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Eric Smith

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Eric Krabbe Smith

Candidate

Biology

Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

Blair O. Wolf, Chairperson

Alexander R. Gerson

Janet M. Ruth

Christopher C. Witt

AVIAN THERMOREGULATION IN THE HEAT: RESTING METABOLISM, EVAPORATIVE COOLING AND LIMITS TO ACTIVITY IN SONORAN DESERT BIRDS

by

Eric Krabbe Smith

B.S., Electrical Engineering, Stanford University, 1984

M.A., History, University of California Santa Cruz, 1990

M.S., Biology, University of New Mexico, 2017

DISSERTATION

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Abstract

Birds in subtropical deserts face significant thermoregulatory challenges as environmental temperatures regularly exceed avian body temperature. To understand the differing susceptibility of desert birds to increasing temperatures, this dissertation initially examined thermoregulatory performance in seven passerine bird species varying in body mass from 10 to 70g – Lesser Goldfinch, House Finch, Pyrrhuloxia, Cactus Wren, Northern Cardinal, Abert's Towhee and Curve-billed Thrasher – and three larger Sonoran Desert nesting bird species – Mourning Dove (104 g), White-winged Dove (147 g) and Gambel's Quail (161 g).

Daytime resting metabolism, evaporative water loss and real-time body temperature were measured using flow-through respirometry at air temperatures (T_{air}) from 30° to 66°C. Marked increases in resting metabolism were found at the upper critical temperature (T_{uc}), which for six of the seven passerine species fell within a relatively narrow range (T_{air}=36.2° - 39.7°C), but which was considerably higher in the largest, the Curve-billed Thrasher (42.6°C); the T_{uc} of the quail (41.1°C) was similar to that of the thrasher but considerably lower than in both dove species (45.9° - 46.5°C). Resting metabolism and evaporative water loss were minimal below the T_{uc} and increased with T_{air} above the T_{uc} in all species to maximum values of 0.38 - 1.62 W and 0.87 - 4.02 g H_2O hr^{-1}, respectively, among the passerines, 0.94 W and 3.21 g H_2O hr^{-1} in the Gambel's Quail, and 0.77 - 1.17 W and 3.73 - 6.59 g H_2O hr^{-1} in the Mourning and White-winged Doves. The passerines maintained relatively high rates of resting metabolism and evaporative water loss and reached heat tolerance limits (HTL) that did not scale with body mass but were ~50°C for all species. Gambel's Quail maintained low resting metabolic rates and low rates of evaporative water loss and reached their HTL at T_{air} of 52°C. Mourning Doves and White-winged Doves maintained low resting metabolic rates, but high rates of evaporative water loss and reached their HTL at T_{air} of 58° - 60°C. Body temperatures reached maximum values of 43.5° to 45.3°C in the passerines, 43.6°C in Gambel's Quail but only 41.9° - 42.7°C in Mourning and White-winged Doves. Among the passerines the ratio of evaporative heat loss to metabolic heat production reached maximum values ranging from 1.39-2.06, similar to that found here for the quail (2.14) but much lower than that found for the doves (3.08-3.69).

Desert birds reduce their activity during the heat of the day, supporting predictions that daily activities and thus fitness and survival will be increasingly impacted by climate warming. Improving confidence in these predictions requires a detailed, mechanistic understanding of functional limits on activity and variability in these limits across taxa. The Heat Dissipation Limit (HDL) theory posits that levels of activity are determined by maximal rates of heat dissipation. This dissertation next examined how high air temperatures, the capacity for evaporative heat loss (EHL) and resting metabolic rate (RMR) restrict activity in 13 species of Sonoran Desert birds. It found that the primary pathway relied upon for evaporative cooling (panting, gular flutter, cutaneous) and its metabolic efficiency (EHL/RMR) predict variation in sustained metabolic scope in the heat. Among nightjars and doves, which use gular flutter and cutaneous water loss, respectively, EHL carries very low metabolic costs. These species can sustain much higher workloads in the heat than passerines, which depend upon the metabolically more costly pathway of panting to achieve evaporative cooling. Climate warming will increasingly impact the activities of all desert birds, but this new model suggests that the impacts to desert passerines will be disproportionately high.

INTRODUCTION

Thermoregulation in birds

Birds are endotherms that balance heat loss with heat gain in order to maintain a high, relatively constant body temperature (T_b), ranging from 39° to 42°C among species. At air temperatures (T_{air}) below T_b, they lose "dry heat" through convection, conduction and radiation according to the gradient between T_b and T_{air}, as well as through evaporative heat loss. Once T_{air} exceeds T_b, the gradient between T_b and T_{air} reverses and the avenues for dry heat loss become avenues for heat gain, leaving only evaporative heat loss to balance heat gain from the environment. Scholander et al. (1950) used Newton's law of cooling as the "natural basis" for modeling heat loss in endotherms, arguing that heat loss in still air was proportional to the gradient $T_b - T_{air}$. The authors defined the critical temperature -- later to become known as the lower critical temperature (T_{lc}) -- as the lowest T_{air} an endotherm can maintain without increasing metabolism. Below the T_{lc} the animal balances heat loss due to the increasing gradient by increasing metabolic heat production, primarily via shivering thermogenesis; above the T_{lc} an animal resides in a thermoneutral zone (TNZ), where it adjusts heat balance behaviorally and maintains a constant, basal metabolic rate (BMR). Later authors expanded the zone of the thermoneutrality to reach an "upper limit of thermoneutrality" or "upper critical temperature" (Wallgren, 1954; Dawson, 1954), above which an endotherm typically loses heat by increasing evaporative water loss, accompanied by increases in metabolic rate.

Thermoregulation in birds at high air temperatures

Despite decades of research on thermoregulation in birds, our information on the thermoregulatory performance of wild birds exposed to $T_{air} > T_b$ is limited. In part this is due to an emphasis on measurement of basal metabolic rates (BMR) at cooler temperatures and in part due to inherent limitations in the methodologies of past studies. Evaporative water loss, if measured, used gravimetric measurements of evaporative water loss over intervals of 30 to 60 minutes. Metabolic rates were calculated from measurements of O_2 consumption, but oxygen analyzers of the time typically required a depression in measured O_2 values of 0.5% (5000 ppm) or more for best accuracy. Achieving this depression in O_2 in the animal chamber required relatively low air flow rates, typically 150-750 mL min^{-1}, which at higher T_{air} increased chamber humidities enough to cause "a marked influence on the effectiveness of evaporative cooling" (p. 452, Lasiewski et al., 1966). Also, experimental birds were generally hand-raised in captivity or kept for periods in the laboratory at standard temperatures (e.g. 25-30°C; Lasiewski and Seymour 1972; Weathers, 1981). Thus earlier studies may have underestimated the heat tolerance of birds; both because heat-acclimated birds tolerate significantly higher temperatures (Marder and Arieli, 1988; McKechnie and Wolf, 2004) and because high chamber humidities impede their ability to evaporate water (Webster and King, 1987; Gerson et al., 2014).

It was thought that the absence of sweat glands in the skin and the thick plumage boundary layer in birds precluded significant cutaneous evaporative water loss (Calder and Schmidt-Nielsen, 1967), and panting was thus seen as the primary means of evaporative heat dissipation in birds. Heat loss through panting is an active process, requiring muscular movement of the respiratory apparatus and is thus costly and produces significant metabolic heat (Dawson, 1982). To counter the environmental and metabolic heat loads, rates of water loss via panting are typically very high. For instance, water loss by panting in a small desert passerine can exceed 5% of M_b per hour (Wolf and Walsberg, 1996). Not all birds pant, however; despite their lack of sweat glands, most doves are able to dissipate significant heat loads via non-glandular cutaneous evaporation (Smith and Suthers, 1969). Cutaneous evaporation -- in contrast to panting – is largely passive, requiring little or no metabolic increase (Marder and Ben-Asher, 1983) and has been shown to be primarily responsible for Rock Doves maintaining nearly constant body temperatures (41° – 42°C) up to T_{air} of 60°C (Marder and Arieli, 1988).

Chapter 1 used flow-through respirometry to measure daytime resting metabolic rate (RMR, W), whole-animal evaporative water loss (EWL, g H_2O hr^{-1}) and T_b as a function of T_{air} from 30° to 66°C in desert-nesting granivores. We found that the thermoregulatory performance and water balance of Mourning and White-winged doves differed greatly from that of the Gambel’s quail. The quail showed lower heat tolerance limits (52°C) due to lower RMR and lower mass-specific EWL at high T_{air}, which allows them to conserve water and energy -- but also potentially makes them vulnerable to increasing temperatures, especially during heat waves. Doves, in contrast, demonstrated higher relative rates of evaporation when environmental temperatures exceeded normothermic T_b. Thus, at a T_{air} of 48°C, Mourning and White-winged Doves lose 10% M_b in water over a period of 4–5 h, while this takes 6 h or more in Gambel’s quail. Greater rates of EWL in these doves could reduce their abundance if water were unavailable, for example, because of longer or more intense droughts; but it also provides them with greater heat tolerance limits (58° – 60°C). With their more constrained EWL and greater reliance on respiratory EWL, Gambel’s quail appear to have heat tolerance limits that are significantly lower than those observed in doves – but may persist without water for longer periods in moderate heat.

