above normothermic levels, during heat exposure, importantly affects the water economy and heat balance of terrestrial endotherms. We currently lack a mechanistic understanding of the benefits hyperthermia provides for avian taxa.

2. Facultative hyperthermia has been proposed to minimize rates of water loss via three distinct mechanisms: M1) by maintaining body temperature ($T_b$) above environmental temperatures ($T_e$), heat can be lost non-evaporatively, saving water; M2) by minimizing the thermal gradient when $T_e > T_b$, environmental heat gain and evaporative water loss rates are reduced; and M3) by storing heat via increases in $T_b$ which reduces evaporative heat loss demands and conserves water.

3. Although individuals may benefit from all three mechanisms during heat exposure, the relative importance of each mechanism has not been quantified among species that differ in their body size, heat tolerance and mechanisms of evaporative heat dissipation.

4. We measured resting metabolism, evaporative water loss and real-time $T_b$ from 33 species of birds representing nine orders ranging in mass from 8 to 300 g and estimated the water savings associated with each proposed mechanism. We show that facultative hyperthermia varies in its benefits among species.

5. Small songbirds with comparatively low evaporative cooling capacities benefit most from (M1), and hyperthermia maintains a thermal gradient that allows non-evaporative heat losses. Other species benefited most from (M2) minimizing evaporative losses via a reduced thermal gradient for heat gain at high $T_e$. We found that (M3), heat storage, only improved the water economy of the sandgrouse, providing little benefit to other species.

6. We propose that differences in the frequency and magnitude of hyperthermia will drive taxon-specific differences in temperature sensitivity of tissues and enzymes and that the evolution of thermoregulatory mechanisms of evaporative heat dissipation.
1 | INTRODUCTION

Life in arid terrestrial environments represents a constant challenge for small endotherms, which are persistently subject to a desiccating environment. Under modest environmental temperatures where $T_{air} < T_b$, high mass-specific metabolic rates and the need to frequently ventilate the respiratory surfaces produce rapid dehydration in both mammals and birds (Bartholomew & Cade, 1963; Schmidt-Nielsen, 1964; Wolf & Walsberg, 1996b). At higher environmental temperatures, when operative temperatures ($T_o$), a value that integrates the effects of conduction, convection and radiation on an animal's heat balance, exceeds an animal's body temperature ($T_b$), both metabolic and environmental heat loads must be dissipated through evaporation, which increases rapidly at high environmental temperatures (Bakken, 1976; Wolf & Walsberg, 1996b).

Water conservation is thus a high priority for desert animals and has importantly shaped their behaviour, morphology and physiology. Most small mammals, for example, are nocturnal and thus directly avoid the high temperatures associated with the desert environment (Schmidt-Nielsen, 1964; Walsberg, 2000). Birds, in contrast, are largely diurnal and must routinely confront extremely high air temperatures and intense solar heat loads during their daily activity (Wolf & Walsberg, 1996a).

It is well known that average body temperatures of birds (~41°C) are substantially higher than those of mammals (~37°C; Wetmore, 1921; Wislocki, 1933; Dawson & Schmidt-Nielsen, 1964). Although mammals and birds are often characterized as strict homeotherms, many species have the ability to both increase and decrease $T_b$ over diel and seasonal time-scales (Boyles et al., 2013). Furthermore, patterns of $T_b$ variation can differ among and within species and may be correlated with physiological factors such as body condition or hydration status, and/or environmental factors such as food availability, environmental temperature and precipitation (Schmidt-Nielsen, Schmidt-Nielsen, Jarnum, & Haupt, 1956; Smit, Harding, Hockey, & McKechnie, 2013). Thus, endothermy manifests as a range of thermoregulatory phenotypes, but a lack of understanding of the adaptive significance of these thermoregulatory phenotypes limits our understanding of the role of endothermy as a whole (Angilletta, Cooper, Schuler, & Boyles, 2010; Boyles et al., 2013; Levesque, Menzies, Landry-Cuerrier, Larocque, & Humphries, 2017).

