

RESEARCH ARTICLE

Avian thermoregulation in the heat: is evaporative cooling more economical in nocturnal birds?

Ryan S. O'Connor¹, Ben Smit², William A. Talbot³, Alexander R. Gerson⁴, R. Mark Brigham⁵, Blair O. Wolf³ and Andrew E. McKechnie^{1,6,*}

ABSTRACT

Evaporative cooling is a prerequisite for avian occupancy of hot, arid environments, and is the only avenue of heat dissipation when air temperatures (T_a) exceed body temperature (T_b). Whereas diurnal birds can potentially rehydrate throughout the day, nocturnal species typically forgo drinking between sunrise and sunset. We hypothesized that nocturnal birds have evolved reduced rates of evaporative water loss (EWL) and more economical evaporative cooling mechanisms compared with diurnal species, permitting nocturnal species to tolerate extended periods of intense heat without becoming lethally dehydrated. We used phylogenetically informed regressions to compare EWL and evaporative cooling efficiency [ratio of evaporative heat loss (EHL) and metabolic heat production (MHP); EHL/MHP] among nocturnal and diurnal birds at high T_a . We analyzed variation in three response variables: (1) slope of EWL at T_a between 40 and 46°C, (2) EWL at $T_a=46^\circ\text{C}$ and (3) EHL/MHP at $T_a=46^\circ\text{C}$. Nocturnality emerged as a weak, negative predictor, with nocturnal species having slightly shallower slopes and reduced EWL compared with diurnal species of similar mass. In contrast, nocturnal activity was positively correlated with EHL/MHP, indicating a greater capacity for evaporative cooling in nocturnal birds. However, our analysis also revealed conspicuous differences among nocturnal taxa. Caprimulgids and Australian owl-nightjars had shallower slopes and reduced EWL compared with similarly sized diurnal species, whereas owls had EWL rates comparable to those of diurnal species. Consequently, our results did not unequivocally demonstrate more economical cooling among nocturnal birds. Owls predominately select refugia with cooler microclimates, but the more frequent and intense heat waves forecast for the 21st century may increase microclimate temperatures and the necessity for active heat dissipation, potentially increasing owls' vulnerability to dehydration and hyperthermia.

KEY WORDS: Caprimulgiformes, Dehydration tolerance, Diurnal, Evaporative water loss, Heat tolerance, Strigiformes

INTRODUCTION

Maintaining heat balance can present a significant physiological challenge for animals, particularly when inhabiting very hot environments (Porter and Gates, 1969). When environmental temperature exceeds body temperature (T_b), animals experience a net heat gain and evaporative water loss (EWL) becomes the only mechanism whereby they can dissipate internal heat loads (Dawson, 1982; Tattersall et al., 2012). The quantity of water lost, relative to body mass (M_b), can become substantial at high air temperatures (T_a) in small birds (McKechnie and Wolf, 2010). For example, EWL can exceed 5% of M_b per hour in verdins (*Auriparus flaviceps*) experiencing air temperatures approaching 50°C (Wolf and Walsberg, 1996). Consequently, during extreme heat waves, the thermoregulatory requirements necessary to avoid lethal hyperthermia can exceed physiological limits of birds and other animals, an occurrence that sometimes leads to large-scale mortality events (Welbergen et al., 2008; McKechnie et al., 2012; Fey et al., 2015).

Like many physiological traits, a large proportion of the variation in avian EWL can be attributed to scaling with M_b (Bartholomew and Dawson, 1953; Crawford and Lasiewski, 1968). However, substantial mass-independent variation remains among similarly sized species (Lasiewski and Seymour, 1972; Smit et al., 2017). Climate has frequently been invoked as an ultimate driver of adaptive variation in avian EWL (Williams, 1996; Tieleman et al., 2002). For instance, measurements of EWL at moderate T_a (e.g. 25°C) suggest that arid-zone species have evolved reduced rates of water loss compared with their mesic counterparts (Williams and Tieleman, 2005). Although fewer data exist for hot conditions, rates of water loss at $T_a>T_b$ exhibit similar trends, at least intraspecifically, with EWL rates lower in arid-zone populations compared with those inhabiting more mesic habitats (Trost, 1972; Noakes et al., 2016; O'Connor et al., 2017). However, climate and M_b scaling may not be the only ecological factors influencing variation in EWL (e.g. diet; Bartholomew and Cade, 1963).

One additional factor that could conceivably exert a strong influence on evaporative cooling economy is the timing of activity (i.e. nocturnality versus diurnality). Diurnal birds can potentially gain water through drinking and/or foraging during the course of the day, thereby offsetting water losses via evaporation (Willoughby and Cade, 1967; Fisher et al., 1972). In contrast, nocturnal birds often experience zero water gain aside from metabolic water for as long as 12–14 h between sunrise and sunset (Brigham, 1991). Consequently, if daytime environmental temperature exceeds T_b , roosting nocturnal birds are subjected to extended periods of elevated requirements for evaporative cooling (Grant, 1982). Birds in the family Caprimulgidae (nightjars and nighthawks) have frequently been reported roosting/nesting in unshaded sites where environmental temperature can approach 58°C (Cowles and Dawson, 1951; Weller, 1958; Grant, 1982; Ingels et al., 1984).

¹DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa. ²Department of Zoology and Entomology, Rhodes University, P.O. Box 94, Grahamstown 6140, South Africa. ³Department of Biology, University of New Mexico, MSC03-2020, Albuquerque, NM 847131-0001, USA. ⁴Department of Biology, University of Massachusetts, Amherst, MA 01003, USA. ⁵Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada. ⁶South African Research Chair in Conservation Physiology, National Zoological Garden, South African National Biodiversity Institute, P.O. Box 754, Pretoria 0001, South Africa.

*Author for correspondence (aemckechnie@zoology.up.ac.za)

 R.S.O., 0000-0002-5831-7006; A.E.M., 0000-0002-1524-1021

List of symbols and abbreviations

EHL	evaporative heat loss
EWL	evaporative water loss
M_b	body mass
MHP	metabolic heat production
T_a	air temperature
T_b	body temperature
PGLS	phylogenetic generalized least squares
\dot{V}_{CO_2}	carbon dioxide production

Even owls, which typically select thermally buffered refugia, can experience T_a approaching or exceeding T_b in hot habitats (Soule, 1964; Ligon, 1968). Given these behavioral constraints, we predicted that nocturnal species in hot environments have experienced strong selection for efficient evaporative cooling and reduced EWL to minimize dehydration risk during the day.

A parameter often used to quantify thermoregulatory capacity at $T_a > T_b$ is evaporative cooling efficiency, calculated as the ratio of evaporative heat loss to metabolic heat production (EHL/MHP; Lasiewski et al., 1966). An EHL/MHP value greater than 1 signifies that an individual can dissipate all its metabolic heat through evaporation, with higher EHL/MHP ratios indicating more efficient evaporative cooling. One of the major determinants of EHL/MHP ratios appears to be the primary pathway of evaporative heat dissipation: panting, gular flutter or cutaneous evaporation. Species using either gular flutter or cutaneous evaporation as their predominant mechanism for heat dissipation generally exhibit high EHL/MHP values (e.g. Marder and Arieli, 1988; McKechnie et al., 2016; O'Connor et al., 2017). In contrast, species that rely on panting as their primary avenue of EWL typically display lower EHL/MHP values (Weathers, 1981; Weathers and Greene, 1998). Thus, when compared at the same T_a , species that employ gular flutter or cutaneous EWL as their main avenue of heat dissipation tend to have higher EHL/MHP values than species that pant (e.g. Smith et al., 2015; Whitfield et al., 2015; O'Connor et al., 2017).