Chapter 2 presents thermoregulatory data for 7 species of Sonoran Desert passerine birds, across a range of body sizes (10-70g), naturally acclimatized to summer heat and exposed to high T_{air} at low chamber humidities, thereby providing a favorable water vapor gradient for evaporative heat loss. We asked how RMR, EWL, and T_b changed in response to T_{air}, contributed to heat tolerance, scaled with M_b and differed among species. We found marked increases in RMR 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). In contrast to the early finding of Dawson (1954) that passerines dissipate less than half their total heat load through evaporation, we found that evaporative heat dissipation at high T_{air} accounted for 139% to 206% of metabolic heat production in these species. These maximum values occurred at heat tolerance limits (HTL) that did not scale with M_b among species, but were ~50°C for all species except the Pyrrhuloxia and Abert's Towhee (HTL = 48°C). These passeriforms were less heat tolerant than other orders of birds found in the Sonoran Desert in large part due to their reliance on respiratory EWL at high T_{air}, which produces high mass-specific rates of EWL and makes them vulnerable to dehydration. Perhaps more importantly, respiratory EWL is metabolically costly and adds to heat load that must be dissipated through evaporation. The benefits of larger body size and more efficient evaporative cooling are shown when comparing the passerines in this study to Mourning Dove and Gambel's Quail. Overall, passerine birds (< 100g) may be in a poor position to persist in hot deserts, relative to other taxa, due to their smaller size, reliance on respiratory EWL and lower heat tolerance, potentially limiting their occupancy of hot dry desert environments during much of the year.

Chapter 3 reviews empirically estimated limits to performance in endothermic animals and hypotheses that seek to explain these limits: the central limitation hypothesis, in which the capacity of the alimentary tract (digestion or absorption) limits the assimilation or use of energy by animals; the peripheral limitation hypothesis, in which various tissues, especially mammary glands, limit animal performance; and the Heat Dissipation Limit (HDL) theory, in which animal performance is determined by maximal rates of passive heat dissipation. The remainder of the chapter extends the central idea of the HDL theory – that capacities for heat dissipation limit levels of activity in animals – to avian activity in the heat. We used thermoregulatory data collected during the summer from a suite of 13 species of Sonoran Desert birds, representing five avian orders, to inform a heat balance model and estimate maximum metabolic scope for desert birds at high air temperatures. In contrast to HDL theory, the model incorporates evaporative heat loss as a pathway for heat dissipation and recognizes that hyperthermia is a common response in exercising and heat-stress birds. Using this model we argue that evaporative heat loss has the potential to strongly limit activity in desert birds at high air temperatures, and that the primary pathway of evaporative cooling and its metabolic efficiency predict variation among species in sustainable metabolic scope. Climate warming will increasingly impact the activities of all desert birds; our new model suggests that the impacts to desert passerines – which depend upon the metabolically costly pathway of panting for evaporative cooling – will be disproportionately high.

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CHAPTER 1

Avian thermoregulation in the heat: Resting metabolism, evaporative cooling, and heat tolerance In Sonoran Desert doves and quail

Eric Krabbe Smith[1*], Jacqueline O'Neill[1], Alexander R. Gerson[1, 2], Blair O. Wolf[1]

1. Department of Biology, University of New Mexico, Albuquerque, NM USA
2. Department of Biology, University of Massachusetts, Amherst, MA USA

*Author for correspondence (ericsm@unm.edu)

Citation

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Running title

Avian thermoregulation and heat tolerance

SUMMARY

Birds in subtropical deserts face significant thermoregulatory challenges as environmental temperatures regularly exceed avian body temperature. To understand the differing susceptibility of desert birds to increasing temperatures, we examined thermoregulatory performance and estimated heat tolerance limits (HTL) for three Sonoran Desert nesting bird species – Gambel's Quail, Mourning Doves, and White-winged Doves. Using flow-through respirometry we measured daytime resting metabolism, evaporative water loss and real-time body temperature at air temperatures (T_{air}) from 30° to 66°C. We found marked increases in resting metabolism at the upper critical temperature (T_{uc}), which was significantly lower in the quail (T_{air}=41.1°C) than in both dove species (T_{air}=45.9° - 46.5°C). Gambel's Quail maintained low resting metabolic rates and low rates of evaporative water loss at their T_{uc} (0.71 W and 1.20 g H_2O hr^{-1} respectively), but were more sensitive to increasing air temperature, reaching their HTL at T_{air} of 52°C. Mourning Doves and White-winged Doves maintained low resting metabolic rates (0.66 and 0.94 W), but higher rates of evaporative water loss (1.91 and 2.99 g H_2O hr^{-1}) at their T_{uc} and reached their HTL at T_{air} of 58° - 60°C. Mass-specific evaporative water loss in White-winged Doves (147 g) and Mourning Doves (104 g) was 45% and 30% greater, respectively, than the rate observed in Gambel's Quail (161 g) at T_{air} of 48°C. Higher rates of evaporation and higher T_{uc} made the doves exceptionally heat tolerant, allowing them to maintain body temperatures at least 14°C below air temperatures as high as 60°C (140°F).

KEYWORDS

evaporative water loss; resting metabolic rate; upper critical temperature; body temperature; thermoregulation; heat tolerance limit; Sonoran Desert; doves; quail

INTRODUCTION

Birds in hot environments face significant physiological challenges when environmental temperatures exceed body temperature, a situation where evaporation is the only avenue for heat dissipation (Calder and King, 1974). Increasing air temperatures drive increases in avian body temperature, metabolism, and evaporative water loss in an effort to offset increasing heat loads, but the costs incurred can affect survival and fitness (McKechnie and Wolf, 2010; Cunningham, 2013a, 2013b). Warmer and more frequent hot days over land are virtually certain by the late 21st century (IPCC, 2013) and will be accompanied by hotter, longer, and more frequent heat waves (Meehl and Tebaldi, 2004; IPCC, 2011; Rahmstorf and Coumou, 2011). These rapid increases in environmental temperatures over the coming century will increasingly tax the abilities of animals to thermoregulate effectively and may dramatically influence community structure and the distribution of animals (McKechnie et al., 2012; Diffenbaugh and Field, 2013; Quintero and Wiens, 2013).

The high solar heat loads and high air temperatures of the world's deserts already routinely expose birds to environmental or operative environmental temperatures (T_e) that greatly exceed avian body temperature (Bakken, 1976; Robinson et al., 1976). Gambel's Quail (*Callipepla gambelii*) foraging on a typical hot summer day in the Sonoran Desert, for example, experience T_e approaching 50°C (Goldstein, 1984). Desert nesting doves often place their nests in sites with high solar heat loads, where the nest environment can reach T_e of 50° - 60°C, which demands that incubating birds cool their eggs to maintain viable egg temperatures (B.O. Wolf, *pers. obs.*; Russell, 1969; Walsberg and Voss-Roberts, 1983; Marder and Gavrieli-Levin, 1986).

Despite decades of research on thermoregulation in birds, our information on the thermoregulatory performance of wild birds exposed to air temperatures above body temperature is limited. Early research on avian thermoregulation in the heat focused on passerines, which evaporate water from their respiratory surfaces by panting (Dawson and Bartholomew, 1968). Heat loss through panting is an active process, requiring muscular movement of the respiratory apparatus, a metabolically costly effort that produces heat. Rates of water loss via panting are very high and in small passerines may exceed 5% of body mass per hour (Wolf and Walsberg, 1996). A lack of sweat glands and the thick plumage were thought to impede significant evaporation from the skin in birds (Calder and Schmidt-Nielsen, 1967). Smith and Suthers (1969) showed that pigeons and doves dissipate large heat loads by cutaneous evaporation with little increase in metabolism, allowing Rock Doves (*Columba livia*) to raise young at air temperatures as high as 60°C (Marder and Arieli, 1988). The strong reliance on cutaneous evaporation in the heat is apparently widespread in columbiform birds, where it has been observed in two of this study's species, Mourning Doves (*Zenaida macroura*) and White-winged Doves (*Z. asiatica*) (Hoffman and Walsberg, 1999; McKechnie and Wolf, 2004), but not in galliform birds (Marder, 1983; Marder and Ben-Asher, 1983). Other mechanisms that enhance evaporative heat loss such as gular flutter, deep esophageal pulsation, and cloacal evaporation remain poorly understood (Calder and King, 1974; Gaunt, 1980; Dawson, 1982; Baumel et al., 1983; Schleucher et al., 1991; Hoffman et al., 2007).

Among the modest number of studies that have examined heat tolerance of birds, differences in methodologies make it difficult to draw broad conclusions. These studies often relied on birds raised or held in captivity for long periods at standard temperatures (e.g. 25° - 30°C; see Hudson and Brush, 1964; Lasiewski and Seymour, 1972; Weathers, 1981; Hoffman and Walsberg, 1999; Hoffman et al., 2007). Because heat acclimated birds can tolerate significantly higher temperatures than birds acclimated to lower standard temperatures (Marder and Arieli, 1988;

McKechnie and Wolf, 2004), prior heat stress studies may have greatly over-estimated the susceptibility of subjects to elevated temperatures.

Here, we present data on the thermoregulatory performance of the Gambel's Quail, a galliform, and two species of columbiforms, the Mourning Dove and White-winged Dove, with the aim of quantifying responses to heat stress in birds summer-acclimatized to a hot subtropical desert. We continuously measured body temperature (T_b, °C), whole animal rates of evaporative water loss (EWL, g H_2O hr^{-1}) and daytime resting metabolism (RMR, W) in response to chamber air temperature (T_{air}, ranging from 30° to 66°C) in birds on the day they were captured. We hypothesized that like Rock Doves, White-winged Doves and Mourning Doves would demonstrate high tolerances for heat, and nearly constant T_b and RMR with increasing T_{air}. Because galliforms lack the cutaneous evaporative cooling of columbiforms, we anticipated that Gambel's Quail would demonstrate lower tolerances for heat and show more rapid increases in T_b and RMR with increasing T_{air}. We present these species together because of their ecological similarities as large (> 100g), desert nesting granivores with overlapping distributions, but make no inferences about adaptive differences. Thus, we examine their relative thermoregulatory performance without yet a sufficient number of species to consider their evolutionary histories (Garland et al., 1992, 1993, 2005; Blomberg et al., 2003).

MATERIALS AND METHODS

Site description

Birds were captured in June and July of 2012 (White-winged and Mourning Doves) and in July of 2013 (Gambel's Quail) in northwest Tucson, Arizona, USA. Experiments were conducted the same day as capture. During June and July of 2012, temperatures at the Tucson AZMET weather station ranged from 14-42°C, daily maximum temperatures ranged from 31-42°C, and the dew point ranged from -15° to 22°C. During July of 2013, temperatures ranged from 21-41°C, daily maximum temperatures ranged from 32-41°C, and the dew point ranged from 7-23°C.