Many studies of mammals and birds have investigated the adaptive role of facultative, regulated hyperthermia, usually in the extreme cases of daily torpor and seasonal hibernation (McKechnie & Lovegrove, 2002; Ruf & Geiser, 2014). The adaptive significance of regulated hyperthermia is readily apparent as a mechanism that reduces energy demand and increases survival. In contrast, although variation in $T_b$ above normothermic values has been well documented in a wide variety of endotherms, from pioneering studies of heat tolerance in camels (Schmidt-Nielsen et al., 1956), boweels and mourning doves (Bartholomew & Dawson, 1954; Dawson, 1954), to more recent studies on fluctuations in $T_b$ in tropical mammals (Levesque, 2018), the data available for a direct assessment of the benefits of hyperthermia to the heat balance and water economy across avian taxa, with body size, and its association with heat tolerance have been very limited (Calder & King, 1974; Tieleman & Williams, 1999; Weathers, 1981).

Birds experiencing high environmental temperatures often exhibit hyperthermia, with $T_b$ increasing above typical active-phase values of ~40-41°C, reaching levels as high as 45-47°C, the upper range of which is thought to represent avian lethal limits (Dawson, 1954). These increases in $T_b$ above normothermic values are often not a failure of thermoregulation (i.e. pathological hyperthermia) but rather represent a facultative physiological response involving a temporarily increased set point, as has been shown in a number of early (e.g. Dawson, 1954; Bartholomew & Dawson, 1958; Dawson & Fisher, 1969 and more recent studies Gerson, Smith, Smit, McKechnie, & Wolf, 2014; O’Connor, Wolf, Brigham, & McKechnie, 2017; Smit et al., 2013; Smith, O’Neill, Gerson, & Wolf, 2015; Whitfield, Smit, McKechnie, & Wolf, 2015). These recent studies have evaluated $T_b$ under conditions of high $T_p$ and have shown that a stepwise increase in $T_b$ results in a corresponding increase in $T_p$.

This pattern continues with increasing $T_b$ until a maximal heat load is reached, beyond which a controlled, stable $T_b$ can no longer be maintained and $T_b$ steadily rises to lethal levels. This final stage is very similar to typical, well-documented patterns of $T_b$ in response to high heat loads in many species of endotherms (Leon & Helwig, 2010).

Facultative, regulated hyperthermia has been proposed to benefit the water economy of birds by one or more mechanisms (Figure 1). The first of these mechanisms (M1) maintains a gradient for passive heat loss by increasing $T_b$ with increasing $T_p$. Maintaining
T_b > T_e allows for dissipation of excess heat by the animal via dry heat loss (conduction, convection and radiation) and reduces evaporative demands by delaying or avoiding the scenario where T_e exceeds T_b. The second mechanism (M2) applies most when T_e exceeds T_b as increasing T_b minimizes the thermal gradient between the animal and the environment, reducing heat gain, and lower rates of evaporative water loss are required to maintain heat balance. The third mechanism (M3) maintains that as T_b increases, heat is stored in body tissues and represents heat that was not dissipated evaporatively, saving water, as long as stored heat is dissipated non-evaporatively once the thermal gradient is again favourable to dry heat loss from the animal to the environment (T_b > T_e). This would allow animals to save water during the hottest parts of the day by tolerating a temporarily high T_b (Bartholomew & Cade, 1963; Schmidt-Nielsen et al., 1956; Tieleman & Williams, 1999).

Here, we investigate the functional significance of hyperthermia in 33 species of bird representing nine orders, and we use these data to empirically quantify each of the proposed benefits of hyperthermia and how they vary with body mass and phylogeny. Our analysis includes a phylogenetically and biogeographically diverse sample of metabolic rate, water loss and real-time T_b data from desert birds in response to ecologically relevant high temperatures. Prior studies (see data sources below; Table S2) have focused on the physiological performance of individual species that regularly experience high temperatures; however, each of these studies alone does not capture the diversity of thermoregulatory strategies employed in response to high temperature across avian taxa. Therefore, a broad-scale phylogenetic and mechanistic analysis of the use of hyperthermia is needed to assess the broad patterns of physiological responses to heat from which we can then deduce the ecological and evolutionary significance of hyperthermia.