The evolution of an evaporative cooling mechanism that increases thermoregulatory capacity would thus have considerable adaptive significance for species subjected to long periods of heat stress. Here, we hypothesized that nocturnal birds have evolved reduced EWL and more efficient evaporative cooling (i.e. higher EHL/MHP at a given T_a) compared with diurnal species of similar M_b in response to extended periods without drinking. We tested three specific predictions regarding EWL and EHL/MHP ratios at T_a approaching and exceeding T_b : (1) nocturnal species display more gradual increases in EWL with increasing T_a (i.e. shallower slopes of EWL against T_a) when the latter exceeds T_b , (2) nocturnal species have lower EWL at a given T_a above normothermic T_b and (3) nocturnal species have higher EHL/MHP at a given T_a above normothermic T_b .

MATERIALS AND METHODS**Study species and physiological data**

We collated published and unpublished data on T_b , EWL rates and carbon dioxide production (\dot{V}_{CO_2}) at T_a between 10 and 65°C for 39 bird species inhabiting three sub-tropical arid zones: the Sonoran Desert of North America, the Kalahari Desert of southern Africa and the interior of South Australia (Table S1). These data were collected between 2012 and 2015 as part of an ongoing project investigating heat tolerance and evaporative cooling efficiency in arid-zone birds. Therefore, all data were collected using similar

protocols and under similar experimental conditions (e.g. relatively high flow rates to ensure low humidity in the metabolic chambers; see Whitfield et al., 2015 for details). The inclusion of physiological data from only arid zones controlled for the potential influence of climate on physiological estimates. Some of the data for several species included here have recently been published, while the remaining data are currently unpublished (Table S1). For the published studies that investigated seasonal differences in heat tolerance, we only used data collected during summer (e.g. Noakes et al., 2016; O'Connor et al., 2017). All equipment and experimental protocols used to record T_a , T_b , \dot{V}_{CO_2} and EWL rates are described in detail within the recently published studies (Table S1). Additionally, these studies provide details on the thermal equivalents and specific equations used for calculating MHP and EHL.

We opted not to include physiological data on nocturnal species from earlier studies because the methodologies and techniques used during open flow-through respirometry can substantially influence physiological estimates (e.g. Hayes et al., 1992; Page et al., 2011; Gerson et al., 2014; Jacobs and McKechnie, 2014). The impact of methodology is clearly demonstrated when considering the relationship between flow rate, humidity and EHL/MHP. Pioneering investigations into heat tolerance of birds used low flow rates when exposing individuals to increasingly high T_a (see Lasiewski et al., 1966). Consequently, as birds increased EWL with increasing T_a , the low flow rates allowed chamber humidity to build up to high levels, impeding the birds' capacity to dissipate heat. Lasiewski et al. (1966) demonstrated that by increasing flow rates, water vapor pressure inside the chamber decreased, allowing birds to tolerate T_a values that earlier work had found to be lethal. Previous work by investigators measuring EWL among nocturnal species used low flow rates across all T_a [e.g. 830 and 1262 ml min⁻¹ (Ligon, 1968); 1500 ml min⁻¹ (Coulombe, 1970); 2000 ml min⁻¹ (Ganey et al., 1993)], whereas the studies included here all used flow rates ranging from 2000 up to 30,000 ml min⁻¹. Hence, by implementing similar experimental protocols between measurements, we were able to minimize noise in our data and permit direct comparisons among species. Two of the nocturnal species included here (*Caprimulgus rufigena* and *Caprimulgus tristigma*) were measured during their diurnal rest phase, whereas the remaining nocturnal species were measured during their nocturnal active phase. However, the influence of the circadian cycle on EWL among birds appears small, with EWL marginally lower during the rest phase, whereas EHL/MHP is seemingly unaffected (Bartholomew and Trost, 1970; Weathers and Caccamise, 1975; Weathers and Schoenbaechler, 1976). Thus, we do not believe that the inclusion of these two caprimulgids significantly influenced our results. All data included in the final data set represent calm, non-active birds.

Data analysis

To quantify variation in EWL and EHL/MHP, we fitted the following three models, with three continuous predictors – M_b , the thermal gradient between T_a and T_b (i.e. $T_a - T_b$) and the $M_b \times T_a - T_b$ interaction term – and period active representing a two-level categorical predictor (i.e. day or night): (A) slope of EWL (g h⁻¹ °C⁻¹) at T_a between 40 and 46°C = M_b + period active; (B) EWL (g h⁻¹) at 46°C = M_b + period active + $T_a - T_b$ + $M_b \times T_a - T_b$; and (C) EHL/MHP at 46°C = M_b + period active + $T_a - T_b$ + $M_b \times T_a - T_b$.

We included $T_a - T_b$ as a continuous predictor to control for the possible influence that $T_a - T_b$ can have on EWL (see Tieleman and Williams, 1999).

All analyses were performed in R v. 3.3.2 (<https://www.r-project.org/>). For model A, we calculated species-specific slopes of EWL at T_a between 40 and 46°C (specifically, $39.5^\circ\text{C} \leq T_a < 46.5^\circ\text{C}$) by fitting linear mixed-effect models of EWL rates against T_a using the R packages lme4 (Bates et al., 2015) and robustlmm (Koller, 2016). We included bird identity as a random effect to account for repeated measurements within individuals. For models B and C, EWL rates and EHL/MHP ratios represent species averages recorded at $T_a=46^\circ\text{C}$, as this was the best compromise between maximizing sample size and the data available for high T_a . Given that we included T_a-T_b in models B and C, we removed incomplete cases at $T_a=46^\circ\text{C}$ when T_b was not known owing to a bird moving out of range of the antenna receiving the T_b signal. Prior to fitting models, we \log_{10} transformed EWL slopes at T_a between 40 and 46°C, EWL rates at $T_a=46^\circ\text{C}$ and M_b to correct for skewness in the data. For models B and C, we also mean-centered and standardized the M_b and T_a-T_b input variables to units of two standard deviations (Gelman, 2008; Schielzeth, 2010). Lastly, we checked for collinearity among our predictors by calculating correlation coefficients (r) and variance inflation factors (VIF; maximum $r=0.34$ and maximum VIF=2.40).

We analyzed our three models in a phylogenetic generalized least squares (PGLS) regression framework (Symonds and Blomberg, 2014) using the R packages ape (Paradis et al., 2004) and caper (R package version 0.5.2, <https://CRAN.R-project.org/package=caper>). We downloaded a subset of 500 phylogenies that included all species in our dataset from <http://www.birdtree.org> (Jetz et al., 2012) using the Hackett et al. (2008) phylogeny as a back-bone. We subsequently used these 500 phylogenies to obtain a majority consensus tree using Mesquite (<http://mesquiteproject.org>), which was then incorporated into our PGLS models. We followed Revell (2010) and simultaneously estimated the PGLS regression coefficients along with the phylogenetic signal using a maximum likelihood estimation procedure of Pagel's lambda (λ ; Pagel, 1999) bounded by 0 and 1, where 0 indicates phylogenetic independence and 1 indicates that traits follow a Brownian motion model of evolution (Freckleton et al., 2002). The fit of each model was diagnosed by visually inspecting plots of the phylogenetic residuals to assess whether they met the assumptions of normality and homogeneity (Symonds and Blomberg, 2014). Species with a Studentized phylogenetic residual >3.0 or <-3.0 were excluded from the final model as these can overly influence the results of the PGLS regression (Table S1; Jones and Purvis, 1997). Lastly, seven species were represented by one or two individuals at $T_a=46^\circ\text{C}$ (Table S1) and we tested for the influence of sample size by running two analyses, one where all species were included and one excluding species for which the data came from fewer than three individuals (McKechnie and Wolf, 2004a; Londoño et al., 2015). The results from these duplicate analyses were quantitatively similar (i.e. estimated effect sizes with standard errors overlapped) and we therefore present the results for the entire data set only.