Animal capture and handling

The birds were captured using standard walk-in traps baited with seed and held outdoors in shaded, darkened screen cages (model 1450B, 12” X 12” X 12”, BioQuip, Rancho Dominguez, CA, USA). None of the birds received supplemental food after capture. However, they probably continued digesting seed in their crops and were not post-absorptive; thus we assumed for metabolic measurements an RER of 1 and 20.9 joules mL^{-1} CO_2 produced (Gessaman and Nagy, 1988; Walsberg and Wolf, 1995). Free water was provided to the quail but they were not observed to drink. Thus, prior to each experimental run, the quail were provided between 3 and 6 mL of tap water via oral gavage. Five White-winged Doves were also given additional water by gavage prior to high temperature runs and no differences in thermal tolerance were observed compared to un-watered individuals. Prior to each experimental run 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 cool air flow and T_b was monitored until it returned to resting levels (~40°C); Gambel’s Quail were also gavaged with tap water post-exposure to ensure rehydration. Birds were monitored for 1-5 hours after exposure, after which the doves were released at the site of the experiments and quail from their 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). Birds were captured under permits from the US Fish and Wildlife Service and the Arizona Game and Fish Department.

Measurements of resting metabolism and evaporative water loss

Measurements of RMR and EWL were made using a flow-through respirometry system similar to Whitfield et al. (2015). The respirometry chamber consisted of a transparent plastic container (5 L, 22 cm x 25 cm x 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 ±0.5°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) or from a compressor through a membrane dryer (2013: Champion® CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA). Excurrent air was sampled at 250 mL min^{-1} and directed to a $CO_{2/}H_2O$ 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, a 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° - 66°C in 2°C increments) in a stepped pattern of temperature trials over the span of the one to three hour experimental run. In order to keep H_2O content of the respirometry chamber at values that would not impede evaporation (dew point < 5°C), flow rates were maintained between 5 to 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; H_2O and CO_2 production were monitored and observed to drop to resting levels (typically 30 minutes). T_{air} was then increased to higher trial temperatures and birds were allowed to adjust to each temperature for 10-20 minutes 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. A trial was ended and the bird recorded as reaching its thermal limit if it: 1) remained continuously active for 5-10 minutes, 2) showed a T_b approaching or exceeding 45°C, or 3) showed a loss of balance or righting response (extremely rare). In some trials, birds were exposed to T_{air} that were at or near their thermal limits, but these measurements were not designed to elicit mortality. Unlike critical thermal maxima trials where mortality is common (reviewed in Lutterschmidt and Hutchison, 1997), our procedure resulted in rates of mortality of less than 1%. 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 five minutes of baseline data were collected following each temperature trial.

Data analysis

We selected the lowest one minute (doves) or five minute (quail) average of CO_2 ppm readings less baseline values for each trial temperature. Birds noted as active or failing or having mean T_b > 44.7°C or slope of T_b > 0.1°C min^{-1} during a temperature trial were not included in the analysis. Using equation 10.5 of Lighton (2008), we estimated the rate of CO_2 production in mL

CO_2 min^{-1} and whole animal RMR in Watts (W), assuming an RER of 1 (see Animal capture and handling). Rates of whole animal EWL (g H_2O hr^{-1}) were calculated from the H_2O ppt readings (less baseline values) for the same data points using equation 10.9 of Lighton (2008).

Statistical analysis

Statistical analyses and graphs were produced using R (version 3.1; R Development Core Team, 2011) inside of RStudio (version 0.98.932). We used the linear mixed effects model from the nlme package and individual bird as a random factor (Pinheiro et al., 2009) due to the repeated measurement of individuals in an unbalanced design. We used the segmented package (Muggeo, 2009) 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

Initial body mass (M_b) averaged 160.7 ± 11.1 g (mean ± SD; N=19) for Gambel's Quail, 104.0 ± 10.2 g (N=49) for Mourning Doves, and 147.3 ± 17.7 g (N=52) for White-winged Doves (Table 1). M_b ($P < 0.001$), species ($P = 0.002$) and T_{air} ($P < 0.001$) all significantly predicted RMR and EWL in the species tested. We account for the mass-dependence of RMR and EWL by including mass as a covariate in all applicable models and presenting mass-independent residuals of these measures when comparing among the three species (Supplement 1).

Resting metabolism

Segmented regressions of RMR residuals against T_{air} allowed us to identify inflection points of 41.1°C for Gambel's Quail, 45.9°C for Mourning Doves, and 46.5°C for White-winged Doves (Table 1, Figure S1). These inflection points represent the upper critical temperatures (T_{uc}) above which daytime RMR increases sharply (Kendeigh, 1969). Between 30°C and the T_{uc}, RMR decreased as T_{air} increased ($F_{1,44} = 24.3$, $P < 0.001$), but this response differed among species ($F_{1,88} = 21.9$, $P < 0.001$) and was significantly influenced by M_b ($F_{1,88} = 30.8$, $P < 0.001$). Above the T_{uc}, RMR increased as T_{air} increased ($F_{1,65} = 43.4$, $P < 0.001$); this response also differed among species ($F_{1,92} = 11.3$, $P = 0.001$) and was significantly influenced by M_b ($F_{1,92} = 48.1$, $P < 0.001$). Thus, the effects of T_{air} and M_b were assessed for each species independently.

For Gambel's Quail exposed to T_{air} below their T_{uc} of 41.1°C, RMR decreased with increasing T_{air} ($F_{1,5} = 15.5$, $P < 0.05$; Figure 1) but was unaffected by M_b ($F_{1,15} = 0.04$, $P = 0.85$). RMR increased with T_{air} above the T_{uc} ($F_{1,11} = 24.6$, $P < 0.001$; Figure 1) with a slope of 0.022 W $°C^{-1}$ (Table 3), and M_b was a significant covariate ($F_{1,16} = 8.03$, $P < 0.05$). RMR was lowest at the T_{uc} and averaged 0.71 W or 4.55 mW g^{-1} (Table 1) and RMR averaged 0.75 W at T_{air} of 42°C and 0.79 W at 48°C (Table 2).

For Mourning Doves at T_{air} below their T_{uc} of 45.9°C, RMR decreased with increasing T_{air} ($F_{1,16} = 10.1$, $P < 0.01$; Figure 1) and M_b was a significant covariate ($F_{1,40} = 8.42$, $P < 0.01$). RMR increased with T_{air} above the T_{uc} ($F_{1,27} = 22.3$, $P < 0.001$; Figure 1) with a slope of 0.017 W $°C^{-1}$ (Table 3), and M_b was a significant covariate ($F_{1,37} = 9.66$, $P < 0.01$). RMR averaged 0.64 W at T_{air} of 42°C, 0.66 W or 6.07 mW g^{-1} at the T_{uc}, and 0.58 W at 48°C (Tables 1 and 2).

For White-winged Doves at T_{air} below their T_{uc} of 46.5°C, RMR decreased with increasing T_{air} ($F_{1,21} = 7.18$, $P < 0.05$; Figure 1) and M_b was a significant covariate ($F_{1,30} = 18.8$, $P < 0.001$). RMR increased with T_{air} above the T_{uc} ($F_{1,25} = 12.3$, $P < 0.01$; Figure 1) with a slope of 0.019 W $°C^{-1}$ (Table 3), and M_b was a significant covariate ($F_{1,36} = 5.73$, $P < 0.05$). RMR averaged 0.99 W at T_{air} of 42°C, 0.94 W or 6.49 mW g^{-1} at the T_{uc}, and 0.97 W at 48°C (Tables 1 and 2).

Evaporative water loss

For T_{air} below the T_{uc}, there was a significant effect of T_{air} ($F_{1,43} = 197.9$, $P < 0.001$), species ($F_{1,88} = 28.0$, $P < 0.001$), and M_b ($F_{1,88} = 32.2$, $P < 0.001$) – as well as a significant interaction of T_{air} and species ($F_{1,43}= 22.2$, $P < 0.001$) – on EWL (g H_2O hr^{-1}) indicating differences in the slope of this relationship among species. For T_{air} above the T_{uc}, EWL was significantly affected by T_{air} ($F_{1,64} = 475.6$, $P < 0.001$), species ($F_{1,92} = 28.8$, $P < 0.001$), M_b ($F_{1,92} = 67.9$, $P < 0.001$), and an interaction of T_{air} and species ($F_{1,64} = 30.8$, $P < 0.001$). Thus, there was a significant difference in the response of EWL to T_{air} among species both above and below the respective T_{uc}.

For Gambel's Quail at T_{air} below their T_{uc} of 41.1°C, EWL increased with T_{air} ($F_{1,5} = 20.1$, $P < 0.01$; Figure 2) with a slope of 0.035 g H_2O $hr^{-1}°C^{-1}$ (Table 3) but was unaffected by M_b ($F_{1,15} = 0.00$, $P = 0.98$). EWL increased more steeply with T_{air} above the T_{uc} ($F_{1,11} = 176.3$, $P < 0.001$; 0.196 g H_2O $hr^{-1}°C^{-1}$; Figure 2; Table 3). EWL averaged 0.67 g H_2O hr^{-1} at T_{air} of 35°C, 1.71 g H_2O hr^{-1} at 42°C, and 2.46 g H_2O hr^{-1} at 48°C (Table 2).

For Mourning Doves at T_{air} below their T_{uc} of 45.9°C, EWL increased with T_{air} ($F_{1,16} = 63.6$, $P < 0.001$; Figure 2) with a slope of 0.069 g H_2O $hr^{-1}°C^{-1}$ (Table 3) and M_b was a significant covariate ($F_{1,40} = 14.2$, $P < 0.001$). EWL increased more steeply with T_{air} above the

T_{uc} ($F_{1,27} = 286.2$, $P < 0.001$; 0.210 g H_2O $hr^{-1}°C^{-1}$; Figure 2; Table 3) and M_b was a significant covariate ($F_{1,37} = 11.6$, $P < 0.01$). EWL averaged 0.74 g H_2O hr^{-1} at T_{air} of 35°C, 1.27 g H_2O hr^{-1} at 42°C, and 1.96 g H_2O hr^{-1} at 48°C (Table 2).