2 | MATERIALS AND METHODS

2.1 | Data Sources

Data for 32 of the species included in this study were previously published (McKechnie et al., 2017; McKechnie, Smit et al., 2016; McKechnie, Whitfield et al., 2016; McWhorter et al., 2018; Smit et al., 2018; Smith, O’Neill, Gerson, McKechnie, & Wolf, 2017; Smith et al., 2015; Talbot, Gerson, Smith, McKechnie, & Wolf, 2018; Talbot, McWhorter, Gerson, McKechnie, & Wolf, 2017; Whitfield et al., 2015) see Table S2), whereas the remaining species (red-billed buffalo-weaver, Bubalornis niger) has not been published elsewhere. The published studies detail the conditions of capture, holding and how temperature trials were performed, which all followed similar protocols. Briefly, birds were almost always evaluated on the day of capture, but occasionally were held overnight. Following capture, a temperature-sensitive passive integrated transponder (PIT) tag was implanted into the abdominal cavity to measure core T_b continuously, and birds were allowed to recover before being placed in a respirometry chamber where they were exposed to stepwise increases in T_b from 30°C to the upper thermal limit, during which time the rate of carbon dioxide production (VCO₂), water loss (VH₂O) and T_b was measured continuously. At each air temperature (T_a) which approximates T_b under our experimental conditions, birds were allowed time to habituate for 10–30 min to the conditions inside the chamber to ensure both T_b and the gas exchange measurements approximated steady state. Measurements commenced once T_b, VCO₂ and VH₂O stabilized. All energy and water fluxes were converted to mW using appropriate respiratory exchange ratio (RER) and thermal equivalencies as described for each study which followed (Walsberg & Wolf,
1995). We then used standard heat balance equations to evaluate the three hypothesized benefits of hyperthermia. Using these data and standard heat balance equations (Equations 1 & 3 below), we were able to calculate $H$ (dry heat loss; mW) and $h$ (heat transfer coefficient; mW per °C) across a range of temperatures for individuals of each of the species tested (Table S1).

### 2.2 Calculations

Using metabolic rate ($M$), evaporative water loss rate ($E$) and $T_a$ data, dry heat loss ($H$; mW) was calculated for each $T_s$ experienced by each individual bird as follows:

$$ H = M - E - C(dT_b/dt) $$

where $H$ is the dry heat loss when (+) and dry heat gain when (-), $M$ is metabolic rate in mW, $E$ is evaporative heat loss in mW, $C$ is the specific heat capacity for the bird which is simply the product of body mass and the specific heat of tissues (3.35 J g$^{-1}$ °C$^{-1}$), and $dT_b/dt$ is the rate of change in body temperature in °C/s, which was always close to zero indicating the animal was in steady state (Bakken, 1976; Tieleman & Williams, 1999).

The dry heat transfer coefficient ($h$) was calculated by rearranging the heat balance equation.

$$ M - E - C(dT_b/dt) = h(T_b - T_a) $$

(2)

to solve for $h$ to yield.

$$ h = M - E - C(dT_b/dt)/(T_b - T_a) $$

(3)

where $T_a$ is the air temperature in the metabolic chamber and $T_b$ is the body temperature of the bird. For additional details on the calculation of $h$ including our procedure for estimating $h$ where indeterminate forms resulted from our calculations, see Appendix S1.

Once $H$ and $h$ had been calculated, we were able to evaluate the proposed hypotheses in the following ways:

M1) To determine whether birds allow $T_b$ to track $T_a$ as a means to prevent an inversion of the temperature gradient, leading to net heat gain from the environment, we restricted the dataset to instances where $T_a < T_b$ and then determined the upper 95% quantile of $T_b$ reached by each species while still maintaining $T_a < T_b$. We also used general linear mixed models to investigate interspecific variation in the relationship between ($T_a - T_b$) and $T_a$, where the slope of this negative relationship provides a metric for how closely $T_b$ tracks increases in $T_a$ (see Appendix S1). For each of these metrics, we used the statistical approach outlined below, and we investigated the phylogenetic signal for each of these traits by calculating phylogenetic independent contrasts (PIC) to investigate the phylogenetic and body mass as drivers of these traits.