RESULTS

Nocturnal species had significantly shallower EWL slopes at T_a between 40 and 46°C compared with diurnal species (Table 1). However, among nocturnal birds, EWL slopes were noticeably shallower within non-Strigiformes (i.e. caprimulgids and Australian owl-nightjars; Fig. 1). Body mass strongly influenced EWL slopes (Table 1, Fig. 1).

Body mass was the most important predictor of EWL at $T_a=46^\circ\text{C}$ (Table 2). The regression estimate for nocturnal activity was negative, indicating that nocturnal species had lower EWL than

Table 1. Regression estimates from a phylogenetic generalized least squares model explaining variation in the slopes of evaporative water loss rates at air temperatures between 40 and 46°C in 34 avian species

	Estimate	Std. error	t-value	P-value
Intercept	-1.85	0.15	-12.40	<0.001
M_b	0.56	0.07	7.68	<0.001
Period active (nocturnal)	-0.18	0.07	-2.62	0.01
λ	0.262 [n.a., 0.824]	—	—	—
Adjusted R^2	0.69	—	—	—

Predictor variables in the model included $\log_{10} M_b$ and period active [diurnal ($N=28$) versus nocturnal ($N=6$)]. λ is the maximum likelihood estimate of Pagel's lambda with 95% confidence intervals. n.a., not applicable.

diurnal species of a similar mass (Table 2). However, the effect of nocturnal activity was weak given its relatively small effect size (Table 2). Among nocturnal birds, non-Strigiformes members displayed lower EWL at $T_a=46^\circ\text{C}$ compared with diurnal species of comparable M_b , whereas EWL for Strigiformes (i.e. owls) was generally similar to that of diurnal species of similar size (Fig. 2). Consequently, the removal of owls from the data set resulted in nocturnal activity having a stronger effect, although it remained statistically non-significant (period active nocturnal = -0.09 ± 0.07 , $t = -1.28$, $P = 0.21$). Neither T_a-T_b nor the interaction between M_b and T_a-T_b had a significant influence on EWL at $T_a=46^\circ\text{C}$ (Table 2).

Body mass and T_a-T_b were the most important predictors of EHL/MHP at $T_a=46^\circ\text{C}$ based on the larger standardized effect sizes, with M_b having an overall negative effect and T_a-T_b a positive effect (Table 3). Nocturnal activity had a positive effect on EHL/MHP, implying higher EHL/MHP in nocturnal species (Table 3). However, we found considerable variation among nocturnal birds, with owls having lower EHL/MHP ratios compared with non-Strigiformes members (Fig. 3). The removal of owls from the data set resulted in period active having the largest effect and becoming the most

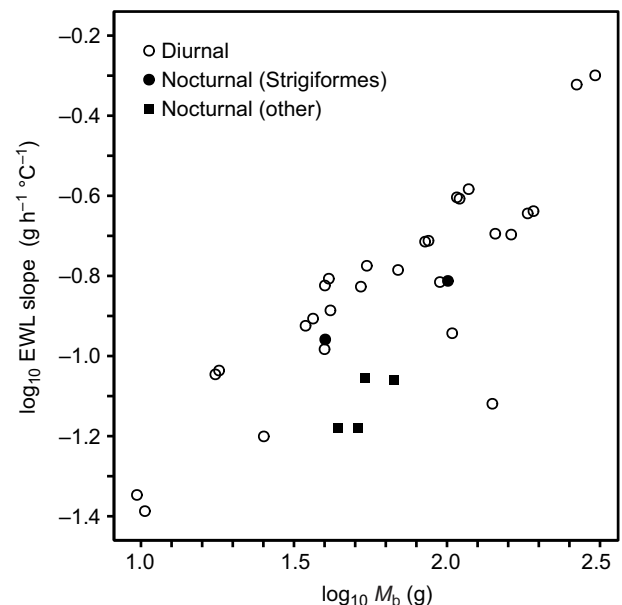


Fig. 1. The relationship between the slope of evaporative water loss (EWL) rate at air temperatures between 40 and 46°C with body mass (M_b) in diurnal ($N=28$) and nocturnal ($N=6$) bird species. Nocturnal Strigiformes represent species in the order Strigiformes (i.e. owls) whereas Nocturnal other represent nocturnal species from other orders of nocturnal birds [i.e. nightjars and nighthawks (Caprimulgiformes) and Australian owl-nightjars (Apodiformes)].

Table 2. Standardized regression estimates from a phylogenetic generalized least squares model explaining variation in evaporative water loss rates at an air temperature of 46°C for 39 avian species

	Estimate	Std. error	t-value	P-value
Intercept	0.20	0.04	4.49	<0.001
M_b	0.49	0.03	14.42	<0.001
Period active (nocturnal)	-0.06	0.06	-0.91	0.37
$T_a - T_b$	-0.04	0.04	-1.07	0.29
$M_b \times T_a - T_b$	0.04	0.06	0.64	0.53
λ	0.725 [0.126, n.a.]	—	—	—
Adjusted R^2	0.87	—	—	—

Predictor variables in the model included $\log_{10} M_b$, period active [diurnal ($N=32$) versus nocturnal ($N=7$)], the thermal gradient between air temperature and body temperature ($T_a - T_b$) and the interaction between $\log_{10} M_b$ and the thermal gradient ($M_b \times T_a - T_b$). Prior to fitting the model, both $\log_{10} M_b$ and $T_a - T_b$ were mean centered and standardized to two standard deviations. λ is the maximum likelihood estimate of Pagel's lambda with 95% confidence intervals.

important predictor of EHL/MHP ratios, but again remaining statistically non-significant (period active nocturnal = 0.24 ± 0.24 , $t=1.03$, $P=0.31$). With the exception of elf owls, all nocturnal birds maintained a lower T_b at $T_a=46^\circ\text{C}$ compared with diurnal species (Fig. 4).

DISCUSSION

Our analysis revealed that increases in EWL with increasing T_a are significantly shallower in nocturnal species, but neither EWL nor EHL/MHP at $T_a=46^\circ\text{C}$ are significantly lower. Although our analyses were constrained by the small number of species for which suitable data are currently available, one pattern to emerge concerns differences between the two major radiations of nocturnal birds for which data are available. Whereas the data for caprimulgids and Australian owl-nightjars appear to be consistent with our

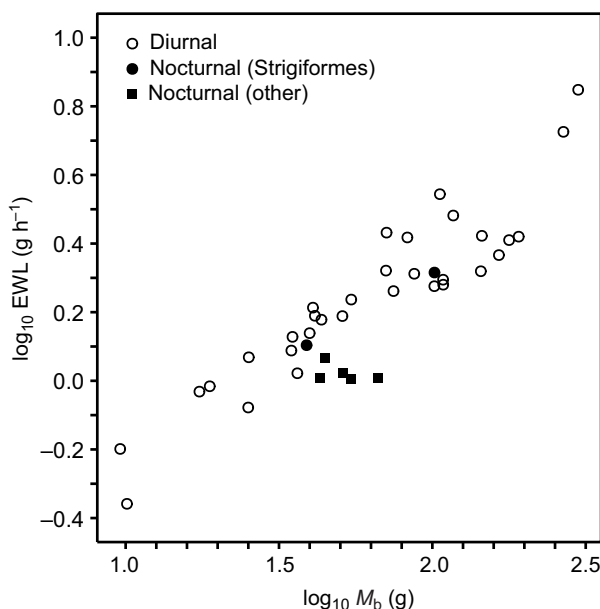


Fig. 2. The relationship between EWL rates at an air temperature of 46°C and M_b in diurnal ($N=32$) and nocturnal ($N=7$) bird species. Nocturnal Strigiformes represent species in the order Strigiformes (i.e. owls) whereas Nocturnal other represent nocturnal species from other orders of nocturnal birds [i.e. nightjars and nighthawks (Caprimulgiformes) and Australian owl-nightjars (Apodiformes)].

