

RESEARCH ARTICLE

Avian thermoregulation in the heat: resting metabolism, evaporative cooling and heat tolerance in Sonoran Desert songbirds

Eric Krabbe Smith^{1,*}, Jacqueline J. O'Neill¹, Alexander R. Gerson^{1,2}, Andrew E. McKechnie³ and Blair O. Wolf¹

ABSTRACT

We examined thermoregulatory performance in seven Sonoran Desert passerine bird species varying in body mass from 10 to 70 g – lesser goldfinch, house finch, pyrrhuloxia, cactus wren, northern cardinal, Abert's towhee and curve-billed thrasher. Using flow-through respirometry, we measured daytime resting metabolism, evaporative water loss and body temperature at air temperatures (T_{air}) between 30 and 52°C. We found marked increases in resting metabolism above the upper critical temperature (T_{uc}), which for six of the seven species fell within a relatively narrow range (36.2–39.7°C), but which was considerably higher in the largest species, the curve-billed thrasher (42.6°C). Resting metabolism and evaporative water loss were minimal below the T_{uc} and increased with T_{air} and body mass to maximum values among species of 0.38–1.62 W and 0.87–4.02 g H₂O h⁻¹, respectively. Body temperature reached maximum values ranging from 43.5 to 45.3°C. Evaporative cooling capacity, the ratio of evaporative heat loss to metabolic heat production, reached maximum values ranging from 1.39 to 2.06, consistent with known values for passeriforms and much lower than values in taxa such as columbiforms and caprimulgiforms. These maximum values occurred at heat tolerance limits that did not scale with body mass among species, but were ~50°C for all species except the pyrrhuloxia and Abert's towhee (48°C). High metabolic costs associated with respiratory evaporation appeared to drive the limited heat tolerance in these desert passeriforms, compared with larger desert columbiforms and galliforms that use metabolically more efficient mechanisms of evaporative heat loss.

KEY WORDS: Evaporative water loss, Resting metabolic rate, Upper critical temperature, Body temperature, Heat tolerance limit, Passerines, Passeriform birds

INTRODUCTION

The thermoregulatory performance of birds in hot deserts has been of interest to biologists for more than 60 years (Dawson and Bartholomew, 1968; Williams and Tieleman, 2001). The extreme challenges produced by the scarcity of water and nutrient resources combined with high air temperatures and aridity has provided a natural laboratory for examining the limits of animal performance

in terrestrial environments (Dawson and Schmidt-Nielsen, 1964). As is common to all terrestrial endotherms, when environmental temperatures exceed body temperature, internal and environmental heat loads must be dissipated by increasing evaporative water loss to ensure that body temperatures remain below lethal limits. Information on thermoregulatory performance, including changes in metabolism, evaporative water loss and body temperature in birds exposed to high air temperatures – and overall heat tolerance – is of urgent interest today, as we seek to understand the effects of rapid warming of the environment on the Earth's biota (Dawson, 1992; Wolf, 2000; Urban et al., 2016).

Early studies during the 1950s and 1960s by G. A. Bartholomew, W. R. Dawson and their students in the deserts of the southwestern United States described some of the basic patterns of thermoregulation in birds (Bartholomew and Dawson, 1953; Dawson, 1954; Bartholomew and Cade, 1963). Prevalent during this era was a view that birds had but a limited capacity to cope with extreme heat. As the field advanced, however, it became clear that methodological and technological constraints had in many cases artificially limited the thermoregulatory performance of experimental subjects in the heat. For example, protocols of the day for measuring metabolic rates in relation to oxygen consumption produced artificially high chamber humidity that likely impeded evaporative heat dissipation (Lasiewski et al., 1966). Oxygen analyzers of the time typically required a depression in O₂ values of 0.5% (5000 ppm) or more for best accuracy; achieving this depression in O₂ in the animal chamber required relatively low air flow rates, typically 150–750 ml min⁻¹, which at higher air temperatures increased chamber humidity enough to have 'a marked influence on the effectiveness of evaporative cooling' (p. 452, Lasiewski et al., 1966). In early experiments, evaporative water loss was only infrequently measured and chamber humidities were unknown, adding to the uncertainty. Dawson's (1954) ground-breaking study, for example, used flow rates that exposed Abert's towhees to chamber relative humidities as high as 50%, substantially inhibiting evaporative cooling, and resulting in comparatively low lethal air temperatures of 39–43°C. In addition, in many experiments, the subjects were hand-raised in captivity and/or kept for weeks or months in the laboratory at standard temperatures (e.g. 22–30°C; Dawson, 1954; Lasiewski and Seymour, 1972; Weathers, 1981; Hoffman et al., 2007). Because heat-acclimated birds tolerate significantly higher temperatures (Marder and Arieli, 1988; McKechnie and Wolf, 2004) and high chamber humidities impede evaporative heat dissipation (Webster and King, 1987; Gerson et al., 2014), early work probably produced a distorted view of avian thermoregulatory capacities.

Given this history, recently we have examined thermoregulation and heat tolerance in a phylogenetically diverse sample of birds inhabiting arid lands on three continents (Gerson et al., 2014;

¹Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA.

²Department of Biology, University of Massachusetts, Amherst, MA 01003, USA.

³DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa.

*Author for correspondence (ericasm@unm.edu)

 E.K.S., 0000-0003-0984-1132

List of symbols and abbreviations

EHL	evaporative heat loss rate (W)
EHL/MHP	evaporative cooling capacity (dimensionless ratio)
EWL	evaporative water loss rate ($\text{g H}_2\text{O h}^{-1}$)
HTL	heat tolerance limit ($^{\circ}\text{C}$)
M_b	initial body mass (g)
MHP	metabolic heat production (=RMR)
RMR	resting metabolic rate (W)
T_{air}	chamber air temperature ($^{\circ}\text{C}$)
T_b	body temperature ($^{\circ}\text{C}$)
T_{uc}	upper critical temperature ($^{\circ}\text{C}$)

Whitfield et al., 2015; Smith et al., 2015; Noakes et al., 2016; O'Connor et al., 2017; McKechnie et al., 2016a,b; McKechnie et al., 2017). Songbirds (oscine passerines) originated in Australia during the Oligocene and diversified in isolation until the early Miocene (20–25 Mya), when islands forming between Australia and Asia allowed dispersal of songbirds to other continents (Moyle et al., 2016). The present study focuses on the thermoregulatory performance of seven songbirds, which diverged 9–26 Mya (Selvatti et al., 2015) and currently inhabit the Sonoran Desert (the hottest of the North American deserts, but which also receives more rainfall than any other desert), and provides an updated perspective of their capacities for evaporative cooling and heat tolerance. Life in hot deserts is a challenge for all birds, but passerines may be exposed to greater challenges than other taxa because of the mechanisms they use to elevate evaporative heat loss. Passerine birds increase evaporative water loss by panting, which also increases metabolic heat production and total heat loads (Wolf and Walsberg, 1996). As a consequence, passerines may be among the most sensitive taxa to increasing global temperatures and the increasing number of severe heat waves, which will accompany these changes (Albright et al., 2017). In an effort to assess the sensitivity of passerine species to extreme heat, we examined thermoregulatory responses under conditions of low humidity in wild, heat-acclimatized birds representing a sevenfold range in initial body mass (M_b , 10–70 g). We continuously measured body temperature (T_b , $^{\circ}\text{C}$), whole-animal rates of evaporative water loss (EWL, $\text{g H}_2\text{O h}^{-1}$) and daytime resting metabolism (RMR, W) in response to chamber air temperature (T_{air} , ranging from 30 to 52 $^{\circ}\text{C}$) in birds on the day they were captured. We ask how RMR, EWL and T_b change in response to T_{air} , contribute to heat tolerance, scale with M_b and differ among species. The EWL data for five of the species presented here formed the basis for the model of dehydration risk recently developed by Albright et al. (2017).

MATERIALS AND METHODS**Site description**

Birds were captured in northwest Tucson, AZ, USA, during the summers of 2012 (6/33 Abert's towhee, 2/12 northern cardinal, 38 house finch) and 2013 (27/33 Abert's towhee, 10/12 northern cardinal, 4 pyrrhuloxia, 17 curve-billed thrasher, 22 cactus wren, 32 lesser goldfinch). Experiments were conducted the same day as capture. During June and July 2012, daily minimum air temperatures at the Tucson AZMET weather station ranged from 14 to 27 $^{\circ}\text{C}$, daily maximum air temperatures ranged from 31 to 42 $^{\circ}\text{C}$, and the dew point ranged from –15 to 22 $^{\circ}\text{C}$. During June and July 2013, daily minimum temperatures ranged from 17 to 29 $^{\circ}\text{C}$, daily maximum temperatures ranged from 32 to 43 $^{\circ}\text{C}$, and the dew point ranged from –21 to 23 $^{\circ}\text{C}$.