For White-winged Doves at T_{air} below their T_{uc} of 46.5°C, EWL increased with T_{air} ($F_{1,21} = 87.9$, $P < 0.001$; Figure 2) with a slope of 0.140 g H_2O $hr^{-1}°C^{-1}$ (Table 3) and M_b was a significant covariate ($F_{1,30} = 12.9$, $P < 0.01$). EWL increased more steeply with T_{air} above the T_{uc} ($F_{1,25} = 174.5$, $P < 0.001$; 0.383 g H_2O $hr^{-1}°C^{-1}$; Figure 2; Table 3). EWL averaged 0.99 g H_2O hr^{-1} at T_{air} of 35°C, 1.95 g H_2O hr^{-1} at 42°C, and 3.41 g H_2O hr^{-1} at 48°C (Table 2).

Ratio of evaporative heat loss to metabolic heat production

We converted EWL to rates of whole animal evaporative heat loss (EHL, W) using a latent heat of vaporization of water of 2.26 J (mg H_2O)$^{-1}$ and define the ratio EHL/MHP – a dimensionless metric for evaporative cooling capacity -- as evaporative heat loss (EHL) relative to metabolic heat production (MHP = RMR). For T_{air} below the T_{uc}, there was a significant effect of T_{air} ($F_{1,43} = 374.7$, $P < 0.001$) and species ($F_{1,89}= 6.50$, $P < 0.05$) – as well as a significant interaction of T_{air} and species ($F_{1,43}= 14.9$, $P < 0.001$) – on EHL/MHP. For T_{air} above the T_{uc}, EHL/MHP showed a significant effect of T_{air} ($F_{1,64} = 282.6$, $P < 0.001$) and species ($F_{1,93} = 6.01$, $P < 0.05$) and a significant interaction of T_{air} and species ($F_{1,64} = 10.6$, $P < 0.01$). Thus, there was a significant difference in the response to T_{air} among species both above and below the respective T_{uc}. There were no significant effects of M_b on EHL/MHP ($P > 0.05$), either above or below the T_{uc}.

In Gambel's Quail EHL/MHP increased with T_{air} both below and above the T_{uc} (Below: $F_{1,5} = 57.4$, $P < 0.001$; Above: $F_{1,11} = 33.9$, $P < 0.001$; Figure 3). EHL/MHP averaged 0.55 at T_{air} of 35°C, 1.42 at 42°C and 1.97 at 48°C, increasing 3.6 fold between 35° and 48°C (Table 2). At

T_{air} of 50°C, just below the HTL (heat tolerance limit, see below), Gambel's Quail reached a maximum EHL/MHP of 2.14 (Table 1).

In Mourning Doves EHL/MHP increased with T_{air} both below and above the T_{uc} (Below: $F_{1,16} = 123.8$, $P < 0.001$; Above: $F_{1,27} = 159.1$, $P < 0.001$; Figure 3). EHL/MHP averaged 0.65 at T_{air} of 35°C, 1.26 at 42°C and 2.19 at 48°C, increasing 3.4 fold between 35° and 48°C (Table 2). At T_{air} of 56°C, just below the HTL, Mourning Doves reached a maximum EHL/MHP of 3.08 (Table 1).

In White-winged Doves EHL/MHP increased with T_{air} both below and above the T_{uc} (Below: $F_{1,21} = 122.9$, $P < 0.001$; Above: $F_{1,25} = 84.5$, $P < 0.001$; Figure 3). EHL/MHP averaged 0.62 at T_{air} of 35°C, 1.22 at 42°C and 2.27 at 48°C, increasing 3.7 fold between 35° and 48°C (Table 2). At T_{air} of 58°C, just below the HTL, White-winged Doves reached a maximum EHL/MHP of 3.69 (Table 1).

Body temperature

For T_{air} below 39°C there were no significant effects of M_b, species, T_{air}, or the interaction of T_{air} and species on T_b ($P > 0.05$) and thus T_b in this range were considered normothermic. For T_{air} above 39°C, however, T_b increased with T_{air} differentially among species (T_{air}: $F_{1,148} = 79.2$, $P < 0.001$; species: $F_{1,107} = 4.9$, $P < 0.05$; T_{air} x species: $F_{1,148} = 4.9$, $P < 0.05$). Thus above T_{air} of 39°C, there was a significant difference in the response of T_b to T_{air} among species.

T_{air} below 39°C did not affect T_b in Gambel's Quail ($F_{1,14} = 0.08$, $P = 0.78$) and normothermic T_b averaged 41.1°C (Table 1). T_b increased with T_{air} above 39°C ($F_{1,17} = 67.8$, $P < 0.001$; Figure 4) with a fairly steep slope of 0.170°C $°C^{-1}$ (Table 3). T_b averaged 41.8° and 42.5°C at T_{air} of 42° and 48°C respectively (Table 2) and 43.6° at T_{air} of 50°C (Table 1). Thus at

T_{air} of 50°C, just below the HTL (heat tolerance limit, see below), Gambel's Quail maintained a $T_a - T_b$ gradient of 6.4°C.

T_{air} below 39°C did not affect T_b in Mourning Doves ($F_{1,9} = 0.01$, $P = 0.93$) and normothermic T_b averaged 41.0°C (Table 1). T_b increased with T_{air} above 39°C ($F_{1,68} = 42$, $P < 0.001$; Figure 4) with a fairly shallow slope of 0.041°C $°C^{-1}$ (Table 3). T_b averaged 42.0° and 42.1° at T_{air} of 42° and 48°C respectively (Table 2) and 41.9° at T_{air} of 56°C (Table 1). Thus at T_{air} of 56°C, just below the HTL, Mourning Doves maintained a $T_a - T_b$ gradient of 14.1°C.

T_{air} below 39°C did not affect T_b in White-winged Doves ($F_{1,9} = 0.40$, $P = 0.54$) and normothermic T_b averaged 41.4°C (Table 1). T_b increased with T_{air} above 39°C ($F_{1,62} = 25$, $P < 0.001$; Figure 4) with a fairly shallow slope of 0.056°C $°C^{-1}$ (Table 3). T_b averaged 41.9° and 41.7° at T_{air} of 42° and 48°C respectively (Table 2) and 42.7° at T_{air} of 58°C (Table 1). Thus at T_{air} of 58°C, just below the HTL, White-winged Doves maintained a $T_a - T_b$ gradient of 15.3°C.

Heat tolerance limit

The results presented thus far pertained to data collected from birds that were inactive and maintaining stable T_b (see Materials and Methods). To investigate heat tolerance, we examined the final 5 minutes of all temperature trials above 39°C with regard to T_b maximum and T_b slope (Figure 5). The T_b (maximum, slope) for Gambel's Quail (45.1°C, 0.27 C min^{-1}) and Mourning Doves (46.1°C, 0.24 C min^{-1}) resulted from individuals in 52°C and 54°C temperature trials, respectively; the values for White-winged Doves (46.0°C, 0.39 C min^{-1}) were recorded by different individuals in trials of 54°C and above. Individual birds passed a given trial if T_b and slope of T_b remained less than or equal to 44.7°C and 0.1°C min^{-1}, respectively; individuals that exceeded either of these limits were classified as failing, indicating that the heat load experienced by an individual exceeded its thermoregulatory capacity and it had reached its heat tolerance limit (HTL). Once the majority of individuals failed in a trial at a given T_{air}, a species was considered to have reached its HTL. Thus, the HTL of Gambel's Quail was 52°C (1/9 pass), of Mourning Doves was 58°C (3/8 pass) and of White-winged Doves was 60°C (1/4 pass; Figure 5; Table 1).

DISCUSSION

In this study we examined the thermoregulatory ability of wild doves and quail under conditions that normally persist during the summer in hot subtropical deserts. We maintained low chamber humidities (dew point < 5°C) to maximize the evaporative gradient and used summer-acclimatized birds in order to make measurements under ecologically relevant conditions. White-winged and Mourning Doves demonstrated a heat tolerance and ability to thermoregulate at T_{air} as high as 60°C, while Gambel's Quail did so successfully up to 50°C.

Earlier studies often did not provide conditions conducive for examining natural responses to heat stress. Hudson and Brush (1964), for example, found that Mourning Doves died at T_{air} above 41°C and that California Quail (*Callipepla californica*) could not survive T_{air} above 44°C. Birds exposed to very high environmental temperatures in nature are typically subject to very low atmospheric humidity. High chamber humidity impeded these birds' ability to evaporate water and severely limited their ability to cope with heat stress (see Lasiewski et al., 1966, and Whitfield et al., 2015, for more discussion of these issues).

In addition, most studies of thermoregulation in these taxa have focused on responses to T_{air} below normothermic T_b. Prior to this study, thermoregulatory performance at T_{air} above 40°C had only been quantified in 9 of the 300+ species of columbiform birds and 7 of the 170+

species of galliform birds (see Figures 6 and 7). Of these, only 4 columbiform and 3 galliform species were exposed to T_{air} above 45°C. Below, we discuss the thermoregulatory performance of each study species in detail and compare our observations to earlier relevant studies in galliform and columbiform birds as well as speculate on their future performance in a warmer and dryer environment.