Table 3. Standardized regression estimates from a phylogenetic generalized least squares model explaining variation in evaporative cooling efficiency at an air temperature of 46°C for 39 avian species

	Estimate	Std. error	t-value	P-value
Intercept	1.62	0.13	12.29	<0.001
M_b	-0.23	0.11	-2.04	0.05
Period active (nocturnal)	0.15	0.19	0.81	0.42
$T_a - T_b$	0.24	0.13	1.80	0.08
$M_b \times T_a - T_b$	-0.12	0.21	-0.56	0.58
λ	0.596 [0.116, n.a.]	—	—	—
Adjusted R^2	0.20	—	—	—

Predictor variables in the model included $\log_{10} M_b$, period active [diurnal ($N=32$) versus nocturnal ($N=7$)], the thermal gradient between air temperature and body temperature ($T_a - T_b$) and the interaction between $\log_{10} M_b$ and the thermal gradient ($M_b \times T_a - T_b$). Prior to fitting the model, both $\log_{10} M_b$ and $T_a - T_b$ were mean centered and standardized to two standard deviations. λ is the maximum likelihood estimate of Pagel's lambda with 95% confidence intervals.

predictions of more efficient evaporative cooling in nocturnal birds, the EWL of owls is similar to that of diurnal species. Consequently, the lower period active estimates within our EWL models appear to be driven by caprimulgids and Australian owl-nightjars, rather than being representative of a generalized evolutionary response to nocturnal activity. Indeed, the removal of owls from the data set resulted in a more negative effect of period active on EWL at $T_a=46^\circ\text{C}$, although the effect remained statistically non-significant, likely a corollary of the small sample size.

We did not find consistent support for our prediction that nocturnal species have higher EHL/MHP ratios at a given T_a compared with diurnal species of comparable mass. The distinction

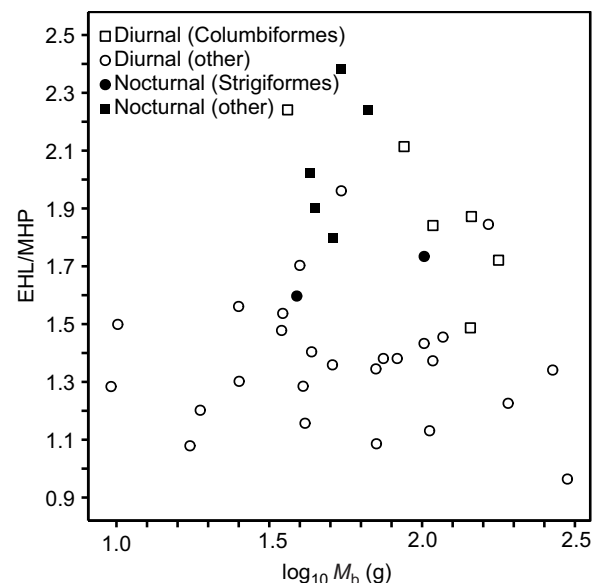


Fig. 3. The relationship between the ratio of heat lost through evaporation (EHL) to heat produced through metabolism (MHP; i.e. evaporative cooling efficiency) at an air temperature of 46°C with M_b in diurnal ($N=32$) and nocturnal ($N=7$) bird species. Values above 1 signify species that dissipated >100% of their metabolic heat through evaporation. Diurnal Columbiformes represent species in the order Columbiformes (i.e. doves and pigeons) whereas Diurnal other represent diurnal species from other orders of diurnal birds. Nocturnal Strigiformes represent species in the order Strigiformes (i.e. owls) whereas Nocturnal other represent nocturnal species from other orders of nocturnal birds [i.e. nightjars and nighthawks (Caprimulgiformes) and Australian owl-nightjars (Apodiformes)].

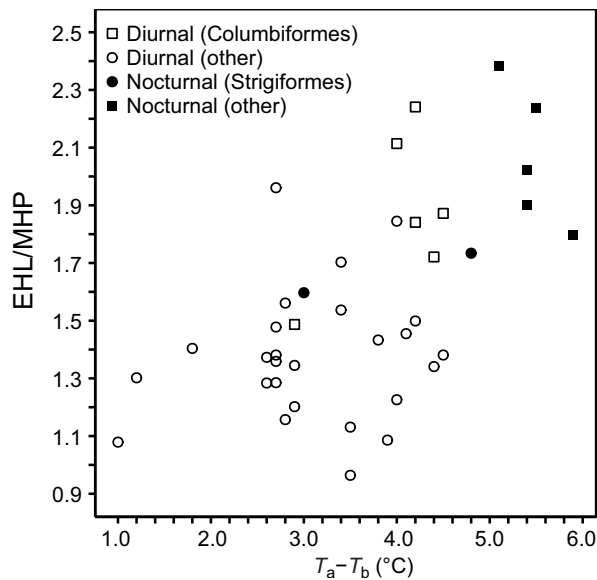


Fig. 4. The relationship between EHL/MHP ratio at an air temperature of 46°C with the thermal gradient between air temperature and body temperature ($T_a - T_b$) in diurnal ($N=32$) and nocturnal ($N=7$) birds. Values above 1 signify species that dissipated >100% of their metabolic heat through evaporation. Diurnal Columbiformes represent species in the order Columbiformes (i.e. doves and pigeons) whereas Diurnal other represent diurnal species from other orders of diurnal birds. Nocturnal Strigiformes represent species in the order Strigiformes (i.e. owls) whereas Nocturnal other represent nocturnal species from other orders of nocturnal birds [i.e. nightjars and nighthawks (Caprimulgiformes) and Australian owlet-nightjars (Apodiformes)].

between nocturnal and diurnal birds was particularly influenced by the high EHL/MHP values of columbids, a result that supports earlier findings that caprimulgids and columbids exhibit high EHL/MHP ratios (e.g. Bartholomew et al., 1962; Dawson and Fisher, 1969; Dawson and Bennett, 1973; Marder and Arieli, 1988; McKechnie et al., 2016). The extraordinary effectiveness of evaporative cooling among caprimulgids and columbids presumably stems in part from their capacity to dissipate heat by gular flutter and cutaneous evaporation, respectively, which manifests in a rapid elevation in EWL with little or no metabolic cost (Lasiewski and Bartholomew, 1966; Dawson and Fisher, 1969; Marder and Arieli, 1988; Marder et al., 2003; McKechnie and Wolf, 2004b).

Among nocturnal birds, EHL/MHP ratios were lower in owls compared with caprimulgids and Australian owlet-nightjars. Indeed, when owls were excluded from the data set, both the effect size and relative importance for period active increased, suggesting that the inclusion of data for owls reduced the overall effect. These observed differences may represent the varying contributions of panting to gular flutter among these nocturnal groups. When exposed to increasing heat loads under laboratory conditions, panting and gular flutter rates became synchronized with each other in barn owls (*Tyto alba*), burrowing owls (*Athene cunicularia*) and great horned owls (*Bubo virginianus*; Bartholomew et al., 1968; Coulombe, 1970). Despite the concurrent use of gular fluttering, the implementation of rapid panting should increase a bird's total heat load because of the consequent increase in endogenous heat production associated with moving the thoraco-abdominal structure (Dawson and Whittow, 2000). In contrast, gular flutter appears to be asynchronous and

occurs at a greater frequency than breathing rate among caprimulgids (Lasiewski and Bartholomew, 1966; Bartholomew et al., 1968; Dawson, 1982; Dawson and Whittow, 2000). Rapid vibrations of the gular region are believed to have a lower energetic cost than panting because the anatomical structures involved are moved more efficiently than those used for panting (Lasiewski and Bartholomew, 1966). Additionally, the enlarged, highly vascularized gular area of caprimulgids provides a larger surface area for evaporative heat dissipation, further enhancing evaporative cooling efficiency (Lasiewski and Bartholomew, 1966).