Animal capture and handling

House finch [*Haemorrhous mexicanus* (Müller 1776)], pyrrhuloxia (*Cardinalis sinuatus* Bonaparte 1838), northern cardinal [*Cardinalis cardinalis* (Linnaeus 1758)], Abert's towhee [*Melospiza aberti* (Baird 1852)] and curve-billed thrasher [*Toxostoma curvirostre* (Swainson 1827)] were captured using standard walk-in traps baited with seed. Lesser goldfinch [*Spinus psaltria* (Say 1823)] were caught with a drop-trap hung outside a thistle seed feeder. Cactus wren (*Campylorhynchus brunneicapillus* Lafresnaye 1835) roosting overnight in cholla cactus (*Cylindropuntia imbricata*) were captured *in situ* early in the morning. Following capture, birds were held outdoors in shaded, darkened screen cages for up to 14 h. Most individuals (141/158=89%) were tested within 6 h of capture. In the summer of 2013, prior to each experimental run, birds were provided with up to 3 ml of tap water via oral gavage. Food was withheld from most birds for more than an hour prior to experimental runs and we thus assumed in these birds a metabolic substrate consisting entirely of lipids, corresponding to a respiratory exchange ratio (RER) of 0.71 and a CO_2 thermal equivalent (CO_2eq) of 27.8 J ml^{-1} CO_2 produced (Walsberg and Wolf, 1995; Whitfield et al., 2015). However, lesser goldfinch were usually tested within an hour of capture; thus, we assigned RER/ CO_2eq of 0.76/26.6 to birds tested within 40–60 min of capture and 0.83/24.9 to birds tested within 20–40 min of capture, in accordance with RER versus time data from another small granivorous passerine (zebra finch, *Taeniopygia guttata*; E.K.S., unpublished data). Two pyrrhuloxia and a single house finch were also similarly assigned RER/ CO_2eq for data points collected within an hour of capture. Prior to all experimental runs, a temperature-sensitive PIT tag (model TX1411BBT, Biomark, Boise, ID, USA) was injected into each bird's abdominal cavity. Use and accuracy of these tags for T_b measurement is detailed in Whitfield et al. (2015). Following experimental runs, where birds were exposed to high temperatures, birds were placed in front of a cool air stream and T_b was monitored until it returned to resting levels ($\sim 40^{\circ}\text{C}$). In the summer of 2013, birds were also gavaged with tap water post-exposure to ensure rehydration. Birds were monitored for 1–5 h after exposure, after which they were released at the site of capture. Animal care protocols were approved by the Institutional Animal Care and Use Committee of the University of New Mexico (protocol no. 12-100537-MCC) and the Animal Ethics Committee of the University of Pretoria (protocol EC054-16). Birds were captured under permits from the US Fish and Wildlife Service (MB756730) and the Arizona Game and Fish Department (SP561214).

Measurements of resting metabolic rate and evaporative water loss

Measurements of RMR and EWL were made using a flow-through respirometry system similar to that used by Smith et al. (2015). The respirometry chamber consisted of a transparent plastic container (4 liters, 22 \times 19 \times 12 cm, Rubbermaid, Atlanta, GA, USA) sealed by an opaque lid, modified by addition of inlet and outlet ports, and containing a plastic mesh platform above a 2 cm layer of medium weight mineral oil to trap excreta. The chamber was placed inside a modified ice chest where temperature was controlled to $\pm 0.5^{\circ}\text{C}$. Mass-flow controllers (Alicat, Tucson, AZ, USA) provided dry air to the chamber from a pump through columns of silica gel and drierite connected in series (2012 season) or from a compressor through a membrane dryer (2013 season: Champion[®] CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA). Excurrent air was sampled at 250 ml min^{-1} and directed to a $\text{CO}_2/\text{H}_2\text{O}$ gas analyzer (model LI-840A, LICOR, Lincoln, NE, USA).

Gas analyzer outputs were sampled once per second by Expedata (version 1.4.15, Sable Systems, Las Vegas, NV, USA).

Following PIT tag insertion, each bird was weighed (model V31XH2, accuracy=0.1 g, Ohaus, Parsippany, NJ, USA) and placed in the darkened respirometry chamber, where an infrared light and video camera enabled continuous viewing. The bird was exposed to one or more thermoneutral temperatures (30 or 35°C) and one or more higher temperatures (40–52°C in 2°C increments) in a stepped pattern of temperature trials over the span of the 1 to 3 h experimental run. In order to keep H₂O content of the respirometry chamber at values that would not impede evaporation (dew point<5°C), flow rates were maintained between 1 and 40 l min⁻¹ depending on T_{air} and the bird's evaporative rate. The initial thermoneutral temperature trial allowed a bird to calm from handling; H₂O and CO₂ production were monitored and observed to drop to resting levels (typically 30 min). T_{air} was then increased to higher trial temperatures and birds were allowed to adjust to each temperature for 10–20 min and stabilize before moving to the next temperature. Most birds remained calmer when flow rates were higher and chamber humidity was lower (<5 ppt water vapor).

As T_{air} was increased above thermoneutrality, T_b and activity were monitored closely to prevent mortality. In the summer of 2013, the behavior of birds during temperature trials was scored on a scale of 0 to 5, where 0 represented a calm, still bird, 2 a pacing bird, and 5 a highly active bird, demonstrating escape behavior. A trial was

ended if the bird: (1) remained continuously active for 5–10 min, (2) showed a T_b approaching or exceeding 45°C or (3) showed a loss of balance or righting response (extremely rare). In addition, the experimental runs were timed to end before a bird had lost more than 10% of M_b during a trial (including any fecal losses). Approximately 5 min of baseline data were collected following each temperature trial.

Data analysis

We selected the lowest 5-min average of chamber CO₂ readings less baseline values for each trial temperature. Data from birds noted as being active (2012 season) or having an activity score >2 (2013 season) were excluded from analyses. Except for our estimates of heat tolerance, data from birds having mean T_b>44.7°C or slope of T_b>0.1°C min⁻¹ during a temperature trial were also excluded. Using eqn 10.5 of Lighton (2008), we determined the rate of CO₂ production in ml CO₂ min⁻¹ and whole-animal RMR in watts (W), assuming an RER of 0.71 and 27.8 J ml⁻¹ CO₂ for most birds (see Animal capture and handling). Rates of whole-animal EWL (g H₂O h⁻¹) were calculated from the H₂O ppt readings (less baseline values) for the same data points using eqn 10.9 of Lighton (2008). We converted EWL to rates of whole-animal evaporative heat loss (EHL, W) using a latent heat of vaporization of water of 2.41 J mg⁻¹ H₂O, corresponding to T_{air}=40°C (Tracy et al., 2010). We defined the ratio EHL/MHP – a dimensionless metric for

Table 1. Mean±s.d. (n) of variables related to thermoregulation at high air temperature (T_{air}) in seven Sonoran Desert passerine bird species