Resting metabolism and upper critical temperature

Understanding changes in RMR with changes in T_{air} is critical to quantifying thermoregulatory capacity in the heat. We found similar slopes in doves and quail for changes in RMR and mass independent RMR at T_{air} above the T_{uc} (Table 3, Table S1). However, the T_{uc} — the T_{air} at which heat dissipation becomes an active process and marked increases in daytime RMR occur (Kendeigh, 1969) — was significantly lower in the quail (41.1°C) than observed in both dove species (45.9 - 46.5°C; Supplement 1). These differences in the T_{uc} among doves and quail are importantly related to pathways of evaporative heat dissipation. At a T_{air} of 30°C evaporative losses in most birds are more or less evenly distributed between respiratory and cutaneous pathways (Bernstein, 1971; Ro and Williams, 2010). At a $T_{air} \geq 40$°C, the primary evaporative pathway is respiratory in passerines (≥75%, Wolf and Walsberg, 1996) and galliforms (75%, Richards, 1976), and cutaneous in doves (≥70%, McKechnie and Wolf, 2004). Since metabolic heat contributes to total heat load, birds that actively dissipate heat via panting (quail, passerines) tend to have lower limits of heat tolerance and relatively high rates of water loss compared with doves, which dissipate most of their heat load using cutaneous evaporation.

Other studies of columbiforms have reported responses of metabolic rate to temperature similar to those reported in the current study (Figure 6). In Rock Doves acclimated to very high

T_{air} (up to 62°C) metabolic rate remained constant from 30° to 60°C, and no T_{uc} is apparent (Marder and Arieli, 1988). White-winged Doves acclimated to 43°C showed no significant difference in RMR between 35° and 45°C (McKechnie and Wolf, 2004), but these T_{air} were below the T_{uc} found in this study. Spinifex Pigeons (89 g, *Geophaps plumifera*; Withers and Williams, 1990) and Crested Pigeons (186 g, *Ocyphaps lophotes*; B.O. Wolf, unpublished), like the two species of dove tested here, show T_{uc} of 46°C. However, three columbiforms, including the Diamond Dove (~40g, *Geopelia cuneata*), Crested Pigeon (174g), and Brush Bronzewing (224g, *Phaps elegans*), show T_{uc} close to normothermic T_b, which is contrary to the pattern we observed and may be due to acclimation history or measurement dates or conditions (Schleucher, 1999; Larcombe et al., 2003). In each of these cases, the experimental birds were housed outdoors at T_{air} below 25°C, suggesting a seasonal adjustment of T_{uc} like that of BMR (McKechnie, 2008). Given their capacities for cutaneous heat dissipation, doves in the wild may only rarely experience heat loads that require panting and an increase in RMR.

Galliform birds such as quail, pheasants and partridges, in contrast, show clear well-defined T_{uc} where metabolic rate increases markedly with increasing heat stress. T_{uc} values for galliforms in the heat tend to cluster around normothermic T_b and show only modest variability (Figure 6). Data from eight studies encompassing six species show that T_{uc} range from 35° - 42°C with only the Sand Partridge (*Ammoperdix heyi*) showing no increase in metabolic rate with T_{air} ranging from 35° - 50°C. Sand Partridges, thus, appear more similar to columbiform birds in that their metabolic rate does not increase steeply at any point (Frumkin et al., 1986), which suggests that an elaborated gular mechanism or enhanced cutaneous evaporation may occur in this species. Our T_{uc} value for Gambel's Quail is similar to other studies for the same species (Goldstein and Nagy, 1985; Weathers, 1981), indicating that T_{uc} in galliform birds tends to fall just below or slightly above T_b.

Given the differences in individual birds, their acclimation history, the time of year and experimental conditions, the lowest metabolic rates we measured are similar to previous measurements of RMR and BMR in these species. For Gambel's Quail in this study RMR was 4.6 mW g^{-1} at the T_{uc} (Table 1), which is less than the BMR of 6.0 mW g^{-1} found for birds acclimated to 25°C (Weathers, 1981) and comparable with an RMR of 5.0 ± 1.7 mW g^{-1} (n=24; $33°C \leq T_{air} \leq 47°C$) found in wild birds -- as in this study – acclimatized to the Sonoran Desert summer (Goldstein and Nagy, 1985). For Mourning Doves in this study RMR was 6.1 mW g^{-1} at the T_{uc}, which is less than the BMR of 7.1 mW g^{-1} observed in birds at higher humidities and acclimated to 25°C (Hudson and Brush, 1964; Appendix A of McNab, 2009). For White-winged Doves in this study RMR was 6.5 mW g^{-1} at the T_{uc}, which compares favorably with the metabolic rate (6.3 ± 0.8 mW g^{-1}; n=15; $35°C \leq T_{air} \leq 45°C$) found for birds acclimated to 43°C (McKechnie and Wolf, 2004).

Evaporative water loss

Gambel's Quail showed a significant increase in EWL at the T_{uc} of 41.1°C (Table 3, Figure 2). The marked increase in RMR and EWL together indicate an increase in respiratory evaporation at a T_{air} coinciding with their normothermic T_b. Doves also increased EWL at their T_{uc}, but this value was ~46°C. Their reliance on cutaneous evaporation, which has negligible metabolic costs (Marder and Ben-Asher, 1983; Marder and Gavrieli-Levin, 1987), allowed these doves to defer active heat dissipation via panting and/or gular flutter to a T_{air} approximately 5°C higher than normothermic T_b.

Despite their differences in M_b, Mourning Doves and Gambel's Quail showed similar responses of EWL above their respective T_{uc} (Table 3, Table S1). However, as a percentage of M_b, EWL was 30% greater in Mourning Doves (2.1% M_b hr^{-1}) and 45% greater in White-winged Doves (2.3% M_b hr^{-1}) than that observed in Gambel's Quail (1.6 % M_b hr^{-1}) at a T_{air} of 48°C (Table 2). White-winged Doves increased their EWL with T_{air} more steeply than the other two species, both above and below T_{uc} (Table 3, Table S1). Compared with similarly sized Gambel's Quail, White-winged Doves evaporated water at higher rates than over a range of high T_{air}, which provided a greater cooling capacity, but resulted in greater rates of water loss.

Evaporative water loss generally scales with M_b with increasing T_{air} in both galliforms and columbiforms (Figure 7). At the highest T_{air} measured among columbiforms, c.a. 55-60°C, EWL ranges from 2-3% M_b hr^{-1} in Rock Doves to 4-5% M_b hr^{-1} in the smaller dove species (39-147g). At the highest T_{air} frequently measured among galliforms, c.a. 44-45°C, EWL ranges from 0.7% M_b hr^{-1} in the large Bedouin fowl (~1400g, *Gallus domesticus*) to 3% M_b hr^{-1} in the small King Quail (40g, *Coturnix chinensis*). In this study EWL in Gambel's Quail at T_{air} of 50°C measured about 2% M_b hr^{-1}.

Ratio of evaporative heat loss to metabolic heat production

At T_{air} just below their respective HTL we found that Gambel's Quail are able to produce EHL/MHP of 2.14 at 50°C, with Mourning Doves producing ratios of 3.08 at 56°C, and White-winged Doves showing ratios of 3.69 at 58°C (Table 1). In prior studies only the larger Rock Doves exhibit ratios approaching 3.0 at 60°C (Marder and Arieli, 1988). The smaller Spinifex Pigeons had EHL/MHP ratios of 1.25-1.5 at 45°C and 1.75 at 50°C (Dawson and Bennett, 1973; Withers and Williams, 1990). Data for small doves (~40g) show that these species can produce

EHL/MHP ratios of 1.0 (Diamond Dove), 1.1-1.2 (Inca Dove, *Columbina inca*), and 1.6 (Namaqua Dove, *Oena capensis*) at 44°C (Schleucher et al., 1991; Lasiewski and Seymour, 1972; MacMillen and Trost, 1967; Schleucher, 1999; Gerson et al., 2014). Among these smaller doves, the Namaqua Doves appear to be more heat tolerant than the other smaller species, although this could be an artifact of acclimation or measurement conditions, producing EHL/MHP of 3.55 at 56°C (Gerson et al., 2014), which is comparable to the value we found for White-winged Doves at 58°C. Overall, heat acclimatized doves exposed to T_{air} of 55-60°C dissipate heat through evaporation at 3 - 3.7 fold their rates of metabolic heat production and thus are able to cope with extremely high environmental heat loads.

Excluding the Gambel's Quail used in this study, galliforms ranging in size from 40-1400g have not been shown to produce EHL/MHP ratios > 2.0 or tolerate T_{air} above 48°C. Large Sinai and Bedouin fowls (~1300-1400g) produce a maximum EHL/MHP of 1.65 at 44°C and apparently tolerate maximum T_{air} of 48°C (Marder, 1973; Arad and Marder, 1982). Chukar Partridge (475g, *Alectoris chukar*) are able to produce EHL/MHP of 1.82 at 48°C and reached their heat tolerance limits in trials >48°C (see below; Marder and Bernstein, 1983). Japanese Quail (~100g, *Coturnix japonica*) produce a maximum EHL/MHP of 1.12 at a T_{air} of 43°C. The smallest galliform that has been studied, King Quail (~40g), produced a EHL/MHP ratio of 1.17 at 45.2°C (Lasiewski et al., 1966) and 1.23 at 44°C (Lasiewski and Seymour, 1972). In general, it appears that galliforms are able to tolerate maximum T_{air} of ~48-50°C and are able to evaporate water at rates that can account for slightly more than two times their RMR at the highest T_{air}.