The apparent disparity in EWL and EHL/MHP ratios among the nocturnal birds in our study likely reflects the ecological differences between these groups. During their diurnal rest phase, owls often select cavities and/or shaded sites with cooler microclimates (Barrows, 1981; Hardy and Morrison, 2001; Charter et al., 2010), a behavior presumably necessary because of a physiological constraint in their capacity to reduce EWL at high T_a . Ganey (2004), for example, suggested that spotted owls (*Strix occidentalis*) select nest sites with thermal properties conferring a positive water balance. Elf owls nesting in the Sonoran Desert of Arizona, USA, prefer north-facing cavities inside saguaro cacti, where maximum internal cavity temperatures may be 2.8–6.0°C below maximum T_a (Soule, 1964; Hardy and Morrison, 2001), a thermal gradient that would reduce total heat loads and, consequently, EWL. However, it is noteworthy that temperatures inside refugia still do, on occasion, approach or exceed T_b (Soule, 1964; Ligon, 1968). Interestingly, Australian owlet-nightjars also make use of cavities during the diurnal period (Doucette et al., 2011), but their physiological responses to heat appear more similar to that of caprimulgids and may reflect these two groups sharing a more recent common ancestor (Hackett et al., 2008). The occupancy of unshaded sites with high operative temperatures by some caprimulgids is no doubt possible through their ability to minimize EWL while maintaining high EHL/MHP ratios via a metabolically efficient mechanism of heat dissipation, namely gular flutter. Furthermore, the use of open nest sites by ground nesting species is believed to aid in predator detection and increased survival (Amat and Masero, 2004). Thus, the ability of caprimulgids to roost and nest in the open may translate into increased fitness.

We acknowledge that our sample size of 39 species is relatively small for a phylogenetic analysis, particularly when compared with past avian EWL reviews (e.g. Crawford and Lasiewski, 1968; Williams, 1996). However, our data set addresses an important, long-standing issue among biological and ecological studies, that of biological versus statistical significance (Yoccoz, 1991; Johnson, 1999; Martínez-Abraín, 2008). Statistical significance is strongly dependent on sample size, and frequently investigators obtain a result that is biologically important but statistically non-significant, or vice versa (Gerrodette, 2011). Currently, the small and unbalanced sample size of our nocturnal species (two Strigiformes and five non-Strigiformes) precludes rigorous statistical comparisons between these two nocturnal evolutionary radiations, but the observed variation in EWL and EHL/MHP ratios between them is arguably biologically relevant with regards to water conservation and dehydration avoidance.

Conclusions

We found limited evidence for more economical evaporative cooling in nocturnal species. Although slopes of EWL were significantly shallower in nocturnal birds, EWL and EHL/MHP at a given T_a were not. Our data do, however, suggest considerable

variation in physiological responses to high T_a between owls and caprimulgids. When compared with diurnal species of similar mass, caprimulgids and Australian owllet-nightjars had lower EWL rates, whereas owls displayed EWL rates comparable to those of diurnal species. Despite having higher EWL rates, owls tended to have lower EHL/MHP ratios compared with caprimulgids and Australian owllet-nightjars. This trend may represent an increased contribution of panting relative to gular fluttering among owls, resulting in increased MHP relative to EHL. The noticeable thermoregulatory differences among the nocturnal species in our study presumably reflects ecological differences in their roost and nest selection. Typically, owls use thermally buffered refugia during their diurnal rest phase. Barrows (1981), for example, observed spotted owls in the wild occupying roost sites that were 1–6°C cooler than the surrounding open areas. However, it is noteworthy that heat waves are predicted to increase in occurrence, duration and intensity throughout the 21st century (Meehl and Tebaldi, 2004). Consequently, refugia used by owls that currently provide favorable microclimates may no longer adequately buffer them from heat stress in the future, causing them to become more susceptible to dehydration risk during extreme weather events compared with other nocturnal birds. Although based on a small sample size, we argue our results allude to a biologically important difference among nocturnal birds in their capacity to conserve water at high T_a . More data for nocturnal species could provide additional support as to whether owls indeed lack physiological adaptations for reducing EWL. Similarly, investigations on physiological adaptations conferring water conservation among mammals would be worthwhile given their use of various shelter types (e.g. underground burrows, tree cavities or leaf nests above ground; Reichman and Smith, 1990).

Acknowledgements

This study represents the culmination of several years of data collection and we are grateful for all the assistants that helped with fieldwork. Michelle Thompson assisted with the ggplot2 code for figure construction.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: B.O.W., A.E.M.; Formal analysis: R.S.O., B.S.; Investigation: R.S.O.; Data curation: R.S.O., W.A.T., A.R.G., B.O.W.; Writing - original draft: R.S.O.; Writing - review & editing: B.S., A.R.G., M.B., B.O.W., A.E.M.; Supervision: M.B., A.E.M.

Funding

This material is based on work supported by the National Science Foundation under IOS-1122228 to B.O.W. Any opinions, findings and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. This work is also partly based on research supported in part by the National Research Foundation of South Africa (grant number 110506). The opinions, findings and conclusions are those of the authors alone, and the National Research Foundation accepts no liability whatsoever in this regard.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.181420.supplemental>