	Lesser goldfinch <i>Spinus psaltria</i>	House finch <i>Haemorhous mexicanus</i>	Pyrrhuloxia <i>Cardinalis sinuatus</i>	Cactus wren <i>Campylorhynchus brunneicapillus</i>	Northern cardinal <i>Cardinalis cardinalis</i>	Abert's towhee <i>Melospiza aberti</i>	Curve-billed thrasher <i>Toxostoma curvirostre</i>
Body mass (M _b , g)	9.7±0.6 (32)	18.1±1.3 (38)	33.6±2.6 (4)	34.5±2.6 (22)	39.4±2.7 (12)	41.8±2.9 (33)	70.9±8.0 (17)
Resting metabolic rate (RMR)							
Upper critical temperature (T _{uc} , °C)	36.2	39.3	39.7	37.0	37.0	36.7	42.6
RMR at T _{uc} (W)	0.23	0.39	0.55	0.40	0.58	0.68	0.81
RMR at T _{uc} (mW g ⁻¹)	23.5	21.6	16.4	11.5	14.7	16.2	11.4
Min. RMR (W)	0.27±0.07 (25)	0.38±0.07 (14)	0.60±0.15 (3)	0.53±0.16 (16)	0.68±0.13 (15)	0.71±0.13 (18)	0.87±0.12 (28)
Slope RMR vs T _{air} >T _{uc} (W °C ⁻¹)	0.009	0.016	0.025	0.018	0.040	0.019	0.097
Max. T _{air} (°C)	50 (5)	50 (7)	48 (2)	50 (4)	50 (3)	48 (5)	50 (3)
		52 (1)	50 (1)			50 (1)	
Max. RMR (W)	0.38±0.06 (5)	0.62±0.15 (7)	0.78±0.14 (2)	0.67±0.07 (4)	1.19±0.26 (3)	0.97±0.28 (5)	1.62±0.31 (6)
		0.71 (1)	0.65 (1)			0.92 (1)	
Max. RMR/min. RMR	1.43	1.63	1.32	1.26	1.76	1.37	1.86
		1.86 (1)	1.10 (1)			1.29 (1)	
Metabolic heat production (MHP=RMR) and evaporative water loss (EWL) and heat loss (EHL) rates							
Min. EWL (g H ₂ O h ⁻¹)	0.18±0.07 (25)	0.13±0.05 (13)	0.58±0.26 (3)	0.24±0.08 (16)	0.33±0.10 (15)	0.41±0.12 (31)	0.39±0.16 (15)
Min. EWL (mg H ₂ O h ⁻¹ g ⁻¹)	19.06	7.44	17.15	7.00	8.40	9.84	5.53
Slope EWL vs T _{air} >36°C (g H ₂ O h ⁻¹ °C ⁻¹)	0.052	0.098	0.132	0.137	0.180	0.151	0.270
Max. EWL (g H ₂ O h ⁻¹)	0.87±0.09 (5)	1.26±0.21 (7)	1.70±0.03 (2)	2.06±0.33 (4)	2.60±0.03 (3)	2.10±0.31 (5)	4.02±0.74 (6)
		1.55 (1)	1.90 (1)			2.15 (1)	
Max. EWL/min. EWL	4.73	9.35	2.95	8.53	7.86	5.10	10.26
		11.52 (1)	3.29 (1)			5.21 (1)	
Min. EHL/MHP	0.47±0.14 (25)	0.23±0.07 (13)	0.63±0.13 (3)	0.31±0.10 (16)	0.34±0.11 (15)	0.35±0.09 (31)	0.30±0.11 (15)
Slope EHL/MHP vs T _{air} >36°C (°C ⁻¹)	0.083	0.111	0.095	0.124	0.085	0.099	0.090
Max. EHL/MHP	1.55±0.21 (5)	1.39±0.26 (7)	1.47±0.23 (2)	2.06±0.20 (4)	1.50±0.31 (3)	1.48±0.17 (5)	1.68±0.30 (6)
		1.46 (1)	1.94 (1)			1.57 (1)	
Body temperature (T _b)							
Min. T _b (°C)	41.2±1.0 (25)	40.8±0.6 (13)	40.7±1.0 (3)	41.0±0.9 (16)	40.8±0.6 (15)	41.9±1.0 (31)	40.4±0.6 (15)
Slope T _b vs T _{air} >36°C	0.210	0.177	0.273	0.271	0.268	0.194	0.316
Max. T _b (°C)	44.5±0.3 (5)	44.8±1.3 (7)	43.7±0.1 (2)	44.5±0.3 (4)	44.6±0.3 (3)	43.9±0.6 (5)	44.3±0.4 (6)
		45.3 (1)	43.7 (1)			43.5 (1)	
Max. T _b -min. T _b (°C)	3.3	4.0	3.0	3.5	3.9	2.0	3.9
		4.4 (1)				1.6 (1)	

Table 2. Upper critical temperature (T_{uc}) and inflection point of EWL (T_{ec}) derived from segmented regressions of residuals of resting metabolic rate and evaporative water loss, respectively, against air temperature in 10 species of Sonoran Desert birds

Species	T_{uc} (°C)	T_{ec} (°C)
Lesser goldfinch	36.17 (33.98–38.36)	43.41 (41.99–44.83)
House finch	39.33 (35.06–43.61)	38.57 (37.01–40.14)
Pyrrhuloxia	39.73 (17.48–61.97)	40.21 (37.10–43.31)
Cactus wren	37.00 (35.03–38.97)	38.09 (36.36–39.81)
Northern cardinal	37.03 (33.75–40.31)	37.78 (36.12–39.45)
Abert's towhee	36.73 (34.22–39.24)	37.62 (36.32–38.92)
Curve-billed thrasher	42.61 (40.22–45.00)	45.55 (44.68–46.41)
Gambel's quail	41.09 (39.05–43.13)	
Mourning dove	45.89 (43.47–48.27)	
White-winged dove	46.47 (42.79–50.14)	

Values are means, with 95% confidence intervals in parentheses. The data for the last three species are from Smith et al. (2015).

evaporative cooling capacity – as evaporative heat loss (EHL) relative to metabolic heat production (MHP=RMR).

Statistical analysis

Statistical analyses and graphs were produced using R (version 3.2; www.r-project.org) inside RStudio (version 0.99.467). We used the linear mixed-effects model from the nlme package and individual bird as a random factor (<http://CRAN.R-project.org/package=nlme>) owing to the repeated measurement of individuals in an unbalanced design. We used the segmented package (Muggeo, 2008) to determine inflection points in the metabolic data. The main effects examined in all analysis were T_{air} and species. M_b was used as a covariate in all analysis. Backwards-stepwise model selection was used where the initial model included all covariates, random factors and main effects, including two-way interactions between main effects.

RESULTS

Body mass

M_b averaged 9.7 ± 0.6 g (mean \pm s.d.; $N=32$ individuals) for lesser goldfinch, 18.1 ± 1.3 g ($N=38$) for house finch, 33.6 ± 2.6 g ($N=4$) for pyrrhuloxia, 34.5 ± 2.6 g ($N=22$) for cactus wren, 39.4 ± 2.7 g ($N=12$) for northern cardinal, 41.8 ± 2.9 g ($N=33$) for Abert's towhee, and 70.9 ± 8.0 g ($N=17$) for curve-billed thrasher (Table 1). Whereas these seven species represent a ~ 7 -fold range of M_b (10–70 g), overlap in M_b existed between pyrrhuloxia and cactus wren and between northern cardinal and Abert's towhee. M_b significantly predicted RMR and EWL in the species tested ($P < 0.001$). We account for the mass dependence of RMR and EWL by including M_b as a covariate in all applicable models and presenting mass-independent residuals of these measures when making inter-specific comparisons (Table S1).

Resting metabolism

Segmented regressions of RMR residuals against T_{air} allowed us to identify inflection points for each species that represent the upper critical temperature (T_{uc} ; Table 2) – the T_{air} at which evaporative heat dissipation becomes an active process and marked increases in daytime RMR occur (Kendeigh, 1969). T_{uc} for these species all occurred at T_{air} above 36°C (Fig. 1). For T_{air} above 36°C , RMR increased as T_{air} increased ($F_{1,103}=225.7$, $P < 0.001$); this response differed among species ($F_{6,136}=210.0$, $P < 0.001$) and was significantly affected by M_b ($F_{1,103}=46.3$, $P < 0.001$), as well as the interaction between T_{air} and species ($F_{6,103}=9.31$, $P < 0.001$). Thus, there was a significant difference in the response of RMR to T_{air} among species and the effects of T_{air} and M_b were assessed for each species independently.

Minimum RMR values below the T_{uc} varied from 0.27 W in the lesser goldfinch to 0.87 W in the curve-billed thrasher (Table 1). All