Body temperature and heat tolerance limit

Facultative hyperthermia represents a means of partially offsetting heat gain in hot environments and reducing EWL and, as a consequence, is a well-developed response in heat stressed and exercising birds. We found that the normothermic T_b for Mourning and White-winged Doves averaged 41.0 and 41.4°C, respectively (Table 1). The T_b of both species increased linearly with T_{air} above this range, staying well below lethal temperatures and reaching a value of 41.9°C for T_{air} of 56°C in Mourning Doves and 42.7°C for T_{air} of 58°C in White-winged Doves (Table 1). This increase of 0.9°C for Mourning and 1.3°C for White-winged Doves from normothermic T_b falls below the 1.6° to 4.2°C range of T_b increases found for other columbiform birds exposed to lower T_{air} of 44° - 45°C (Lasiewski and Seymour, 1972; MacMillen and Trost, 1967; Schleucher, 1999; Withers and Williams, 1990; Larcombe et al., 2003), while it exceeds the 0.8°C variation in T_b found for heat acclimated Rock Doves between T_{air} of 30° and 60°C (Marder and Arieli, 1988). At ~41°C, the normothermic T_b of Gambel's Quail and the dove species were very similar. As T_{air} increased, however, T_b of Gambel's Quail had a significantly steeper slope and lower intercept than that of both dove species (Figure 4, Table 3), reaching 43.6° at T_{air} of 50°C (Table 1). Thus, just below the HTL, Gambel's Quail maintained a T_{air} - T_b gradient of just 6.4°C versus 14.1° and 15.3°C, respectively, for Mourning and White-winged Doves.

Establishing the thermal tolerance of animals to heat stress is a prerequisite for understanding how heat exposure and its severity may impact wild animal populations. Historically, these determinations have taken a variety of forms, but the assays typically produced high mortality in the subjects and most have tended to focus on ectotherms (98% of 604 animal taxa reviewed by Lutterschmidt and Hutchison, 1997). In this study we measured core T_b continuously, rather than recording a single T_b measurement at the end of a temperature trial, which allowed us to determine both maximum T_b of individuals as well as the response of

T_b to changes in T_{air}. Thus, we could determine real time if an individual had reached its thermal limits and terminate the trial without harming the bird. The HTL metric provided a clear T_{air} above which birds could not maintain a constant T_b. Using a protocol similar to ours, Marder and Bernstein (1983) found that Chukar Partridges exposed to T_{air} of 48°C maintained a stable T_b for 2 to 4.5 hours, but could not maintain T_b below lethal levels at T_{air} of 52°C. Thus, like the quail observed in our study, this large galliform (475g) reached its limit of heat tolerance at a T_{air} of 52°C. Our findings and those of others provide strong evidence that desert-dwelling columbiform birds, primarily due to their high rates of cutaneous evaporation, cope better with high heat loads than galliforms in the same environment.

Ecological aspects of thermoregulatory performance in doves and quail

Williams et al. (2012) has suggested that desert birds need the capacity to increase EWL during periods of extreme heat in order to maintain sub-lethal T_b, while minimizing dehydration over the long term. In this study, we found that the thermoregulatory performance and water balance of Mourning and White-winged Doves differed greatly from that of the sympatric Gambel's Quail. The quail showed lower RMR and lower mass-specific EWL at T_{air} above normothermic T_b, which serves to conserve water and energy, but also potentially makes them vulnerable to increasing temperatures, especially during heat waves. Doves, in contrast, support a high water use "lifestyle" when environmental temperatures exceed normothermic T_b. Thus at a T_{air} of 48°C, Mourning and White-winged Doves lose 10% M_b in water over a period of four to five hours, while this takes six hours or more in Gambel's Quail. Greater rates of EWL in doves could reduce their abundances if water were unavailable, for example, due to longer or more intense droughts (IPCC, 2013; Albright et al., 2010); but it also allows them to survive at temperatures of 60°C or more. With their more constrained EWL and greater reliance on respiratory EWL, Gambel's Quail appear to have heat tolerance limits that are significantly lower than those observed in doves — but may persist without water for longer periods in moderate heat.

The differing thermoregulatory responses among the three species to high T_{air}, in part, may reflect their differing ecologies within the Sonoran Desert. Mourning and White-winged Doves often nest in exposed locations with significant solar heat loads, where the nest environment can reach T_e of 50° - 60°C and incubating birds must cool rather than warm their eggs to maintain viability (B.O. Wolf, *pers. obs.*; Russell, 1969; Walsberg and Voss-Roberts, 1983). Doves require access to preformed water almost daily and travel up to 20 km or more access water holes (Gubanich, 1966; Brown, 1989); their strong flight capabilities allow them to nest many miles from water sources (Bartholomew and Dawson, 1954). In addition, doves are able to rapidly drink by suction, placing their bills in water sources and drinking continuously. Mourning Doves deprived of water for 24 hours can drink 17% of their M_b in water in 10 minutes (Bartholomew and Dawson, 1954). Gambel's Quail are much less mobile and typically range about ½ a kilometer from their roost sites (Gorsuch, 1934). During the Sonoran Desert summer, they constrain their activities to shaded microsites during the heat of the day, with only intermittent exposure to the sun when moving between shaded sites or flying short distances (Goldstein, 1984; Goldstein and Nagy, 1985). Gambel's Quail often live independent of surface water resources and rely on vegetation and insects in desert valleys far from water (Lowe, 1955; Hungerford, 1960; Bartholomew and Cade, 1963). Very high air temperatures, however, may constrain the ability of quail to forage and potentially limit their distribution in future climates (Goldstein, 1984; McKechnie and Wolf, 2010).

It is critical that we understand the thermoregulatory and water balance challenges that birds face in a rapidly warming world. Such understanding might allow us predict and perhaps mitigate such events; it is a prerequisite for understanding avian distributions now and in a warmer future. This study is a first step in examining the relative responses of birds to higher temperatures and gives us some baseline measure of their ecological performance. Given the apparent differences among species in physiological responses to heat stress, examining tolerances of naturally occurring avian communities in similar ways will be critical for understanding their composition and persistence.

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COMPETING INTERESTS

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

B.O.W. designed the study. B.O.W., E.K.S. and A.R.G. designed the experimental set up. E.K.S., J.O., A.R.G., and B.O.W. collected data. E.K.S. analyzed the data. E.K.S., A.R.G., and B.O.W. wrote the manuscript.

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SYMBOLS AND ABBREVIATIONS

BMR	basal metabolic rate (Watts or W)
EHL	whole animal evaporative heat loss rate (Watts or W)
EHL/MHP	evaporative cooling capacity (dimensionless ratio)
EWL	whole animal evaporative water loss rate (g H_2O hr^{-1})
HTL	heat tolerance limit (°C)
M_b	initial body mass (g)
MHP	whole animal metabolic heat production (= RMR)
ppm	parts per million
ppt	parts per thousand
RMR	whole animal resting metabolic rate (Watts or W)
T_{air}	chamber air temperature (°C)
T_b	body temperature (°C)
T_e	operative environmental temperature (°C)
T_{uc}	upper critical temperature (°C)

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TABLES

Table 1. Mean values and ± SD for variables measured in three Sonoran Desert nesting bird species.

Species	Body mass (g)	Normothermic T_b[1] (°C)	T_{uc} (°C)	RMR[2] (W)	RMR[2] (mW g^{-1})	EWL[2] (g H_2O hr^{-1})	HTL (°C)	T_b[3] (°C)	EHL/MHP[3]
Gambel's Quail	160.7 ± 11.1 (N=19)	41.1 ± 0.5	41.1	0.71 ± 0.09	4.55 ± 0.63	1.20 ± 0.43	52	43.6 ± 0.8	2.14 ± 0.30
Mourning Dove	104.0 ± 10.2 (N=49)	41.0 ± 0.8	45.9	0.66 ± 0.10	6.07 ± 0.72	1.91 ± 0.21	58	41.9 ± 0.9	3.08 ± 0.48
White-winged Dove	147.3 ± 17.7 (N=52)	41.4 ± 0.6	46.5	0.94 ± 0.29	6.49 ± 1.78	2.99 ± 0.66	60	42.7 ± 0.9	3.69 ± 1.24

1. $T_{air} \leq 39°C$. Sample sizes (n) ranged between 11 and 16.
2. Tair (± 1°C) = T_{uc} (upper critical temperature). Sample sizes (n) ranged between 7 and 15.
3. T_{air} (± 1°C) = HTL (heat tolerance limit) - 2°C. Sample sizes (n) ranged between 5 and 6.

Table 2. Mean values and ± SD for resting metabolic rate (RMR), rate of evaporative water loss (EWL), evaporative cooling capacity (EHL/MHP), and body temperature (T_b) in Gambel's Quail, Mourning Doves, and White-winged Doves at three air temperatures (T_{air} ± 1°C).

	Gambel's Quail			Mourning Dove			White-winged Dove		
T_{air} (°C)	35°C (n=8)	42°C (n=6)	48°C (n=7)	35°C (n=7)	42°C (n=19)	48°C (n=12)	35°C (n=8)	42°C (n=12)	48°C (n=15)
RMR (W)	0.78 ± 0.08	0.75 ± 0.10	0.79 ± 0.09	0.75 ± 0.22	0.64 ± 0.18	0.58 ± 0.14	0.98 ± 0.39	0.99 ± 0.25	0.97 ± 0.28
RMR (mW g^{-1})	4.77 ± 0.58	4.50 ± 0.46	5.00 ± 0.54	7.37 ± 2.32	6.32 ± 1.71	6.11 ± 1.72	6.90 ± 1.81	6.76 ± 1.54	6.57 ± 1.70
EWL (g H_2O hr^{-1})	0.67 ± 0.15	1.71 ± 0.37	2.46 ± 0.37	0.74 ± 0.16	1.27 ± 0.44	1.96 ± 0.42	0.99 ± 0.49	1.95 ± 0.72	3.41 ± 0.85
EWL (% of Mb hr^{-1})	0.42 ± 0.09	1.03 ± 0.22	1.57 ± 0.25	0.72 ± 0.12	1.24 ± 0.36	2.05 ± 0.40	0.69 ± 0.23	1.32 ± 0.47	2.31 ± 0.51
EHL/MHP	0.55 ± 0.11	1.42 ± 0.22	1.97 ± 0.31	0.65 ± 0.19	1.26 ± 0.25	2.19 ± 0.47	0.62 ± 0.12	1.22 ± 0.28	2.27 ± 0.47
T_b (°C)	41.1 ± 0.6	41.8 ± 0.6	42.5 ± 0.8	41.0 ± 0.7	42.0 ± 0.5	42.1 ± 0.8	41.3 ± 0.6	41.9 ± 0.7	41.7 ± 0.9

Table 3. Slope (m) and intercept (b) for the relationships of resting metabolic rate (RMR), rate of evaporative water loss (EWL), evaporative cooling capacity (EHL/MHP) and body temperature (T_b) in response to air temperature (T_{air}) below and above the upper critical temperature (T_{uc}) in Gambel's Quail, Mourning Doves, and White-winged Doves.