References

- Amat, J. A. and Masero, J. A. (2004). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Anim. Behav.* **67**, 293–300.
- Barrows, C. W. (1981). Roost selection by spotted owls: an adaptation to heat stress. *Condor* **83**, 302–309.
- Bartholomew, G. A. and Cade, T. J. (1963). The water economy of land birds. *Auk* **80**, 504–539.
- Bartholomew, G. A. and Dawson, W. R. (1953). Respiratory water loss in some birds of southwestern United States. *Physiol. Zool.* **26**, 162–166.
- Bartholomew, G. A. and Trost, C. H. (1970). Temperature regulation in the speckled mousebird, *Colius striatus*. *Condor* **72**, 141–146.
- Bartholomew, G. A., Hudson, J. W. and Howell, T. R. (1962). Body temperature, oxygen consumption, evaporative water loss, and heart rate in the poor-will. *Condor* **64**, 117–125.
- Bartholomew, G. A., Lasiewski, R. C. and Crawford, E. C. (1968). Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. *Condor* **70**, 31–34.
- Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1–48.
- Brigham, R. M. (1991). Apparent drinking by the common poorwill (*Phalaenoptilus nuttallii*). *Northwest. Nat.* **72**, 82–84.
- Charter, M., Meyrom, K., Leshem, Y., Aviel, S., Izhaki, I. and Motro, Y. (2010). Does nest box location and orientation affect occupation rate and breeding success of barn owls *Tyto alba* in a semi-arid environment? *Acta Ornithol.* **45**, 115–119.
- Coulombe, H. N. (1970). Physiological and physical aspects of temperature regulation in the burrowing owl (*Speotyto cunicularia*). *Comp. Biochem. Physiol.* **35**, 307–337.
- Cowles, R. B. and Dawson, W. R. (1951). A cooling mechanism of the Texas nighthawk. *Condor* **53**, 19–22.
- Crawford, E. C. and Lasiewski, R. C. (1968). Oxygen consumption and respiratory evaporation of the emu and rhea. *Condor* **70**, 333–339.
- Dawson, W. R. (1982). Evaporative losses of water by birds. *Comp. Biochem. Physiol. A* **71**, 495–509.
- Dawson, W. R. and Bennett, A. F. (1973). Roles of metabolic level and temperature regulation in the adjustment of western plumed pigeons (*Lophophaps ferruginea*) to desert conditions. *Comp. Biochem. Physiol. A* **44**, 249–266.
- Dawson, W. R. and Fisher, C. D. (1969). Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* **71**, 49–53.
- Dawson, W. R. and Whittow, G. C. (2000). Regulation of body temperature. In *Sturkie's Avian Physiology Fifth Edition* (ed. G. C. Whittow), pp. 357–404. London: Academic Press.
- Doucette, L. I., Brigham, R. M., Pavey, C. R. and Geiser, F. (2011). Roost type influences torpor use by Australian owllet-nightjars. *Naturwissenschaften* **98**, 845–854.
- Fey, S. B., Siepielski, A. M., Nusslé, S., Cervantes-Yoshida, K., Hwan, J. L., Huber, E. R., Fey, M. J., Catenazzi, A. and Carlson, S. M. (2015). Recent shifts in the occurrence, cause, and magnitude of animal mass mortality events. *Proc. Natl. Acad. Sci. USA* **112**, 1083–1088.
- Fisher, C. D., Lindgren, E. and Dawson, W. R. (1972). Drinking patterns and behavior of Australian desert birds in relation to their ecology and abundance. *Condor* **74**, 111–136.
- Freckleton, R. P., Harvey, P. H. and Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726.
- Ganey, J. L. (2004). Thermal regimes of Mexican spotted owl nest stands. *Southwest. Nat.* **49**, 478–486.
- Ganey, J. L., Balda, R. P. and King, R. M. (1993). Metabolic rate and evaporative water loss of Mexican spotted and great horned owls. *Wilson Bull.* **105**, 645–656.
- Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873.
- Gerrodette, T. (2011). Inference without significance: measuring support for hypotheses rather than rejecting them. *Mar. Ecol.* **32**, 404–418.
- Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E. and Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiol. Biochem. Zool.* **87**, 782–795.
- Grant, G. S. (1982). Avian Incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithol. Monogr.* **30**, 1–75.
- 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. et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science* **320**, 1763–1768.
- Hardy, P. C. Morrison, M. L. (2001). Nest site selection by elf owls in the Sonoran Desert. *Wilson Bull.* **113**, 23–32.
- Hayes, J. P., Speakman, J. R. and Racey, P. A. (1992). Sampling bias in respirometry. *Physiol. Zool.* **65**, 604–619.
- Ingels, J., Ribot, J. H. and de Jong, B. H. J. (1984). Vulnerability of eggs and young of the blackish nightjar (*Caprimulgus nigrescens*) in Suriname. *Auk* **101**, 388–391.
- Jacobs, P. J. and McKechnie, A. E. (2014). Experimental sources of variation in avian energetics: estimated basal metabolic rate decreases with successive measurements. *Physiol. Biochem. Zool.* **87**, 762–769.
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. and Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature* **491**, 444–448.
- Johnson, D. H. (1999). The insignificance of statistical significance testing. *J. Wildl. Manage.* **63**, 763–772.
- Jones, K. E. and Purvis, A. (1997). An optimum body size for mammals? Comparative evidence from bats. *Funct. Ecol.* **11**, 751–756.

- Koller, M. (2016). robustlmm: an R package for robust estimation of linear mixed-effects models. *J. Stat. Softw.* **75**, 1-24.
- Lasiewski, R. C. and Bartholomew, G. A. (1966). Evaporative cooling in the poor-will and the tawny frogmouth. *Condor* **68**, 253-262.
- Lasiewski, R. C. and Seymour, R. S. (1972). Thermoregulatory responses to heat stress in four species of birds weighing approximately 40 grams. *Physiol. Zool.* **45**, 106-118.
- Lasiewski, R. C., Acosta, A. L. and Bernstein, M. H. (1966). Evaporative water loss in birds-I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. *Comp. Biochem. Physiol.* **19**, 445-457.
- Ligon, J. D. (1968). The biology of the elf owl, *Micrathene whitneyi*. *Museum Zool.* **136**, 6-70.
- Londoño, G. A., Chappell, M. A., Castañeda, M. D. R., Jankowski, J. E. and Robinson, S. K. (2015). Basal metabolism in tropical birds: latitude, altitude, and the "pace of life". *Funct. Ecol.* **29**, 338-346.
- Marder, J. and Arieli, Y. (1988). Heat balance of acclimated pigeons (*Columba livia*) exposed to temperatures up to 60°C T_a. *Comp. Biochem. Physiol. A* **91**, 165-170.
- Marder, J., Withers, P. C. and Philpot, R. G. (2003). Patterns of cutaneous water evaporation by Australian pigeons. *Isr. J. Zool.* **49**, 111-129.
- Martínez-Abraín, A. (2008). Statistical significance and biological relevance: a call for a more cautious interpretation of results in ecology. *Acta Oecol.* **34**, 9-11.
- McKechnie, A. E. and Wolf, B. O. (2004a). The allometry of avian basal metabolic rate: good predictions need good data. *Physiol. Biochem. Zool.* **77**, 502-521.
- McKechnie, A. E. and Wolf, B. O. (2004b). Partitioning of evaporative water loss in white-winged doves: plasticity in response to short-term thermal acclimation. *J. Exp. Biol.* **207**, 203-210.
- McKechnie, A. E. and Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biol. Lett.* **6**, 253-256.
- McKechnie, A. E., Hockey, P. A. R. and Wolf, B. O. (2012). Feeling the heat: Australian landbirds and climate change. *Emu* **112**, 1-7.
- McKechnie, A. E., Whitfield, M. C., Smit, B., Gerson, A. R., Smith, E. K., Talbot, W. A., McWhorter, T. J. and Wolf, B. O. (2016). Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *J. Exp. Biol.* **219**, 2145-2155.
- Meehl, G. A. and Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science* **305**, 994-997.
- Noakes, M. J., Wolf, B. O. and McKechnie, A. E. (2016). Seasonal and geographical variation in heat tolerance and evaporative cooling capacity in a passerine bird. *J. Exp. Biol.* **219**, 859-869.
- O'Connor, R. S., Wolf, B. O., Bringham, R. M. and McKechnie, A. E. (2017). Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J. Comp. Physiol. B* **187**, 477-491.
- Page, A. J., Cooper, C. E. and Withers, P. C. (2011). Effects of experiment start time and duration on measurement of standard physiological variables. *J. Comp. Physiol. B* **181**, 657-665.
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature* **401**, 877-884.
- Paradis, E., Claude, J. and Strimmer, K. (2004). ape: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289-290.
- Porter, W. P. and Gates, D. M. (1969). Thermodynamic equilibria of animals with environment. *Ecol. Monogr.* **39**, 227-244.
- Reichman, O. J. and Smith, S. C. (1990). Burrows and burrowing behavior by mammals. In *Current Mammalogy* (ed. H. H. Genoways), pp. 197-244. New York: Plenum Press.
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods Ecol. Evol.* **1**, 319-329.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods Ecol. Evol.* **1**, 103-113.
- Smit, B., Whitfield, M. C., Talbot, W. A., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2017). Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance. *J. Exp. Biol.* **221**, jeb174870.
- Smith, E. K., O'Neill, J., Gerson, A. R. and Wolf, B. O. (2015). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *J. Exp. Biol.* **218**, 3636-3646.
- Soule, O. H. (1964). The saguaro tree-hole microenvironment in southern Arizona; II, Summer. *MSc thesis*, University of Arizona, Tucson, AZ, USA.
- Symonds, M. R. E. and Blomberg, S. P. (2014). A Primer on phylogenetic generalised least squares. In *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (ed. L. Z. Garamszegi), pp. 105-130. Heidelberg, Germany: Springer.
- Tattersall, G. J., Sinclair, B. J., Withers, P. C., Fields, P. A., Seebacher, F., Cooper, C. E. and Maloney, S. K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperatures. *Compr. Physiol.* **2**, 2151-2202.
- Tieleman, B. I. and Williams, J. B. (1999). The role of hyperthermia in the water economy of desert birds. *Physiol. Biochem. Zool.* **72**, 87-100.
- Tieleman, B. I., Williams, J. B. and Buschur, M. E. (2002). Physiological adjustments to arid and mesic environments in larks (*Alaudidae*). *Physiol. Biochem. Zool.* **75**, 305-313.
- Trost, C. H. (1972). Adaptations of horned larks (*Eremophila alpestris*) to hot environments. *Auk* **89**, 506-527.
- Weathers, W. W. (1981). Physiological thermoregulation in heat-stressed birds: consequences of body size. *Physiol. Zool.* **54**, 345-361.
- Weathers, W. W. and Caccamise, D. F. (1975). Temperature regulation and water requirements of the monk parakeet, *Myiopsitta monachus*. *Oecologia* **18**, 329-342.
- Weathers, W. W. and Greene, E. (1998). Thermoregulatory responses of bridled and juniper titmice to high temperature. *Condor* **100**, 365-372.
- Weathers, W. W. and Schoenbaechler, D. C. (1976). Regulation of body temperature in the Budherygah, *Melopsittacus undulatus*. *Aust. J. Zool.* **24**, 39-47.
- Welbergen, J. A., Klose, S. M., Markus, N. and Eby, P. (2008). Climate change and the effects of temperature extremes on Australian flying-foxes. *Proc. R. Soc. B Biol. Sci.* **275**, 419-425.
- Weller, M. W. (1958). Observations on the incubation behavior of a common nighthawk. *Auk* **75**, 48-59.
- Whitfield, M. C., Smit, B., McKechnie, A. E. and Wolf, B. O. (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* **218**, 1705-1714.
- Williams, J. B. (1996). A phylogenetic perspective of evaporative water loss in birds. *Auk* **113**, 457-472.
- Williams, J. B. and Tieleman, B. I. (2005). Physiological adaptation in desert birds. *Bioscience* **55**, 416-425.
- Willoughby, E. J. and Cade, T. J. (1967). Drinking habits of birds in the central Namib Desert of south west Africa. *Sci. Pap. Namib Desert Res. Stn.* **31**, 1-35.
- Wolf, B. O. and Walsberg, G. E. (1996). Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. *J. Exp. Biol.* **199**, 451-457.
- Yoccoz, N. G. (1991). Use, overuse, and misuse of significance tests in evolutionary biology and ecology. *Bull. Ecol. Soc. Am.* **72**, 106-111.