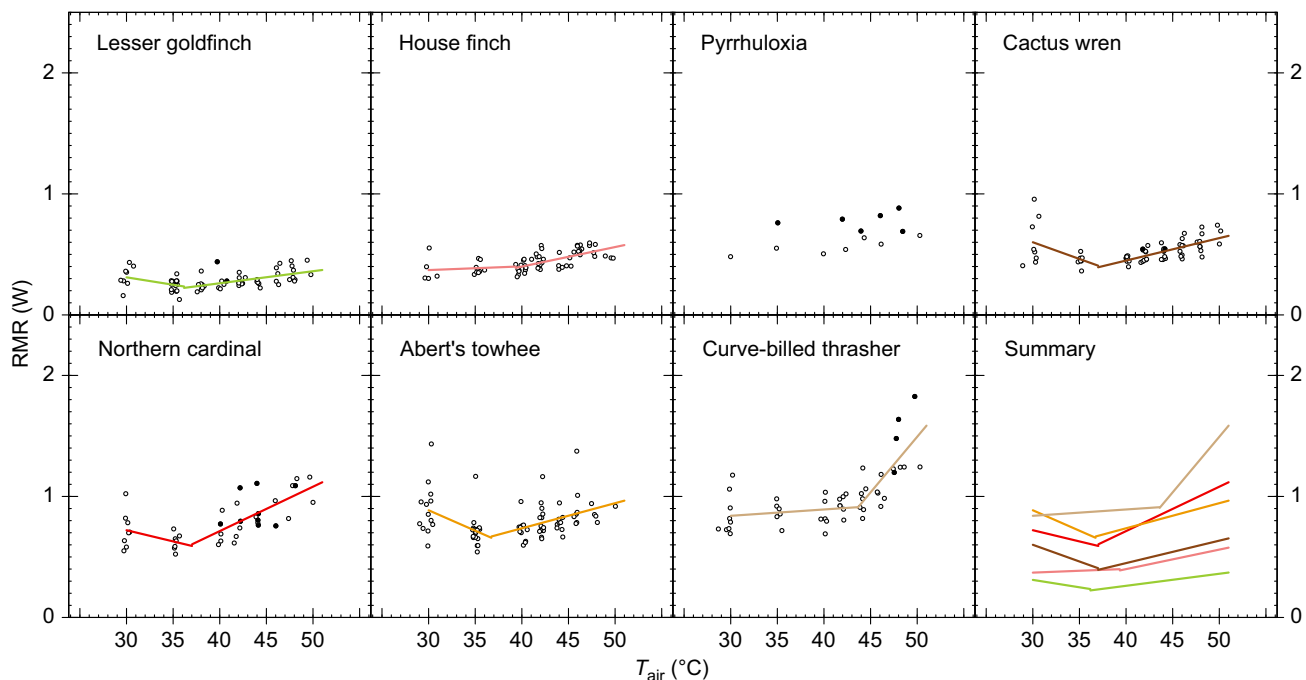


Fig. 1. Resting metabolic rate (RMR) as a function of air temperature (T_{air}) in the lesser goldfinch, house finch, pyrrhuloxia, cactus wren, northern cardinal, Abert's towhee and curve-billed thrasher. RMR was regressed against T_{air} above (all $P < 0.05$) and below the upper critical temperature (T_{uc} ; Abert's towhee significant at $P < 0.05$). The open circles represent inactive birds (activity score < 2 in 2013 season) and the solid circles represent birds that showed limited activity or movement from 2013 season (activity score = 2) and are included in all regressions and parameter estimates. See Table S3 for parameter estimates and Table 2 for determination of T_{uc} using RMR residuals.

seven species showed a clear T_{uc} (Fig. 1), with values for six species falling between 36.2 and 39.7°C, but being substantially higher in the largest species, the curve-billed thrasher (42.6±2.4°C, 95% CI; Table 2). RMR increased significantly with $T_{air}>T_{uc}$ in all species ($P<0.01$); except pyrrhuloxia and Abert's towhee, $P<0.05$; Fig. 1) with slopes ranging from 0.009 W °C⁻¹ in the lesser goldfinch to 0.097 W °C⁻¹ in the curve-billed thrasher; M_b was a significant covariate with T_{air} in the lesser goldfinch, house finch, cactus wren and Abert's towhee. RMR increased to maximum values equivalent to 126–186% of minimum RMR values in six of the species (Table 1). In the pyrrhuloxia, maximum RMR in one individual at $T_{air}=50°C$ was equivalent to 110% of minimum RMR.

Evaporative water loss

Because the T_{uc} for each species occurred at T_{air} above 36°C, EWL was separately regressed against T_{air} above and below 36°C in all species. For $T_{air}≤36°C$, there was a significant effect of species ($F_{6,94}=25.5$, $P<0.001$) and M_b ($F_{1,16}=21.2$, $P<0.001$) but no effect of T_{air} on EWL ($P>0.05$), and thus EWL in this range was considered minimum. For $T_{air}>36°C$, EWL was significantly influenced by T_{air} ($F_{1,103}=1233.0$, $P<0.001$), species ($F_{6,136}=131.6$, $P<0.001$), M_b ($F_{1,103}=33.1$, $P<0.001$), and the interaction between T_{air} and species ($F_{6,103}=40.7$, $P<0.001$). Thus, there was a significant difference in the response of EWL to T_{air} among species and the effects of T_{air} and M_b were assessed for each species independently.

Minimum EWL at $T_{air}≤36°C$ varied in six of the species from an average of 0.13 g H₂O h⁻¹ in the house finch to 0.41 g H₂O h⁻¹ in the Abert's towhee (Table 1). In the pyrrhuloxia, minimum EWL was 0.58 g H₂O h⁻¹ ($n=3$). All seven species showed clear inflection points above which EWL increased rapidly; these varied from $T_{air}=37.6°C$ in the Abert's towhee to $T_{air}=45.6°C$ in the curve-billed thrasher (Table 2). Although determined independently of T_{uc} , the

inflection points for EWL occurred within the 95% CI of the T_{uc} (and vice versa) for five of the seven species, indicating a strong functional link between the steep increase in evaporative water loss and metabolism at these critical temperatures. At T_{air} above 36°C, EWL increased significantly in all seven species ($P<0.001$; Fig. 2); slopes ranged from 0.052 g H₂O h⁻¹ °C⁻¹ in the lesser goldfinch to 0.270 g H₂O h⁻¹ °C⁻¹ in the curve-billed thrasher and – except for a swap in values between the similarly sized northern cardinal (39.4 g) and Abert's towhee (41.8 g) – scaled positively with M_b . M_b was a significant covariate with T_{air} only in the smaller lesser goldfinch and house finch. Maximum rates of EWL ranged from 0.87 g H₂O h⁻¹ in the lesser goldfinch to 4.02 g H₂O h⁻¹ in the curve-billed thrasher. The fractional increase in EWL (i.e. the ratio of maximum to minimum values) ranged from 4.7 in the lesser goldfinch to 10.3 in the curve-billed thrasher, with a larger value of 11.5 in a single house finch at $T_{air}=52°C$ and a smaller value of ~3 ($n=3$) in the pyrrhuloxia (Table 1).

Body temperature

At $T_{air}≤36°C$, T_b varied significantly among species ($F_{6,94}=5.6$, $P<0.001$), there was no effect of M_b ($P>0.05$), and a marginal effect of T_{air} on T_b ($F_{1,16}=5.6$, $P=0.03$). If the house finch was excluded, however, the effect of T_{air} on T_b became non-significant ($F_{1,16}=4.0$, $P=0.06$) and so we considered T_b for $T_{air}≤36°C$ normothermic for all but the house finch. For $T_{air}>36°C$, T_b increased with T_{air} differentially among species (T_{air} : $F_{1,104}=791.3$, $P<0.001$; species: $F_{6,136}=3.4$, $P<0.01$; $T_{air}×species$: $F_{6,104}=5.3$, $P<0.001$). Thus, there was significant variation among species in the response of T_b to T_{air} . However, there were no significant effects of M_b ($P>0.05$).

Minimum T_b varied by ~1.5°C among the seven species from 40.4±0.6°C in the curve-billed thrasher to 41.9±1.0°C in the Abert's towhee (Table 1). At $T_{air}>36°C$, T_b increased significantly in all

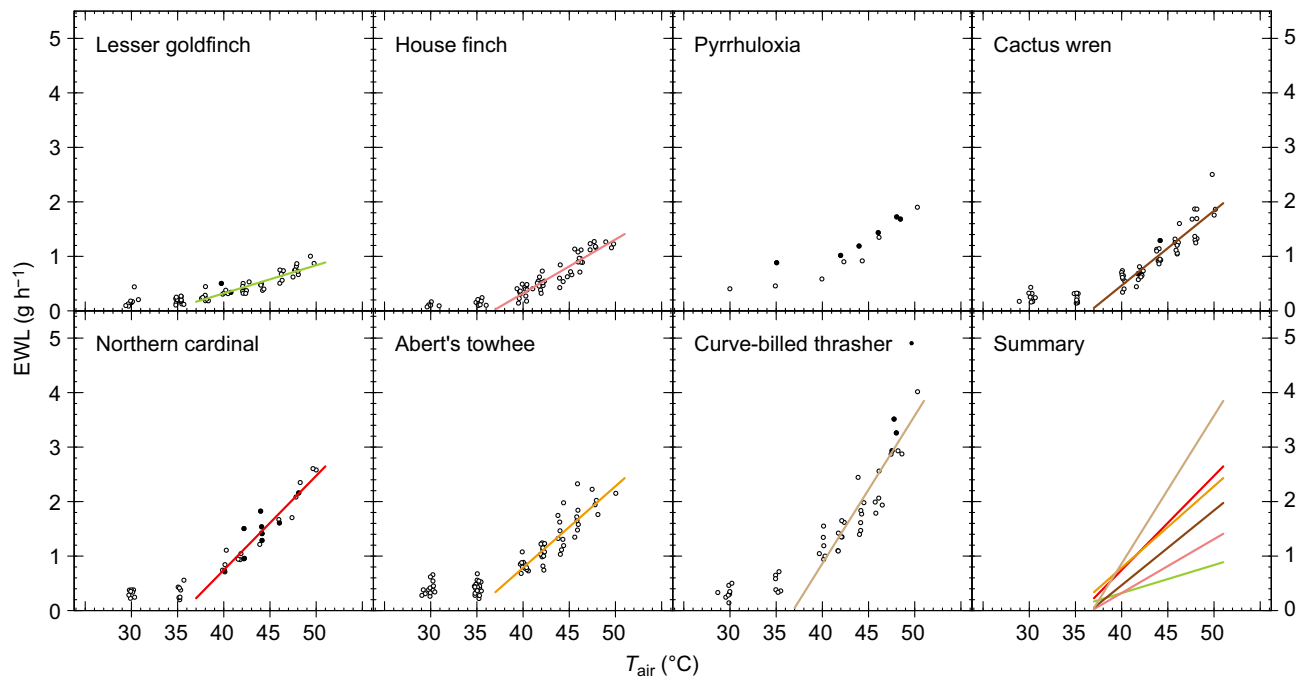


Fig. 2. Rate of evaporative water loss (EWL) as a function of T_{air} in the lesser goldfinch, house finch, pyrrhuloxia, cactus wren, northern cardinal, Abert's towhee and curve-billed thrasher. EWL was regressed against T_{air} above 36°C (all $P<0.001$). The open circles represent inactive birds (activity score<2 in 2013 season) and the solid circles represent birds that showed limited activity or movement from 2013 season (activity score=2) and are included in all regressions and parameter estimates. See Table S3 for parameter estimates.