Species	T_{uc}	regression	m	b	regression	m	b
Gambel's Quail	41.09	RMR ($\leq T_{uc}$)	-0.026 (-0.039 -0.013)	1.76 (1.29 2.22)	RMR ($> T_{uc}$)	0.022 (0.013 0.032)	-0.21 (-0.66 0.24)
Mourning Dove	45.89	RMR ($\leq T_{uc}$)	-0.019 (-0.031 -0.007)	1.49 (0.99 1.99)	RMR ($> T_{uc}$)	0.017 (0.010 0.025)	-0.15 (-0.54 0.25)
White-winged Dove	46.47	RMR ($\leq T_{uc}$)	-0.011 (-0.020 -0.003)	1.41 (1.05 1.78)	RMR ($> T_{uc}$)	0.019 (0.008 0.030)	0.04 (-0.53 0.60)
Gambel's Quail	41.09	EWL ($\leq T_{uc}$)	0.035 (0.019 0.050)	-0.44 (-0.99 0.11)	EWL ($> T_{uc}$)	0.196 (0.166 0.225)	-6.75 (-8.14 -5.36)
Mourning Dove	45.89	EWL ($\leq T_{uc}$)	0.069 (0.051 0.087)	-1.54 (-2.29 -0.79)	EWL ($> T_{uc}$)	0.210 (0.184 0.236)	-7.89 (-9.26 -6.53)
White-winged Dove	46.47	EWL ($\leq T_{uc}$)	0.140 (0.112 0.169)	-3.83 (-5.02 -2.64)	EWL ($> T_{uc}$)	0.383 (0.325 0.441)	-15.19 (-18.21 -12.16)
Gambel's Quail	41.09	EHL/MHP ($\leq T_{uc}$)	0.042 (0.031 0.054)	-0.88 (-1.28 -0.49)	EHL/MHP ($> T_{uc}$)	0.095 (0.062 0.127)	-2.59 (-4.11 -1.07)
Mourning Dove	45.89	EHL/MHP ($\leq T_{uc}$)	0.082 (0.067 0.096)	-2.16 (-2.76 -1.56)	EHL/MHP ($> T_{uc}$)	0.135 (0.113 0.156)	-4.45 (-5.57 -3.33)
White-winged Dove	46.47	EHL/MHP ($\leq T_{uc}$)	0.104 (0.085 0.122)	-2.96 (-3.73 -2.19)	EHL/MHP ($> T_{uc}$)	0.176 (0.137 0.214)	-6.20 (-8.20 -4.21)
Gambel's Quail	na	na	na (na na)	na (na na)	T_b (T_{air} > 39°C)	0.170 (0.129 0.211)	34.61 (32.72 36.50)
Mourning Dove	na	na	na (na na)	na (na na)	T_b (T_{air} > 39°C)	0.041 (0.028 0.053)	40.24 (39.61 40.88)
White-winged Dove	na	na	na (na na)	na (na na)	T_b (T_{air} > 39°C)	0.056 (0.034 0.079)	39.32 (38.22 40.42)

Note: Values are means, with 95% confidence intervals in parentheses. Regressions of body temperature (T_b) are in response to air temperature (T_{air}) above 39°C.

FIGURE CAPTIONS

Figure 1. Resting metabolic rate (W) as a function of air temperature (°C) in Gambel's Quail, Mourning Doves, and White-winged Doves. RMR was regressed against T_{air} below (all $P < 0.05$) and above the T_{uc} (all $P < 0.01$). T_{uc} in Gambel's Quail, Mourning Doves, and White-winged Doves are 41.1°, 45.9°, and 46.5°C respectively. See text for statistical details of linear regressions, Table 3 for parameter estimates, and Supplement 1 for determination of T_{uc} using RMR residuals.

Figure 2. Rate of evaporative water loss (g H_2O hr^{-1}) as a function of air temperature (°C) in Gambel's Quail, Mourning Doves, and White-winged Doves. EWL was regressed against T_{air} below (all $P < 0.01$) and above the T_{uc} (all $P < 0.001$). T_{uc} in Gambel's Quail, Mourning Doves, and White-winged Doves are 41.1°, 45.9°, and 46.5°C respectively. See text for statistical details of linear regressions, Table 3 for parameter estimates, and Supplement 1 for determination of T_{uc} using RMR residuals.

Figure 3. Evaporative cooling capacity (EHL/MHP) as a function of air temperature (°C) in Gambel's Quail, Mourning Doves, and White-winged Doves. EHL/MHP was regressed against T_{air} below and above the T_{uc} (all $P < 0.001$). T_{uc} in Gambel's Quail, Mourning Doves, and White-winged Doves are 41.1°, 45.9°, and 46.5°C respectively. See text for statistical details of linear regressions, Table 3 for parameter estimates, and Supplement 1 for determination of T_{uc} using RMR residuals.

Figure 4. Body temperature (°C) as a function of air temperature (°C) in Gambel's Quail, Mourning Doves, and White-winged Doves. Body temperature was regressed against air temperature above 39°C (all $P < 0.001$). See text for statistical details of linear regressions and Table 3 for parameter estimates. The dotted lines represent $T_b = T_{air}$.

Figure 5. Maximum body temperature (Max $T_{b,}$ °C), the slope of body temperature (Slope $T_{b,}$ °C min^{-1}) during temperature trials (Trial Count, pass versus fail) at air temperatures ≥ 40°C in Gambel's Quail, Mourning Doves, and White-winged Doves. In temperature trials a bird passed until reaching its heat tolerance limit (Fail = HTL, coded in black), when maximum body temperature exceeded 44.7°C or slope of body temperature exceeded 0.1°C min^{-1} during the last 5 minutes of a trial.

Figure 6. Metabolic rate (mW g^{-1}) as a function of air temperature (°C) in galliform and columbiform birds.

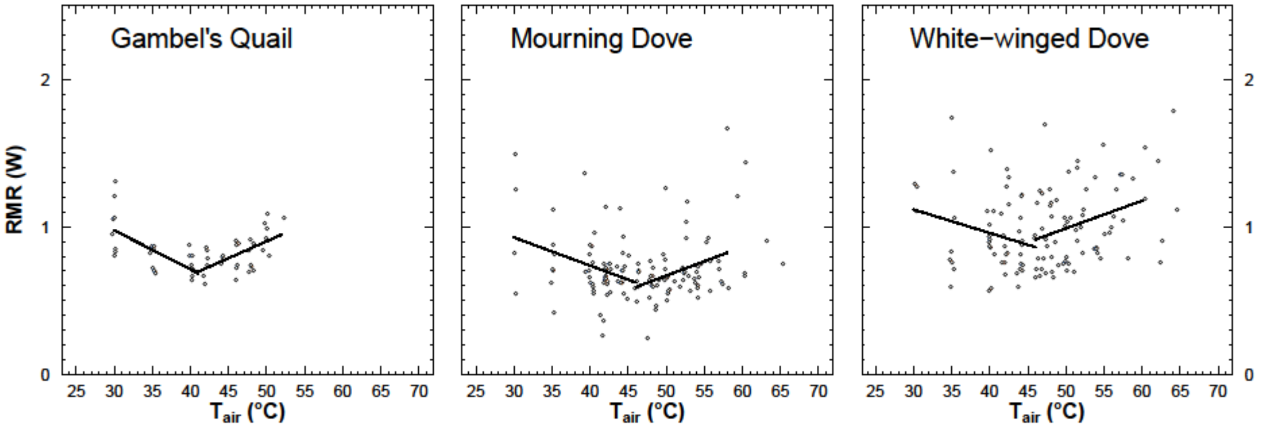
(1. Lasiewski and Seymour, 1972; 2. Roberts and Baudinette, 1986; 3. Pis, 2010; 4. Weathers, 1981; 5. Goldstein and Nagy, 1985 (data from summer of 1981); 6. this study; 7. Frumkin et al., 1986; 8. Marder and Bernstein, 1983; 9. Arad and Marder, 1982; 10. Marder, 1973; 11. Schleucher, 1999; 12. Gerson et al., 2014; 13. Withers and Williams, 1990; 14. McKechnie and Wolf, 2004; 15. Larcombe et al., 2003; 16. Marder and Arieli, 1988).

Figure 7. Rate of evaporative water loss (mg H_2O g^{-1} hr^{-1}) as a function of air temperature (°C) in galliform and columbiform birds. Note difference in scale of ordinate between the two graphs.

(1. Lasiewski and Seymour, 1972; 2. Roberts and Baudinette, 1986; 4. Weathers, 1981; 6. this study; 7. Frumkin et al., 1986; 8. Marder and Bernstein, 1983; 9. Arad and Marder, 1982; 10. Marder, 1973; 11. Schleucher, 1999; 12. Gerson et al., 2014; 13. Withers and Williams, 1990; 14. McKechnie and Wolf, 2004; 15. Larcombe et al., 2003; 16. Marder and Arieli, 1988).

FIGURES

Figure 1.