M2) To quantify the reduction in evaporative water losses because of the use of hyperthermia, equation 3 was rearranged to solve for evaporative water loss ($E$) using our calculated value of $h$ using all empirically measured values. This value of $E$ was compared to measured values as a validation of our calculated $h$ values. We then also calculated normothermic evaporative water loss ($E'$) using normothermic $T_b$ (mean $T_b$ of inactive birds at $T_a < 35^\circ$C) instead of measured $T_b$ to estimate evaporative water loss in the absence of hyperthermia. Thus, $E'$ represents the rate of evaporative water loss that would occur if a constant and normothermic $T_b$ were defended over the entire range of $T_a$ for each species, and assuming all other parameters remain unchanged. The difference between $E$ and $E'$ is the water savings due to hyperthermia and was evaluated among species as a function of $T_a$ above 39°C, and again, we evaluated the phylogenetic signal and generated PIC for the slopes of this relationship to investigate the importance of phylogeny and mass scaling to the variation we found in this trait.

M3) To determine the water savings due to heat storage, we first determined the difference between $T_b$ at a particular $T_a$ and normothermic $T_b$. The product of this difference in $T_b$, body mass ($M_b$) of the bird and the specific heat of body tissues (assumed to be 3.35 J g$^{-1}$ °C$^{-1}$) was divided by the specific heat of vaporization of water (2.43 J/g) to yield an estimate of the mass of water that would have been required to dissipate the stored heat.

### 2.3 Statistics

The relationships for all three mechanisms were evaluated among species using a general linear mixed model with individual as a random factor and all two-way interactions. For all models, nonsignificant (> 0.05) terms were removed using backward stepwise model selection until only significant terms remained. When a significant interaction including species as a factor was identified, the slopes ±95% CI were reported, and overlap of confidence intervals was used to evaluate differences. For each hypothesis, the derived slopes were regressed against $M_b$ to evaluate the scaling of various traits. In these instances, we also determined the phylogenetic signal of these traits and derived phylogenetic independent contrasts (PIC) to remove influence of phylogeny on these data before investigating scaling relationships, using a similar approach to Rodriguez et al. (2015). We downloaded a subset of 100 phylogenies that included all our species in our dataset from http://www.birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) using the Hackett et al., 2008 (Hackett et al., 2008) phylogeny as a backbone. We then derived a consensus tree and determined branch lengths using the ape package in R (Paradis, 2011). Continuous trait figures were developed using the phytools package (Revell, 2013) and phylosig, with PIC tools from this package used to estimate phylogenetic signal as well as phylogenetic independent contrasts.

### 3 RESULTS

We analysed data for 33 species representing nine orders, spanning a ∼ 36-fold $M_b$ range of 8.6–308.0 g (Table S1). We found large variation among species in the maximal thermal gradient ($T_a - T_b$) defended, ranging from −1.4°C at $T_a = 46.2$°C for yellow-plumed
honeyeaters (Lichenostomus ornatus) to -23.2°C at $T_a = 64.6$°C for white-winged doves (Zenaida asiatica). At $T_a > 37$°C, the rate of $T_b$ increase in response to rising $T_a$ differed among species (species x temperature: $F_{32,744} = 14.3, p < 0.001$). Consequently, we evaluated this relationship for each species independently using linear mixed effects models and report parameter estimates with 95% CI for each species in Table S1. All species showed an increase in $T_b$ with increasing $T_a$, with slopes ranging ~7-fold from 0.05°C per °C for the mourning dove to 0.37°C per °C for the scaly-feathered weaver. Due to the scaling of surface area to mass, we hypothesized that the slope of the relationship between $T_a$ and $T_b$ would show strong scaling with $M_b$. To evaluate this possibility, we initially compared natural log-transformed slopes from each species to natural log ($M_b$) using traditional linear models and found no significant relationship ($F_{1,31} = 3.60, p = 0.067$). We then determined the phylogenetic signal for mass ($K = 0.14, p = 0.098$, Lambda = 0.39, $p = 0.03$) and for slope of $T_b$ ($K = 0.17, p = 0.039$; Lambda = 0.27, $p = 0.06$) and calculated phylogenetic independent contrasts both for the log-transformed slope of $T_b$ at $T_a > 37$°C and for log-transformed $M_b$. By correcting for phylogeny, the relationship between body mass and slope of $T_b$ above 37°C became significant ($F_{1,31} = 4.64, p = 0.039$) indicating unique physiological adaptations within some avian taxa that offset the impact of $M_b$ alone on net heat gain from the environment.