seven species ($P < 0.001$; Fig. 3); slopes ranged from 0.177 in the house finch to 0.316°C per 1°C change in T_{air} in the curve-billed thrasher; maximum values varied from 43.5°C ($n=1$) in the Abert's towhee to 45.3°C ($n=1$) in the house finch (Table 1). Neither slope of T_b nor maximum T_b was related to M_b in any consistent way. The magnitude of the hyperthermic response varied among species from 1.6 to 4.0°C, with a single house finch increasing T_b above minimum by 4.4°C at $T_{\text{air}}=52^\circ\text{C}$ (Table 1). Just below their heat tolerance limit (HTL; see below) at T_{air} of 48°C, all seven species maintained a remarkably consistent $T_{\text{air}}-T_b$ gradient of 4.1–4.3°C (Table S2).

Ratio of evaporative heat loss to metabolic heat production

At $T_{\text{air}} > 36^\circ\text{C}$, EHL/MHP showed a significant effect of T_{air} ($F_{1,104}=1263.6$, $P < 0.001$) and species ($F_{6,136}=8.65$, $P < 0.001$) and a significant interaction between T_{air} and species ($F_{6,104}=4.49$, $P < 0.001$). Thus, there was significant variation among species in the response of EHL/MHP to T_{air} . However, there were no significant effects of M_b ($P > 0.05$).

EHL/MHP increased significantly with T_{air} above 36°C in all species ($P < 0.001$; Fig. S1), increasing 2.2–5.6 times among species between 35 and 48°C (Table S2). Maximum EHL/MHP varied from 1.39 in the house finch to 2.06 in the cactus wren, exceeding 2.0 only in the latter species (Table 1), and was not related to M_b in any consistent way.

Heat tolerance limit

The results presented so far pertain to data collected from birds that were inactive and maintaining stable T_b (see Materials and methods). To investigate heat tolerance, we examined all temperature trials above 39°C without constraining T_b or slope of T_b . The maximum 2°C bin of T_{air} reached in each species by more than a single individual (max. T_{air} , Table 1) represents its HTL. The HTL was 48°C for the pyrrhuloxia and Abert's towhee and 50°C for

the other five species (Fig. 4A, includes all but pyrrhuloxia). The values associated with this limit (maximum RMR, maximum EWL, maximum T_b and maximum EHL/MHP) are also shown in Table 1.

DISCUSSION

Most studies of thermoregulation in passerine birds have focused on responses to cold or thermoneutral temperatures. Prior to the present study, thermoregulatory performance at T_{air} above 40°C had been quantified in only 33 of the 5000+ species of passerine birds and, of these, only eight species were exposed to $T_{\text{air}} > 45^\circ\text{C}$ (see Marder, 1973; Wolf and Walsberg, 1996; Williams, 1999; Tieleman et al., 2002; Gerson et al., 2014; Whitfield et al., 2015; Noakes et al., 2016). Approximately a third of the 33 species exposed to T_{air} above 40°C were heat-acclimated, the remainder typically being held at standard T_{air} (e.g. 22–30°C) for weeks to months prior to measurements. Here, we present data from seven Sonoran Desert passerine species, summer-acclimatized to a hot subtropical desert and exposed to high T_{air} at low chamber humidities on the day of their capture. Although we included the pyrrhuloxia in the results for completeness, we omit this species from the discussion because of the small sample size ($N=4$), except to note some similarity to the congeneric northern cardinal.

Resting metabolism and upper critical temperature

Quantifying changes in RMR with changes in T_{air} is crucial to understanding thermoregulatory capacity in the heat because any increase in metabolic heat production above resting levels adds to the total heat load that must be dissipated evaporatively. We found rapid increases in RMR at T_{air} above the T_{uc} in all species. However, the T_{uc} itself was lower in the five smaller species than the value observed for the larger curve-billed thrasher (Table 2), indicating an earlier onset of active heat dissipation in the smaller birds.

The slopes of RMR against T_{air} for the three smallest species, ranging in body size from 9.7 to 34.5 g – lesser goldfinch, house

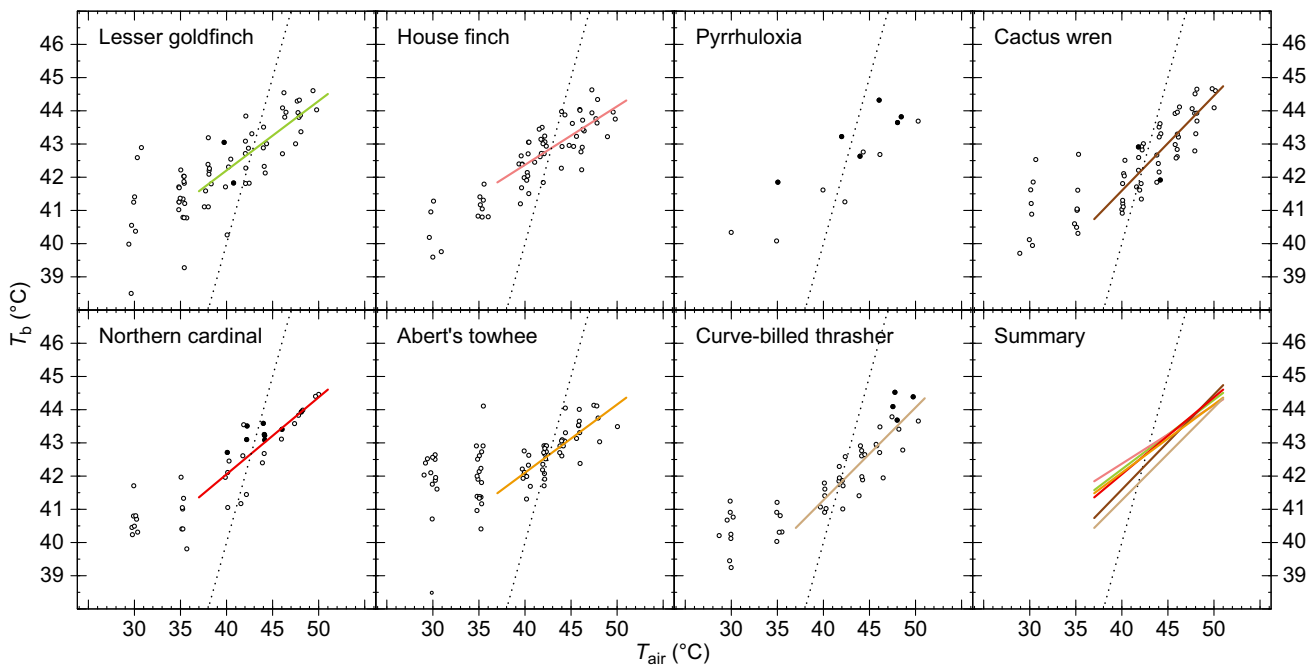


Fig. 3. Body temperature (T_b) as a function of T_{air} in the lesser goldfinch, house finch, pyrrhuloxia, cactus wren, northern cardinal, Abert's towhee and curve-billed thrasher. T_b was regressed against T_{air} above 36°C (all $P < 0.001$). The open circles represent inactive birds (activity score < 2 in 2013 season) and the solid circles represent birds that showed limited activity or movement from 2013 season (activity score = 2) and are included in all regressions and parameter estimates. See Table S3 for parameter estimates. The dotted lines represent $T_b = T_{\text{air}}$.