Table S1. Avian species and data used for phylogenetically-informed analyses of the slope of evaporative water loss rates at air temperatures (T_a) between 40 and 46°C (EWL slope), evaporative water loss rates at 46°C (EWL) and the ratio of evaporative heat loss and metabolic heat production at 46°C (EHL/MHP). “ T_a-T_b ” represents the thermal gradient between T_a and body temperature (T_b) at 46°C. “ M_b slope” represents the average body mass for a species included in the EWL slope analysis and “ M_b EWL” is the average body mass for each species included in the EWL and EHL/MHP analyses. Source represents the published articles from which data were derived. Values in brackets are the number of individuals included in an analysis for a species (e.g., 26 Abert’s Towhees were included in the EWL slope analysis and 9 in the EWL and EHL/MHP analyses).

Species	Period ^a active	M_b (g) slope	EWL slope (g hr ⁻¹ °C ⁻¹)	M_b (g) EWL	EWL (g hr ⁻¹)	EHL/MHP	T_a-T_b (°C)	Source
Abert's Towhee <i>Melospiza aberti</i>	D	41.6	0.130 [26]	41.4	1.547 [9]	1.157	2.8	Smith et al. 2017
African Cuckoo <i>Cuculus gularis</i>	D	109.9	0.247 [6]	108.4	1.971 [3]	1.373	2.6	Smit et al. 2018
Apostlebird <i>Struthidea cinerea</i>	D	117.7	0.261 [7]	117.0	3.032 [3]	1.455	4.1	McKechnie et al. 2017
Australian Owlet-nightjar <i>Aegotheles cristatus</i>	N	44.2	0.066 [22]	44.6	1.162 [8]	1.901	5.4	Talbot et al. 2017
Burchell's Sandgrouse <i>Pterocles burchelli</i>	D	191.7	0.230 [16]	191.2	2.631 [5]	1.226	4.0	McKechnie et al. 2016
Burchell's Starling <i>Lamprolornis australis</i>	D	107.7	0.249 [7]	105.8	3.499 [3]	1.131	3.5	Smit et al. 2018
Cactus Wren <i>Campylorhynchus brunneicapillus</i>	D	34.5	0.119 [21]	34.7	1.225 [9]	1.478	2.7	Smith et al. 2017

Species	Period ^a active	M _b (g) slope	EWL slope (g hr ⁻¹ °C ⁻¹)	M _b (g) EWL	EWL (g hr ⁻¹)	EHL/MHP	T _a -T _b (°C)	Source
Cape Glossy Starling <i>Lamprolornis nitens</i>	D	NA	NA	70.9	2.703 [1]	1.086	3.9	<i>Unpublished data</i>
Chestnut-crowned Babbler <i>Pomatostomus ruficeps</i>	D	52.3	0.149 [17]	50.9	1.544 [8]	1.359	2.7	McKechnie et al. 2017
Common Poorwill ^b <i>Phalaenoptilus nuttallii</i>	N	43.7	0.116 [26]	43.0	1.022 [5]	2.022	5.4	Talbot et al. 2017
Crested Pigeon <i>Ocyphaps lophotes</i>	D	183.5	0.227 [36]	177.9	2.571 [9]	1.721	4.4	McKechnie et al. 2016b
Curve-billed Thrasher <i>Toxostoma curvirostre</i>	D	69.2	0.164 [16]	70.6	2.095 [4]	1.345	2.9	Smith et al. 2017
Elf Owl <i>Micrathene whitneyi</i>	N	40.0	0.110 [12]	38.9	1.270 [3]	1.597	3.0	<i>Unpublished data</i>
Freckled Nightjar <i>Caprimulgus tristigma</i>	N	67.3	0.087 [16]	66.6	1.019 [13]	2.239	5.5	O'Connor et al. 2017
Galah <i>Eolophus roseicapilla</i>	D	265.3	0.476 [7]	267.5	5.316 [3]	1.341	4.4	McWhorter et al. 2018
Gambel's Quail <i>Callipepla gambelii</i>	D	162.1	0.201 [17]	164.8	2.325 [6]	1.845	4.0	Smith et al. 2015
Grey Butcherbird <i>Cracticus torquatus</i>	D	84.8	0.193 [15]	82.9	2.617 [4]	1.381	2.7	McKechnie et al. 2017