3.1 | M1—Maximize non-evaporative heat loss

We found a significant relationship between log 95% quantile $T_b$ and log mean $M_b$ ($F_{1,31} = 11.975, p = 0.001$; $\log(T_b) = 3.806 - 0.0150 \log(M_b)$; Figure 2a). Again, we evaluated this relationship using PIC and this relationship remained significant ($F_{1,31} = 10.99, p < 0.002; m = -0.012$) due to the weak to moderate phylogenetic signal for mass ($K = 0.14, p = 0.09$; Lambda = 0.39, $p = 0.03$) and a moderate phylogenetic signal for 95% quantile of $T_b$ ($K = 0.25, p = 0.002$; Lambda = 0.71, $p < 0.001$; Figure 2b). Species with low $M_b$ attained the highest $T_b$ while still maintaining a net dry heat loss to the environment, compared to large species, but this strategy was dominated by passerines. Mass-independent residuals of Caprimulgiformes (nightjars—poorwills and nighthawks) and Pterocliformes (sandgrouse) tended to be negative, indicating these taxa make less pronounced use of hyperthermia for the purpose of maintaining $T_b > T_a$. Passerines (songbirds) tended to have positive residuals, indicating a high $T_b$ was reached while still maintaining a net positive dry heat loss—evidence in support of this thermoregulatory benefit of hyperthermia in these species (Figure 2a,b).

3.2 | M2—Reduce evaporation rate

The use of hyperthermia results in significant reductions in mass-specific EWL when compared to the hypothetical situation where $T_b$ does not increase with increasing heat load (Figure 3a). The magnitude of the mass-specific savings in relation to chamber $T_b$ differed among species (Temperature x Species: $F_{1,31} = 39.423, p < 0.001$; Figure 3a, Table S2). The greatest water savings accrued from hyperthermia were realized by small passerines, and the relationship between mass-specific savings and $T_b$ showed moderate phylogenetic signal overall ($K = 0.20, p = 0.009$; Lambda = 0.42, $p = 0.003$), and inspection of the continuous trait phylogeny (Figure 3b) revealed dramatic variation among clades. Thus, we used PIC to identify the relationship between phylogenetically independent savings in EWL and mass ($F_{1,31} = 60.48, p < 0.001, m = -0.059$; Standard lm: $F_{1,31} = 38.71, p < 0.001; \log(EWL\text{savings per } ^\circ\text{C}) = -0.639 \log(M_b) + 1.93$).

**FIGURE 2** (a) Maximal body temperature while $T_b$ exceeds $T_a$ scales negatively with body mass (natural log). Small-bodied birds such as songbirds use hyperthermia to a greater degree than large-bodied birds to avoid or delay $T_b$ exceeding $T_a$. (b) This use of hyperthermia differs among taxa, where doves (Columbiformes), sandgrouse (Pterocliformes) and nightjars (Caprimulgiformes) (upper clades) maintain lower $T_b$ as $T_a$ increases (values mapped onto phylogeny are raw data, i.e. not corrected for phylogeny). See Results for statistics.
3.3 | M3—Heat storage

The water savings resulting from heat storage as $T_b$ increased varied among species (Species x $T_c$: $F_{1,734} = 23.09, p < 0.001$; see Table S2). Water savings as a function of $T_b$ had low phylogenetic signal ($K = 0.17, p = 0.033$, Lambda = 0.31, $p = 0.37$), and thus, the differences in slope with increasing $T_b$ were adequately explained by $M_b$ (PIC: $F_{1,21} = 179.4, p < 0.001$; glm: $F_{1,21} = 9.51, p = 0.01$; log (water saved by heat storage per °C) = 2.77 (log $M_b$) – 18.31). For example, among similarly sized birds, water savings resulting from heat storage were greatest in the sandgrouse (Pterocliformes) (67.8 mg/°C) and were among the lowest for white-winged dove (Columbiformes) (12.5 mg/°C) (Table S2; Figure S1). Water savings due to heat storage were most significant for species with high $M_b$ that also employed pronounced hyperthermia (Figure S1).