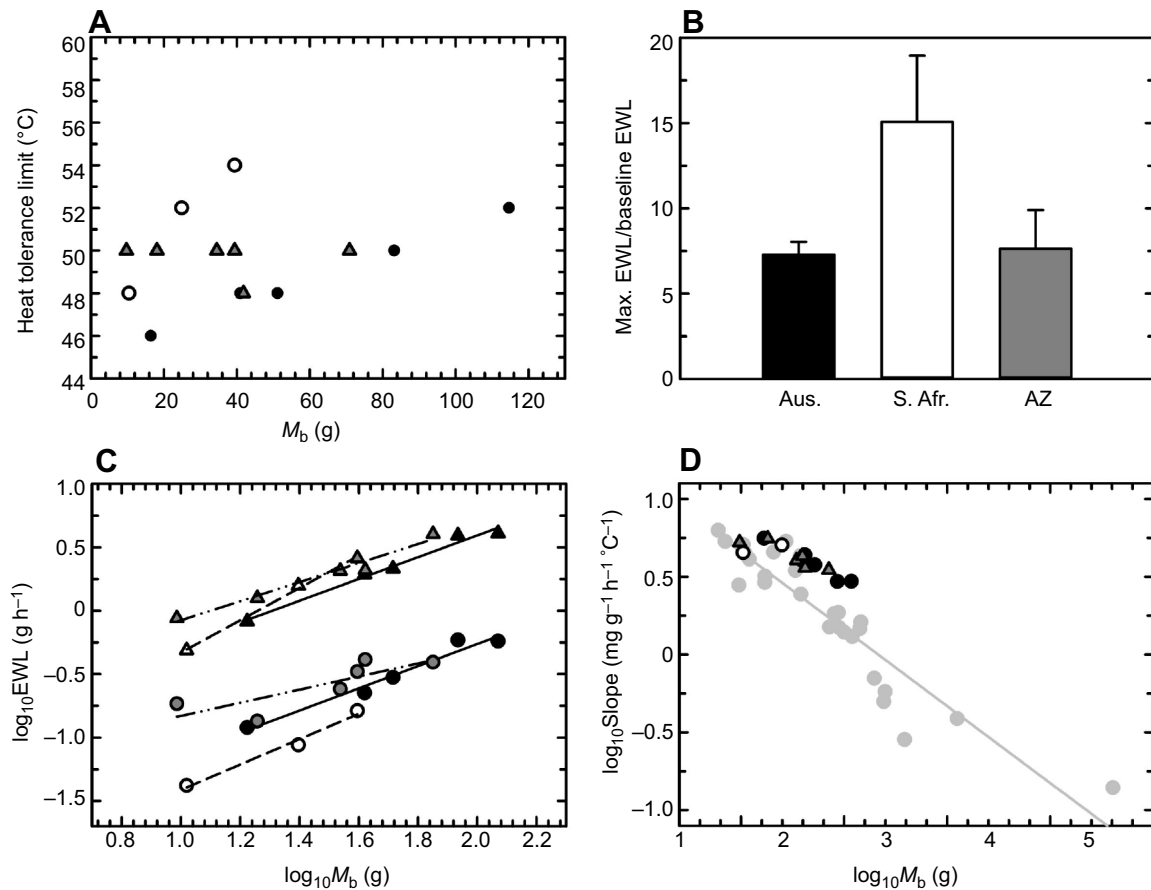


Fig. 4. Scaling of heat tolerance and evaporative cooling parameters in five Australian (data from McKechnie et al., 2017), three southern African (data from Whitfield et al., 2015) and six Sonoran Desert (AZ) passerines. (A) Heat tolerance limits were higher and scaled with body mass in three southern African ploceids (open circles) and scaled with body mass in five Australian species (closed circles) but not in six Sonoran species (gray triangles). (B) The ratio of maximum evaporative water loss (EWL) to baseline EWL at thermoneutrality was substantially higher in southern African ploceids compared with Australian species and the Sonoran species investigated in the present study. (C) This difference in fractional increases in EWL appears to arise from a combination of lower baseline EWL (circles) and higher maximum EWL (triangles) in the southern African ploceids (open symbols) compared with the Australian (closed symbols) and Sonoran species (gray symbols). (D) The slopes of mass-specific EWL versus air temperature (T_{air}) in the six Sonoran species investigated here (gray triangles) are all relatively high compared with allometrically expected values. Data for three southern African ploceids (open circles) and five Australian species (closed circles) are also shown, and the gray circles and line show the avian data included and regression model fitted by McKechnie and Wolf (2010).

finch and cactus wren – were similar, with overlapping 95% CI (Table S3). The slope of RMR in the northern cardinal was the next steepest, overlapping that of the similarly sized Abert's towhee. The larger curve-billed thrasher had the steepest slope of RMR above the T_{uc} and 95% CI that did not overlap those of the other species. Data points from more active birds (dark circles, Fig. 1) contributed to the steeper slope of curve-billed thrasher RMR. The slopes of mass-independent residuals of RMR also overlapped and were similar for lesser goldfinch, house finch, cactus wren and Abert's towhee, and lower than that of northern cardinal and curve-billed thrasher (Table S1).

The RMR values we measured are comparable to previous measurements of daytime metabolic rates in these species, given differences in individual birds, acclimatization, the time of year and experimental conditions. Northern cardinals and pyrrhuloxia investigated by Hinds and Calder (1973) during the summer in the Sonoran Desert had respective daytime metabolic rates averaging 17.6 and 21.8 mW g^{-1} at 45°C, corresponding well to RMR of 21.8±2.9 mW g^{-1} ($n=8$) and 20.3±3.0 ($n=4$) found in this study at T_{air} of 44–46°C. Daytime metabolic rates at T_{air} of 30°C in northern cardinals studied by Ro and Williams (2010) averaged 0.71±0.03 W ($n=6$), indistinguishable from the RMR of

0.72±0.15 W ($n=8$) we found in this species at the same temperature.

Fractional increases in metabolic rate varied with body mass and among taxa. As T_{air} increased from 35 to 48°C, RMR increased by an average of 1.42±0.11 times for the six species examined in this study; this is comparable to the fractional increase in RMR of 1.40±0.24 among two Arabian (Tieleman et al., 2002) and four southern African passerine species (Whitfield et al., 2015; A.E.M., unpublished data) over the same range of T_{air} . Marder (1973) reported larger fractional increases in RMR in brown-necked ravens (*Corvus ruficollis*, 610 g); values increased 1.72±0.36 times over a similar range of T_{air} (32–45°C). Large increases in RMR in passerines with increasing heat stress contrast with the responses of some other taxa; desert-dwelling columbiform birds, for example, use cutaneous evaporation as the primary pathway for evaporative cooling with little or no measurable metabolic cost. Six species of columbiforms studied in South Africa, Australia and North America exhibited fractional changes in RMR ranging from 0.77 to 1.11 as T_{air} increased from 35 to 48°C (Smith et al., 2015; McKechnie et al., 2016b). As a consequence, for a given level of heat stress, smaller passerine birds must cope with much larger metabolic heat loads compared with columbiforms, caprimulgiforms and other groups

that use more metabolically efficient mechanisms of evaporation (Bartholomew et al., 1962; Lasiewski and Seymour, 1972; Smith et al., 2015; O'Connor et al., 2017).

Increases in RMR with increasing T_{air} are typically accompanied by increases in T_b as the animal attempts to maintain a favorable thermal gradient for passive heat transfer. One consequence of increasing T_b is that a fraction of the RMR increase may arise from a temperature effect, whereby a 10°C increase in temperature typically results in a twofold to threefold increase in the rates of biochemical reactions (i.e. $Q_{10}=2-3$). Several studies of larger avian species have partitioned increases in RMR at high T_{air} into the cost of active heat dissipation versus Q_{10} effects associated with increases in T_b ; Marder (1973) assumed a Q_{10} of 2.0 for brown-necked ravens, whereas a $Q_{10}=2.2$ was evident in Burchell's sandgrouse (*Pterocles burchelli*, 193 g) for RMR within the thermoneutral zone (McKechnie et al., 2016a). Our experimental design here did not permit accurate partitioning of increases in RMR, but past work on passerines, including two of our present study species, suggests that temperature-independent metabolism ($Q_{10}=1.0$) may be common in small birds at high T_{air} (Weathers and Schoenbaechler, 1976; Weathers, 1981; Wolf and Walsberg, 1996). Based on these observations, we contend that the vast majority of the increase in RMR that we observed in our study species at T_{air} above the thermoneutral zone reflects the cost of active dissipation via panting, rather than passive temperature effects. Weathers and Schoenbaechler (1976) and Weathers (1981) argued that the ability to uncouple increases in T_b from increases in metabolism confers adaptive advantages on account of hyperthermia in heat-stressed birds increasing the gradient for passive heat loss, and consequently reducing demands for evaporative cooling.