Species	Period ^a active	M _b (g) slope	EWL slope (g hr ⁻¹ °C ⁻¹)	M _b (g) EWL	EWL (g hr ⁻¹)	EHL/MHP	T _a -T _b (°C)	Source
House Finch <i>Haemorhous mexicanus</i>	D	18.0	0.092 [32]	18.8	0.964 [8]	1.202	2.9	Smith et al. 2017
Laughing Dove <i>Spilopelia senegalensis</i>	D	87.0	0.194 [17]	87.3	2.051 [4]	2.114	4.0	McKechnie et al. 2016b
Lesser Goldfinch <i>Spinus psaltria</i>	D	9.7	0.045 [18]	9.6	0.633 [4]	1.284	2.6	Smith et al. 2017
Lesser Nighthawk <i>Chordeiles acutipennis</i>	N	51.2	0.066 [15]	51.2	1.051 [3]	1.798	5.9	Talbot et al. 2017
Lilac-breasted Roller <i>Coracias caudatus</i>	D	94.8	0.153 [7]	101.5	1.887 [4]	1.433	3.8	Smit et al. 2018
Marico Flycatcher <i>Melaenornis mariquensis</i>	D	NA	NA	25.2	1.171 [1]	1.302	1.2	<i>Unpublished data</i>
Mourning Dove <i>Zenaida macroura</i>	D	104.0	0.114 [41]	108.5	1.906 [8]	1.841	4.2	Smith et al. 2015
Mulga Parrot <i>Psephotellus varius</i>	D	54.7	0.168 [16]	54.4	1.725 [7]	1.961	2.7	McWhorter et al. 2018
Namaqua Dove <i>Oena capensis</i>	D	36.5	0.124 [10]	36.3	1.052 [5]	2.241	4.2	McKechnie et al. 2016b
Northern Cardinal <i>Cardinalis cardinalis</i>	D	39.9	0.150 [10]	40.8	1.634 [2]	1.285	2.7	Smith et al. 2017

Species	Period ^a active	M _b (g) slope	EWL slope (g hr ⁻¹ °C ⁻¹)	M _b (g) EWL	EWL (g hr ⁻¹)	EHL/MHP	T _a -T _b (°C)	Source
Pyrhuloxia <i>Cardinalis sinuatus</i>	D	NA	NA	35.0	1.343 [1]	1.537	3.4	Smith et al. 2017
Red-billed Buffalo-Weaver ^b <i>Bubalornis niger</i>	D	71.1	0.030 [5]	74.7	1.826 [1]	1.381	4.5	<i>Unpublished data</i>
Red-billed Spurfowl <i>Pternistis adspersus</i>	D	305.0	0.502 [4]	298.9	7.050 [2]	0.964	3.5	<i>Unpublished data</i>
Ring-necked Dove <i>Streptopelia capicola</i>	D	140.7	0.076 [15]	143.9	2.086 [4]	1.487	2.9	McKechnie et al. 2016b
Rufous-cheeked Nightjar <i>Caprimulgus rufigena</i>	N	53.9	0.088 [16]	54.2	1.014 [8]	2.384	5.1	O'Connor et al. 2017
Scaly-feathered Weaver <i>Sporopipes squamifrons</i>	D	10.3	0.041 [14]	10.1	0.438 [6]	1.499	4.2	Whitfield et al. 2015
Sociable Weaver <i>Philetairus socius</i>	D	25.2	0.063 [14]	25.1	0.836 [5]	1.561	2.8	Whitfield et al. 2015
Spiny-cheeked Honeyeater <i>Acanthagenys rufogularis</i>	D	41.1	0.156 [16]	43.5	1.507 [1]	1.404	1.8	McKechnie et al. 2017
Western Screech Owl <i>Megascops kennicottii</i>	N	100.7	0.154 [13]	101.6	2.068 [7]	1.734	4.8	<i>Unpublished data</i>
White-browed Sparrow-Weaver <i>Plocepasser mahali</i>	D	39.8	0.104 [10]	39.8	1.377 [10]	1.703	3.4	Noakes et al. 2016

Species	Period ^a active	M _b (g) slope	EWL slope (g hr ⁻¹ °C ⁻¹)	M _b (g) EWL	EWL (g hr ⁻¹)	EHL/MHP	T _a -T _b (°C)	Source
White-winged Dove <i>Zenaidura macroura</i>	D	143.8	0.202 [34]	145.0	2.646 [7]	1.872	4.5	Smith et al. 2015
Yellow-plumed Honeyeater <i>Ptilotula ornata</i>	D	17.5	0.090 [11]	17.4	0.930 [3]	1.079	1.0	McKechnie et al. 2017

^a D = Diurnal, N = Nocturnal

^b The Common Poorwill and Red-billed Buffalo-weaver were removed from the final EWL slope regression model because these species had studentized phylogenetic residuals > 3 or < -3.

References

- McKechnie, A. E., Smit, B., Whitfield, M. C., Noakes, M. J., Talbot, W. A., Garcia, M., Gerson, A. R. and Wolf, B. O.** (2016a). Avian thermoregulation in the heat: evaporative cooling capacity in an archetypal desert specialist, Burchell's sandgrouse (*Pterocles burchelli*). *J. Exp. Biol.* **219**, 2137–2144.
- McKechnie, A. E., Whitfield, M. C., Smit, B., Gerson, A. R., Smith, E. K., Talbot, W. A., McWhorter, T. J. and Wolf, B. O.** (2016b). Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *J. Exp. Biol.* **219**, 2145–2155.
- McKechnie, A. E., Gerson, A. R., Mcwhorter, T. J., Smith, E. K., Talbot, W. A. and Wolf, B. O.** (2017). Avian thermoregulation in the heat: evaporative cooling in five Australian passerines reveals within-order biogeographic variation in heat tolerance. *J. Exp. Biol.* **220**, 2436–2444.
- McWhorter, T. J., Gerson, A. R., Talbot, W. A., Smith, E. C., McKechnie, A. E. and Wolf, B. O.** (2018). Avian thermoregulation in the heat: evaporative cooling capacity and thermal tolerance in two Australian parrots. *J. Exp. Biol.* doi: 10.1242/jeb.168930.
- Noakes, M. J., Wolf, B. O. and McKechnie, A. E.** (2016). Seasonal and geographical variation in heat tolerance and evaporative

cooling capacity in a passerine bird. *J. Exp. Biol.* **219**, 859–869.

O'Connor, R. S., Wolf, B. O., Brigham, R. M. and McKechnie, A. E. (2017). Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars. *J. Comp. Physiol. B* **187**, 477–491.

Smit, B., Whitfield, M. C., Talbot, W. A., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2018). Avian thermoregulation in the heat: phylogenetic variation among avian orders in evaporative cooling capacity and heat tolerance. *J. Exp. Biol.* doi: 10.1242/jeb.174870.

Smith, E. K., O'Neill, J., Gerson, A. R. and Wolf, B. O. (2015). Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert doves and quail. *J. Exp. Biol.* **218**, 3636–3646.

Smith, E. K., O'Neill, J. J., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2017). Avian thermoregulation in the heat : resting metabolism , evaporative cooling and heat tolerance in Sonoran Desert songbirds. *J. Exp. Biol.* **220**, 3290–3300.

Talbot, W. A., McWhorter, T. J., Gerson, A. R., McKechnie, A. E. and Wolf, B. O. (2017). Avian thermoregulation in the heat: evaporative cooling capacity of arid-zone Caprimulgiformes from two continents. *J. Exp. Biol.* **220**, 3488–3498.

Whitfield, M. C., Smit, B., McKechnie, a. E. and Wolf, B. O. (2015). Avian thermoregulation in the heat: scaling of heat tolerance and evaporative cooling capacity in three southern African arid-zone passerines. *J. Exp. Biol.* **218**, 1705–1714.