3.4 | Comparing water savings at a common air temperature

A comparison of water savings from reduced EWL (M2) due to an improved thermal gradient to the water saved by heat storage alone (M3) at $T_e = 45°C$ for 1 hr reveals the relative importance of each of these proposed benefits of hyperthermia (Figure 4). The improved thermal gradient associated with hyperthermia results in significant savings due to reduced EWL, especially in small birds, and in orders where cutaneous water loss is low (passerines). Large birds such as sandgrouse seem to be unique in their pronounced use of hyperthermia despite their large $M_b$, and therefore, this group seems to benefit from heat storage more so than others of equal size. Nonetheless, even large birds save proportionally more water through the benefit of a reduced rate of water loss over longer time periods.

4 | DISCUSSION

We found considerable phylogenetic and size-related variation in the functional significance of hyperthermia to the water balance of arid-zone birds experiencing very hot conditions. These results highlight the physiological diversity among desert birds in terms of their capacity for dealing with extreme temperatures, which will importantly affect their persistence in warming ecosystems (McKechnie & Wolf, 2010), while also shedding new light on the potential role of water economy on the evolution of endothermic set points in birds.

Our evaluation of M1, that hyperthermia maximizes non-evaporative heat loss, showed that numerous species maintain $T_b > T_e$ with increasing $T_e$ to maximize dry heat losses to the environment—reducing the amount of water required for evaporative cooling. This process is most pronounced in small songbirds (passerines) and results in significant water savings, but is only feasible up to $T_b$ of ~44–45°C, above which $T_b$ approaches lethal limits. Yellow-plumed honeyeaters, for instance, used this mechanism but were only able to tolerate a thermal gradient where $T_e$ exceeded $T_b$ by 1.47°C, reaching a max $T_e$ of 46°C. These birds are one of the smallest passerines studied and used hyperthermia to maintain $T_b > T_e$ at $T_e$ up to ~45°C. The use of hyperthermia to maximize dry heat losses thus appears to be a primary strategy at moderately hot $T_e$ for smaller birds with limited capacity for evaporation. However, it does not allow small species with high surface area–volume ratios and limited ability to evaporate water to tolerate extremely high $T_e$ (~50°C and above). Most species that heavily utilized this strategy also have low heat tolerance limits (Table S1). Further, this strategy seems to be most utilized by songbirds, parrots and owls, rather than doves, nightjars and sandgrouse.

Our evaluation of M2, that hyperthermia reduces the rate of evaporative water loss, indicates that the most significant benefit to
The slope of $T_b$ against $T_e$ in the sandgrouse is very similar to some of the smallest songbirds (Table S1), and the substantial water savings due to heat storage (M3) set them apart from all other birds in their thermoregulatory strategy (Figure S1). Although not as dramatic, the quail and some of the larger songbirds also appear to follow this strategy.

The difference in the use of hyperthermia to reduce EWL relative to the savings from of heat storage (M2 vs. M3) is illustrated in (Figure 4), which shows the water economies of all species held at $T_e = 45^\circ$C for 1 hr. For all species, even over this relatively short time-scale, the primary benefit of employing hyperthermia is to reduce the rate of evaporative water loss (M2), and only in the Burchell’s sandgrouse does the benefit from heat storage (M3) outweigh that of reduced rates of EWL.