Evaporative water loss

Birds become increasingly reliant on EWL as environmental temperatures approach T_b and the thermal gradient for passive heat transfer disappears. When environmental temperatures exceed T_b , EWL becomes the sole avenue of heat loss and EWL increases rapidly to offset both internal and environmental heat loads. At thermoneutral temperatures, evaporative losses in most birds are approximately evenly divided between respiratory and cutaneous pathways (Bernstein, 1971; Ro and Williams, 2010; Wolf and Walsberg, 1996); as T_{air} exceeds normothermic T_b , however, the majority of evaporative water loss occurs via the respiratory tract in passeriforms (75%; Wolf and Walsberg, 1996) and galliforms (75%; Richards, 1976), but via cutaneous pathways in columbiforms (70%, McKechnie and Wolf, 2004). Passerine birds elevate respiratory EWL by panting, which is a metabolically expensive mechanism of evaporation, and increasing rates of EWL in these passerine species were generally accompanied by steep increases in RMR. However, this observation was not in concordance for all of the present study species, as the lesser goldfinch showed a higher inflection point for EWL than T_{uc} , and we do not have a plausible explanation for this observation. The other five species showed significant increases in EWL at or near their T_{uc} (Table 2). Although the curve-billed thrasher showed a higher inflection point for EWL, this value corresponded with its higher T_{uc} and lay just outside the latter's 95% CI, indicating a direct connection between steeply increasing RMR and EWL at these critical temperatures. We thus found that the curve-billed thrasher elevated its EWL at a higher T_{air} than the other species, perhaps because its larger mass allowed for lower environmental heat gain or because its larger bill allowed for greater rates of non-evaporative cooling (Tattersall et al., 2009; Greenberg et al., 2012; van de Ven et al., 2016).

Rates of EWL for our study species increased an average of 5.9 ± 0.9 times as T_{air} increased from 35 to 48°C. Even larger fractional increases in EWL (i.e. 9.1 ± 3.0) have been observed in two Arabian (Tieleman et al., 2002) and four southern African passerines (Whitfield et al., 2015; A.E.M., unpublished data) over the same range of T_{air} . Marder (1973) found that brown-necked ravens showed a comparable increase in EWL of 6.1 ± 1.8 times over a similar range of T_{air} . In contrast, columbiforms show more modest increases in rates of EWL with increasing T_{air} because of their larger size and reliance on cutaneous rather than respiratory EWL; six species of South African, Australian and North American doves showed fractional increases in EWL ranging from 2.7 to 5.2 as T_{air} increased from 35 to 48°C (Smith et al., 2015; McKechnie et al., 2016b).

Body temperature

In birds, increasing heat stress or exercise produces hyperthermia, which helps to reduce heat gain in hot environments and save valuable body water by reducing evaporative losses (Calder and King, 1974; Tieleman and Williams, 1999). In the six study species, T_b increased linearly at $T_{\text{air}}>36^\circ\text{C}$ and hyperthermic responses between T_{air} of 35 and 48°C averaged $2.65\pm 0.34^\circ\text{C}$, quantitatively similar to the hyperthermic responses of $3.02\pm 1.37^\circ\text{C}$ observed in two Arabian (Tieleman et al., 2002) and four South African passerine species (Whitfield et al., 2015; A.E.M., unpublished data), as well as the much larger brown-necked raven over a similar range of T_{air} ($3.22\pm 1.52^\circ\text{C}$; Marder, 1973). Columbiform birds appear to defend lower T_b as T_{air} increases from 35 to 48°C, with four species of southern African and Australian doves showing mean increases in T_b of $1.45\pm 0.12^\circ\text{C}$ (McKechnie et al., 2016b) and two Sonoran dove species showing increases of $0.75\pm 0.76^\circ\text{C}$ (Smith et al., 2015).

These differences in the overall hyperthermic responses among species are reflected in the slope of T_b with increasing T_{air} . Higher slopes may indicate greater sensitivity to increasing heat stress, but also may provide a more favorable $T_{\text{air}}-T_b$ gradient for passive heat loss and thus save water. In this study, we found that the slope of T_b did not scale directly with body size; the smaller house finch showed the shallowest slope and the larger curve-billed thrasher the steepest slope, suggesting a positive relationship with M_b (Table 1). This range of slopes matches well the range of slopes of $0.21-0.37^\circ\text{C}$ per °C change in T_{air} found for three species of African arid-zone passerine (Whitfield et al., 2015); however, in that study, the slope of T_b scaled inversely with M_b , while heat tolerance scaled directly with M_b . Another possible metric of resistance to heat stress is represented by the thermal gradient maintained between T_b and T_{air} . Two columbiform and one galliform species (>100 g) in the Sonoran Desert maintained gradients between T_b and T_{air} of 14–15°C and 6°C, respectively, below their HTL (Smith et al., 2015). In the present study, Sonoran Desert passerines below their HTL maintained a smaller but uniform $T_{\text{air}}-T_b$ gradient among species of 4.1–4.3°C, revealing relatively modest heat tolerance.

Evaporative heat dissipation and heat tolerance among arid-zone passerines on three continents

The maximum ratio of EHL to MHP provides insight into the upper limit of evaporative cooling capacity. Ratios of EHL/MHP >1 indicate the capacity to cope with environmental heat loads and can range up to values of 4.0+ in species with very efficient evaporative cooling mechanisms (Gerson et al., 2014; Smith et al., 2015; McKechnie et al., 2016b; O'Connor et al., 2017). Early research on passerine birds, however, suggested that low maximum EHL/MHP values (<0.5) were typical, reflecting a limited capacity to cope with environmental heat loads. Dawson (1954) observed maximum

EHL/MHP values of just 0.45 and limits of heat tolerance of approximately 43°C in Abert's towhee, for example, because low chamber air flow rates and associated high relative humidity inhibited evaporative cooling. Other studies measuring EWL at high T_{air} (>40°C) in passerines are rare and, consequently, demonstrations of maximum EHL/MHP ratios exceeding unity have been relatively uncommon. Among the species studied here, house finches were previously observed to have maximum EHL/MHP ratios of 0.88 at T_{air} of 44°C (Weathers, 1981) and 1.3 at 44.4°C (Lasiewski et al., 1966), and the northern cardinal showed EHL/MHP ratios of 0.5 at 41°C (Dawson, 1958) and 1.0 at 45°C (Hinds and Calder, 1973).

We exposed birds to high T_{air} at low chamber humidities (dew point < 5°C), thereby ensuring a favorable water vapor gradient for evaporative heat loss. We recorded maximum EHL/MHP ratios of 1.46 at 52°C in house finches and 1.50 at 50°C in the northern cardinal (Table 1) – higher ratios than found previously in these species. Overall, we found that these passerines achieved maximum EHL/MHP ratios ranging from 1.4 to 2.1 at their HTL, which ranged from 48 to 50°C (Table 1). An even smaller Sonoran Desert passerine, the verdin (*Auriparus flaviceps*, 7 g), also tolerated a maximum T_{air} of 50°C (Wolf and Walsberg, 1996). These findings suggest that heat tolerance may be independent of M_b among passerines in the Sonoran Desert, a pattern that contrasts with three Kalahari Desert and five Australian counterparts (Fig. 4A). The Kalahari species showed a range of maximum EHL/MHP ratios (1.4–2.2) similar to that of the species in the present study, but their HTL ranged from 48 to 54°C and scaled positively with M_b (Whitfield et al., 2015). Working on Australian desert passerines, McKechnie et al. (2017) observed similar maximum EHL/MHP values of 1.2–2.2 with HTL ranging from 46 to 52°C and also scaling positively with M_b . To date, high rates of MHP associated with panting and increased respiratory water loss appear to limit

EHL/MHP ratios in desert passerines to approximately 2.2, and thus the upper bounds of heat tolerance of small species. That the three Kalahari species show somewhat higher heat tolerance may be related to their substantially greater ratios of maximum to minimum EWL, approximately double those of the Sonoran and Australian passerines (Fig. 4B). This larger fractional increase in EWL in the Kalahari passerines reflects greater maximum and lower baseline EWL compared with the Australian species and much lower baseline EWL compared with the Sonoran species (Fig. 4C). These limited data suggest that there may be considerable phylogenetic or biogeographic variation in the scaling of HTL among passerines.