We identify a clear phylogenetic divide in the heat tolerance limits of birds that we posit is functionally linked to the primary avenue of evaporation. Doves (columbids), which rely primarily on transcutaneous evaporation, are often highly tolerant to heat (Marder, 1983; McKechnie & Wolf, 2004). This high HTL appears to be due to the low metabolic cost of non-glandular transcutaneous evaporation, compared to the relatively high metabolic costs of panting. This results in much lower heat loads from metabolism during heat exposure, and thus, evaporative heat loss is only required to dissipate external heat loads. Nightjars (Caprimulgidae), in contrast, use gular flutter, which is the rapid oscillation of the throat pouch (Bartholomew, Lasiewski, & Crawford, 1968), which is also very efficient (O’Connor et al., 2017; Talbot et al., 2017). Currently, it appears that most other orders of birds investigated to date, the songbirds, owls, parrots and sandgrouse, rely primarily on panting (but see Bartholomew et al., 1968). Panting requires substantial metabolic input to contract thoracic muscles to move large volumes of air over the moist respiratory surfaces, and thus, metabolic heat is generated and must be dissipated in addition to the environmental heat load. Further, panting also ventilates the respiratory tract with air that is in many instances at a higher temperature than body temperature, perhaps resulting in additional heat load (Schmidt-Nielsen, Hainsworth, & Murrish, 1970; Seymour, 1972).

Although these findings have very obvious ecological implications, they also raise other questions about how the physiology of these animals has evolved in response to the different thermoregulatory phenotypes present among desert birds. It does appear that small songbirds utilize pronounced hyperthermia frequently during hot summers in deserts, and it is likely that their $T_b$ exceeds
43–44°C for many hours each day. \(T_b\) data from populations of nine species of wild birds held in outdoor aviaries in mid-summer in the Kalahari Desert support this prediction; several small (<50 g) songbirds maintained modal diurnal \(T_b\) values of ~43°C (Thompson, Cunningham, & McKechnie, 2018). In contrast, mean \(T_b\) at \(T_a\) ≥ 38°C in free-ranging populations of two southern African nightjars was lower, 40°C in freckled nightjars (Caprimulgus tristigma) and 42°C in rufous-cheeked nightjars (C. rufigna) (O’Connor et al., 2017), consistent with our conclusions that hyperthermia is relied upon much less by nightjars. When contrasted with doves and nightjars that have high evaporative efficiencies and rely much less on hyperthermia as a heat tolerance strategy, songbirds rely heavily on hyperthermia as a heat tolerance strategy and we therefore predict tissue-level differences in optimal temperatures for various functions that would be due to differences in heat stability and sensitivity of metabolic and other enzymes.

The variation in the occurrence and functional significance of hyperthermia among avian orders is also relevant to recent arguments that the thermal performance of endotherms can, like that of ectotherms, be viewed as a continuum from thermal specialization to generalization (Angilletta et al., 2010). According to this view, endotherms’ thermoregulation should be co-adapted with thermal sensitivity of performance in a similar manner to that of ectotherms, where temperature–performance relationships are commonly measured, and therefore, analogous trade-offs between thermal specialization and generalization should be evident in endotherms (Angilletta et al., 2010) with potentially important consequences for understanding how birds tolerate heat during current and future climates (Boyles, Seebacher, Smit, & McKechnie, 2011; McKechnie & Wolf, 2010). Differences among avian taxa in the ways in which they employ hyperthermia may represent one component of such a thermal specialist–generalist continuum. For instance, the observation that small desert songbirds readily use hyperthermia to maintain \(T_b\) > \(T\)p (and hence probably experience high \(T_b\) on a regular basis during summer at \(T_a = 35°C\) to 45°C) leads to the prediction that performance components, for instance those related to muscle function and cognition, may be less sensitive to temperatures above the normothermic \(T_b\) than other taxa that use high rates of evaporative heat loss to maintain \(T_b\) below \(T\)p such as doves and nightjars as has been found for peripheral and core tissues in mammals which experience wide and narrow ranges of temperature, respectively (James, 2013; James, Tallis, & Angilletta, 2014).

The expression of regulated hyperthermia may be predicted to be more pronounced in species or populations inhabiting hot environments compared to those inhabiting cooler regions. Few data are currently available with which to test this prediction, although among populations of a songbird that showed significantly greater heat tolerance during summer in a desert population, the greater heat tolerance appeared to arise from more efficient evaporative cooling rather than more pronounced hyperthermia (Noakes, Wolf, & McKechnie, 2016). It is also possible that differential expression of hyperthermia is involved in phenotypic plasticity in avian heat tolerance, such as the remarkable developmental plasticity associated with prenatal acoustic communication recently demonstrated for zebra finches (Mariette & Buchanan, 2016).

The pronounced use of hyperthermia to maintain positive \(T_b\)-\(T\)a gradients by songbirds, and their greater reliance on elevated \(T_b\) during thermoregulation at high \(T_a\) compared to other taxa, raises interesting questions about the evolution of thermal physiology in this order. Several authors have noted that songbirds have among the highest avian \(T_b\) (Clarke & Rothery, 2008; Prinzinger, Pressmar, & Schleucher, 1991), and a recent analysis of avian basal metabolic rates (BMR) confirmed early views that passerine BMR is significantly higher than that of other orders (Londoño, Chappell, Castañeda, Jankowski, & Robinson, 2014). Our findings here raise the intriguing, albeit highly speculative, possibility that the evolution of relatively high \(T_b\) and BMR among early songbirds is functionally linked to the use of hyperthermia on account of reliance on panting for evaporative heat loss. We speculate that the use of hyperthermia to compensate for a less efficient mechanism of evaporating water (panting) in passerines could be related to the evolution of higher resting \(T_b\) in this group.

Oscine passerines evolved in Australia during the late Oligocene and underwent rapid diversification during the early Miocene (Moyle et al., 2016). At this time, the Australian arid zone was warm and wet, with sea surface temperatures in the region at least 6–8°C higher than at comparable latitudes today (Byrne et al., 2008). The aridification of Australia commenced in the mid-Miocene (~15 MYA), leading to that continent’s arid-adapted contemporary biota (Byrne et al., 2008). Assuming ancestral oscine passerines, like extant species, relied on panting as the primary avenue of evaporative cooling, which is more efficient under humid conditions (Gerson et al., 2014), higher \(T_b\) may have been selected for in warm, wet and humid conditions in which the group initially diversified, as well as in the arid conditions that subsequently developed across much of the Australian continent. According to this hypothesis, the evolution of relatively high \(T_b\) and accompanying rapid metabolism in early passerines was driven by selection for the maintenance of positive \(T_b\)-\(T\)a gradients in environments where high \(T_b\) constrained thermoregulation in a taxon with high metabolic heat production but lacking more efficient pathways for evaporative heat dissipation.

5 | CONCLUSIONS

Our data reveal that body mass and phylogeny are important sources of variation in the expression and functional significance of hyperthermia. They also support the view that selection may act strongly on thermoregulation during very hot weather and that we expect inter- and/or intraspecific variation in avian heat tolerance correlated with climate. We show clear differences among avian taxa in the mechanism by which hyperthermia is beneficial to the water economy of birds. We identify small songbirds as highly susceptible to high temperatures due to their limited ability to evaporate water
at a high rate and to compensate these birds readily use hyperthermia to maintain temperature gradients favourable to dry heat losses. As a result, this group shows dramatic fluctuations in $T_a$ through a typical day and may therefore have unique adaptations to optimize performance at high $T_a$. However, given the increasing frequency and severity of heat events, it remains important to continue to investigate the long-term physiological, behavioural and ecological costs to animals that are repeatedly being forced to their thermoregulatory limits.

6 | ETHICS

All experimental procedures were approved by the Institutional Animal Care and Use Committee of the University of New Mexico (12-1005370-MCC), the Animal Ethics Committees of the University of Adelaide (S-2013-151A) and the University of Pretoria (EC054-16). The capture of birds was approved by all relevant federal, state and local officials. See [10–19] for details.

ACKNOWLEDGEMENTS

We are grateful to all the landowners in Australia (Birdlife Australia), South Africa (Leeupan Farm) and Tucson (The Cadden and Wolf families), and to our many field and laboratory technicians, at all three sites.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS


DATA ACCESSIBILITY

All individual-level animal data accompany previously published materials [see data sources].

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Gerson AR, McKechnie AE, Smit B, et al. The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. Funct Ecol. 2019:00:1–11. https://doi.org/10.1111/1365-2435.13274