Integrating the physiological responses to high temperatures across species

The strategies that birds employ at any given time to cope with heat stress may vary with reproductive status and availability of water, prey and thermal refugia – as well as T_{air} , M_b and mechanism of EWL. Fig. 5 provides an integrated view of the thermoregulatory performance among Sonoran Desert birds in the heat, showing the distinct evaporative and metabolic responses to the thermal gradient between an animal and its environment ($T_{\text{air}} - T_b$). In addition to the passerines used in this study, we also present data from Smith et al. (2015) on the sympatric mourning dove (columbiform: *Zenaidura macroura*, 104 g) and Gambel's quail (galliform: *Callipepla gambelii*, 161 g). The solid lines (EHL–MHP) represent the environmental heat load that must be dissipated through evaporation, and dashed lines represent rising internal heat load (MHP) associated with the metabolic cost of cooling. For the smallest passerines, the lesser goldfinch and house finch, the environmental heat load (EHL–MHP) increases sharply with increasing temperature, which contrasts with the slower rate of increase in the larger species such as the curve-billed thrasher. The effects of increased M_b are especially apparent in the larger

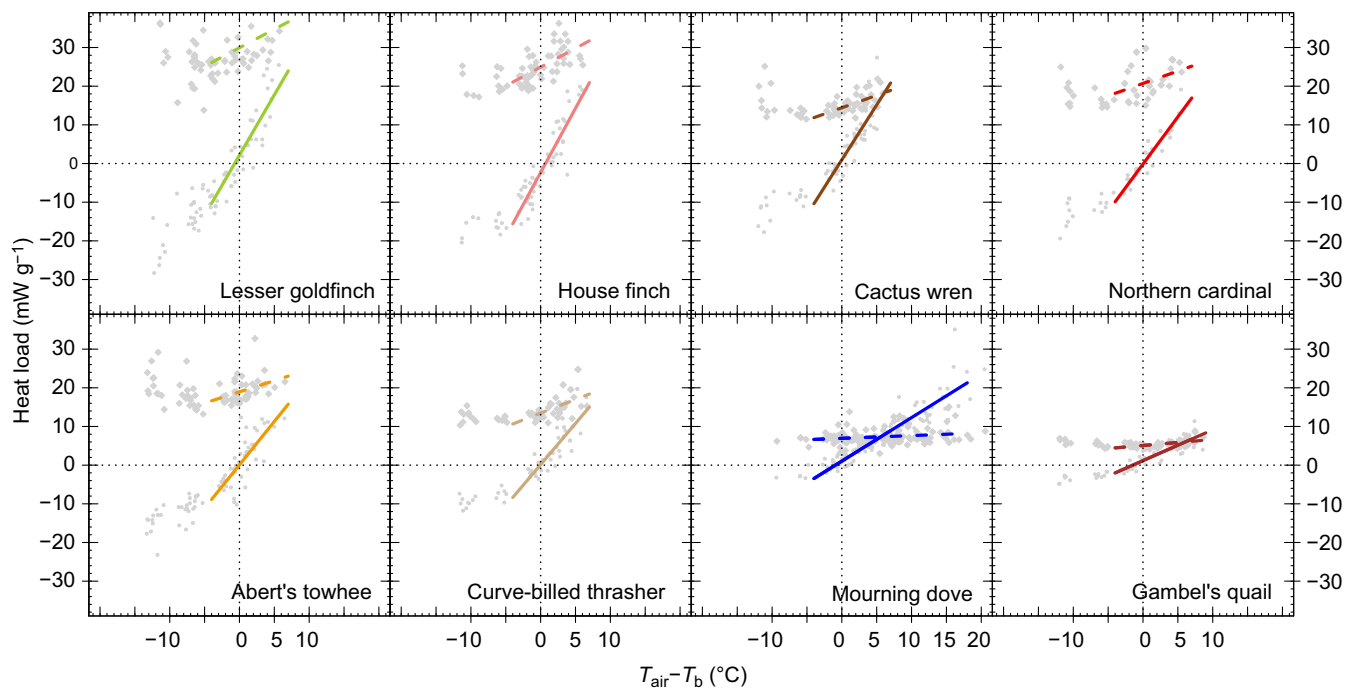


Fig. 5. Environmental heat load (circles, solid lines) and internal/metabolic heat load (diamonds, dashed lines) as a function of the thermal gradient between the animal and its environment in the lesser goldfinch, house finch, cactus wren, northern cardinal, Abert's towhee, curve-billed thrasher, mourning dove and Gambel's quail. The environmental heat load of $[EHL - MHP]/M_b$ (circles, solid lines; all $P < 0.001$) and the internal heat load of MHP/M_b (diamonds, dashed lines; all $P < 0.05$) were regressed against $T_{\text{air}} - T_b$ for T_{air} above 36°C. See Table S4 for parameter estimates.

mourning dove and Gambel's quail, where environmental heat loads increase more slowly with temperature and slopes are <50% than those observed in the passerines (Table S4). These lower slopes provide the larger dove and quail with an advantage; specifically, lower rates of heat gain translate into lower relative water requirements and smaller hyperthermic responses. For doves breeding during the summer in the heat, more modest hyperthermic responses and lower rates of mass-specific EWL allow for the cooling of eggs to maintain viability (Russell, 1969; Walsberg and Voss-Roberts, 1983). In addition, these reduced water requirements may limit time away from the nest or reduce foraging time and risks.

As the thermal gradient increases, each animal responds by increasing T_b and EHL. For the passerines that employ panting as their means of EWL, we observe steep increases in T_b with T_{air} , an acute hyperthermic response that provides the most favorable gradient for passive heat loss and saves water, but may have trade-off effects on reproduction or exercise performance. Increases in EHL are reflected in changes in internal heat production (MHP, dashed lines) and the slope of MHP reflects the efficiency of the evaporative mechanism. For the smaller passerines in this study, MHP is much larger in magnitude than the environmental heat load (when $T_b = T_{air}$), and for all the passerines, MHP increases steeply with the increasing thermal gradient. This is in stark contrast to the relatively low values and trajectory of MHP observed in the mourning dove and the Gambel's quail. For these two species, MHP is more similar in magnitude to the environmental heat load (when $T_b = T_{air}$) and its trajectory is nearly flat, with slopes that are <50% of those observed in the passerines (Table S4). Overall, larger body size and smaller surface-area-to-volume ratios drive the lower values and slope of MHP observed in the doves and quail compared with the passerines. More importantly, these differences in MHP reflect the metabolic efficiency of the evaporative mechanisms of cutaneous evaporation in the dove and gular flutter in the quail. For the passerines, the high metabolic costs associated with respiratory evaporation appear to drive their limited heat tolerance compared with the larger dove and quail, which use metabolically more efficient mechanisms of EWL. In total, the trajectories of MHP, EHL–MHP and T_b in response to increasing T_{air} provide insight into how body size, efficiency of the evaporative mechanism and sensitivity of the hyperthermic response produce limits on the heat tolerance of desert birds and may allow for the evaluation of trade-offs that allow for persistence in increasingly challenging environments.

Conclusions

This study and our recent work show that passerines are less heat tolerant than other orders of birds in large part because of their reliance on respiratory EWL at high T_{air} . This lower level of tolerance appears to be driven by the high metabolic costs of panting and the added heat load that must be evaporatively dissipated, making them susceptible to lethal dehydration. The species observed in the present study, for example, lost 5–9% $M_b h^{-1}$ at their thermal limits (~50°C), which is two to four times the 2% $M_b h^{-1}$ at T_{air} of 48°C (Smith et al., 2015) observed in the larger columbiforms from the same region that primarily use cutaneous evaporation. With increasingly warmer temperatures predicted across deserts of the southwestern United States, smaller desert passerines will be subject to increased risk of dehydration, reductions in daily activity, potential lethal overheating, and changes in geographic distribution and possible local extirpation (Albright et al., 2017). Overall, passerine birds (<100 g) may be in a poor position to persist in hot deserts, relative to other taxa, because of

their smaller size and reliance on respiratory EWL, potentially limiting their occupancy of hot dry desert environments during much of the year.

Acknowledgements

We thank the Cadden and Wolf families for allowing us to conduct this research on their properties. Matt Baumann, Corrie Borgman, Jennifer Clark, Mateo Garcia, Michael Griego, Chuck Hayes, Alex Kusarov, Ben Smit and Bill Talbot provided invaluable assistance in the field and laboratory. We thank Christian P. Giardina for helpful comments early in the writing process. We also thank two anonymous reviewers for constructive comments on the manuscript that greatly improved its quality.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.E.M., B.O.W.; Methodology: E.K.S., A.R.G., B.O.W.; Software: E.K.S., A.E.M.; Formal analysis: E.K.S., A.E.M., B.O.W.; Investigation: E.K.S., J.J.O., A.R.G., B.O.W.; Resources: B.O.W.; Data curation: E.K.S., A.R.G.; Writing - original draft: E.K.S.; Writing - review & editing: E.K.S., J.J.O., A.R.G., A.E.M., B.O.W.; Visualization: E.K.S., A.E.M.; Supervision: B.O.W.; Project administration: B.O.W.; Funding acquisition: B.O.W.

Funding

This research was supported by the National Science Foundation [grant number 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.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.161141.supplemental>

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