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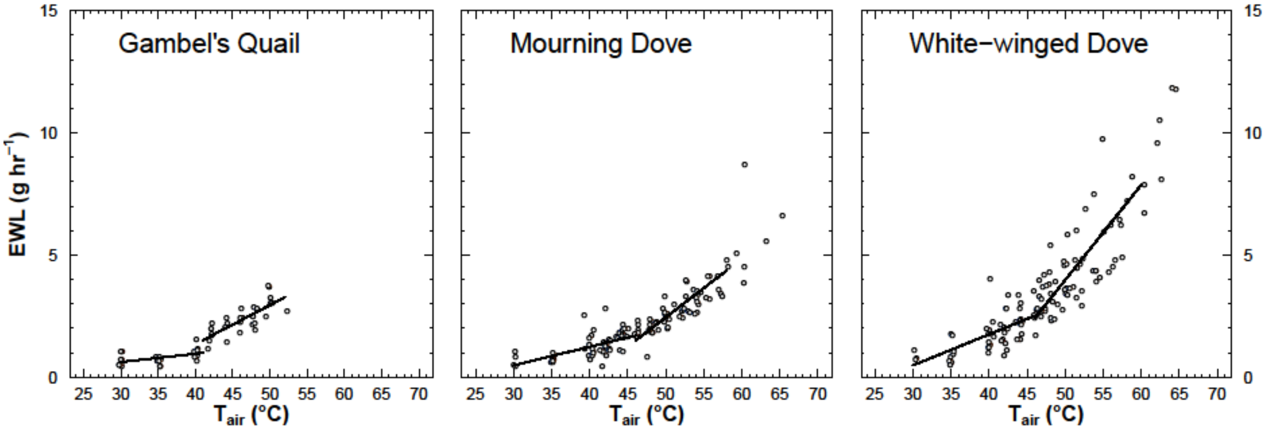

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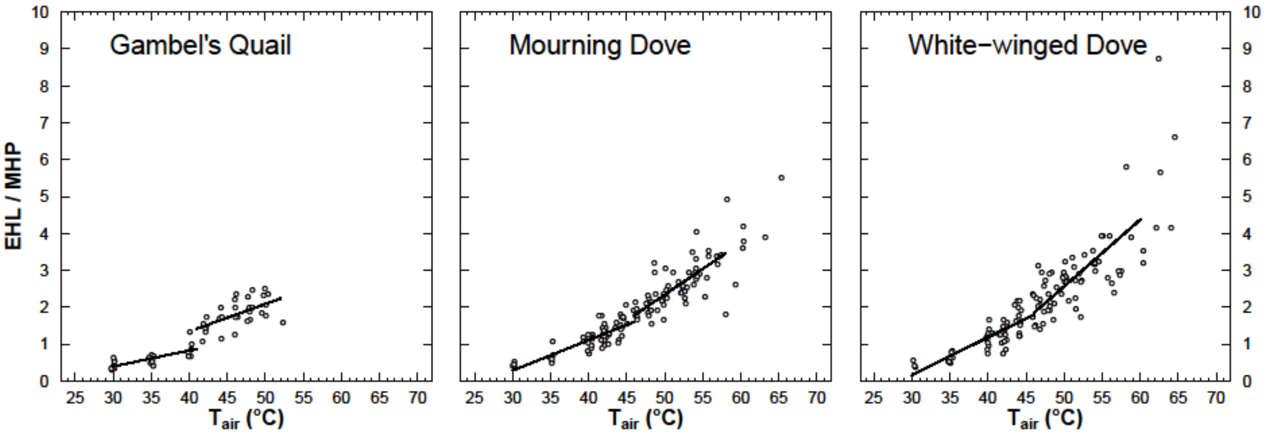

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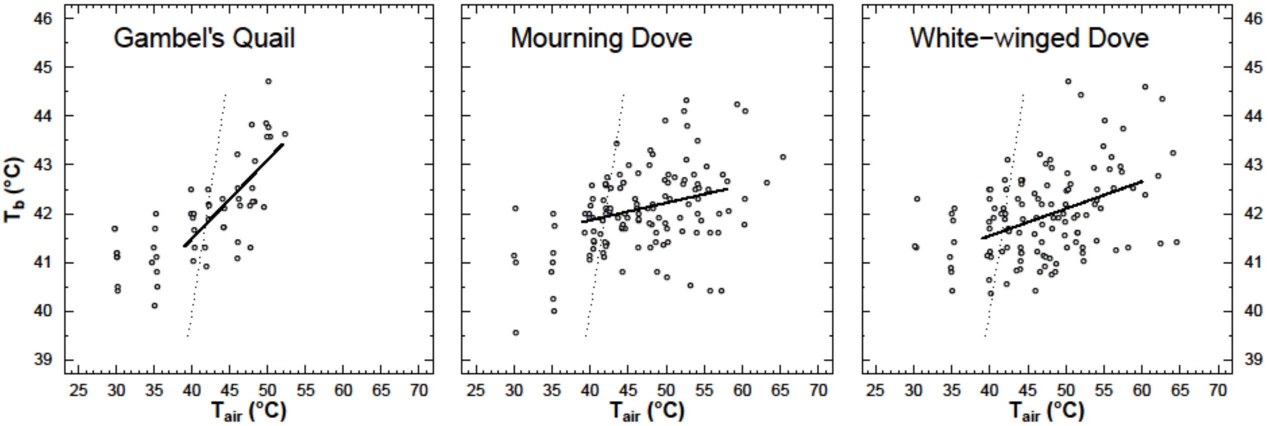

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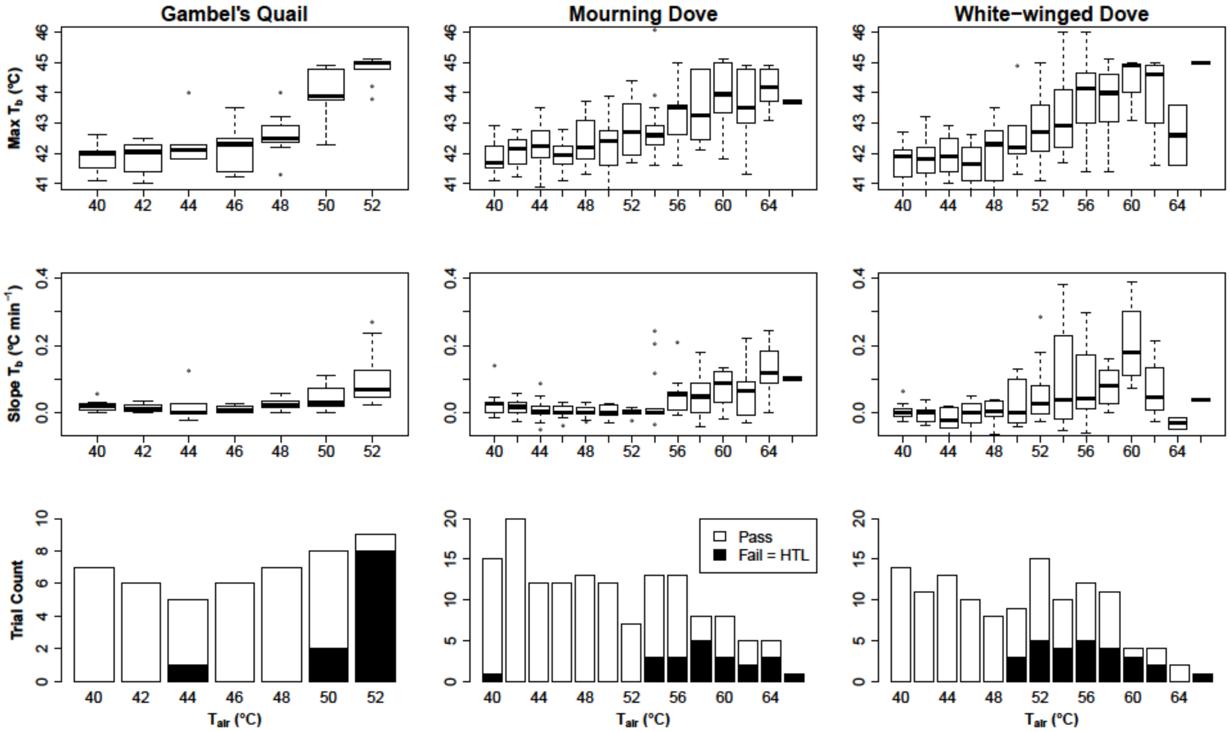


Gambel's Quail
Mourning Dove
White−winged Dove
Max Tb (°C)
41
42
43
44
45
46
Slope Tb (°C min−1)
0.0
0.2
0.4
Trial Count
0
2
4
6
8
10
0
5
10
15
20
40
42
44
46
48
50
52
40
44
48
52
56
60
64
Pass
Fail = HTL
Tair (°C)

Figure 6.

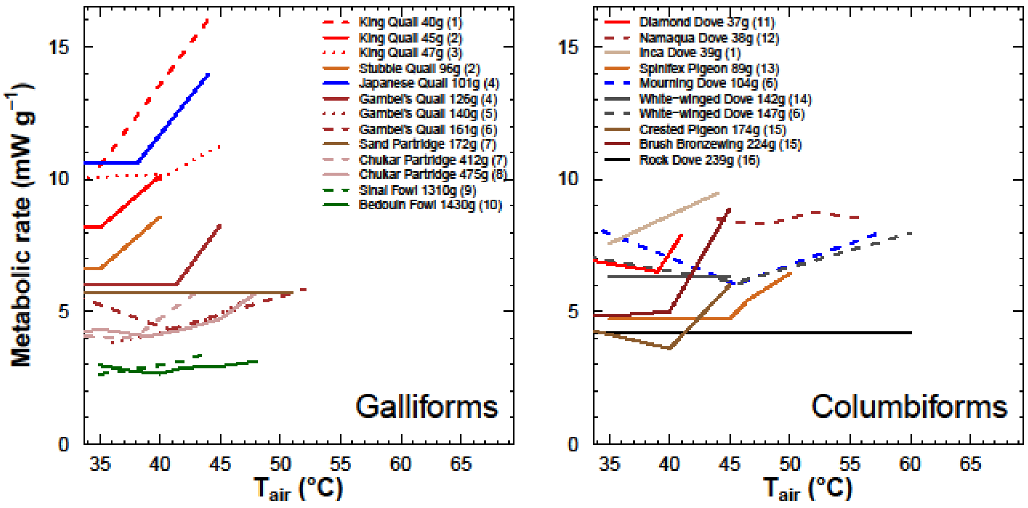
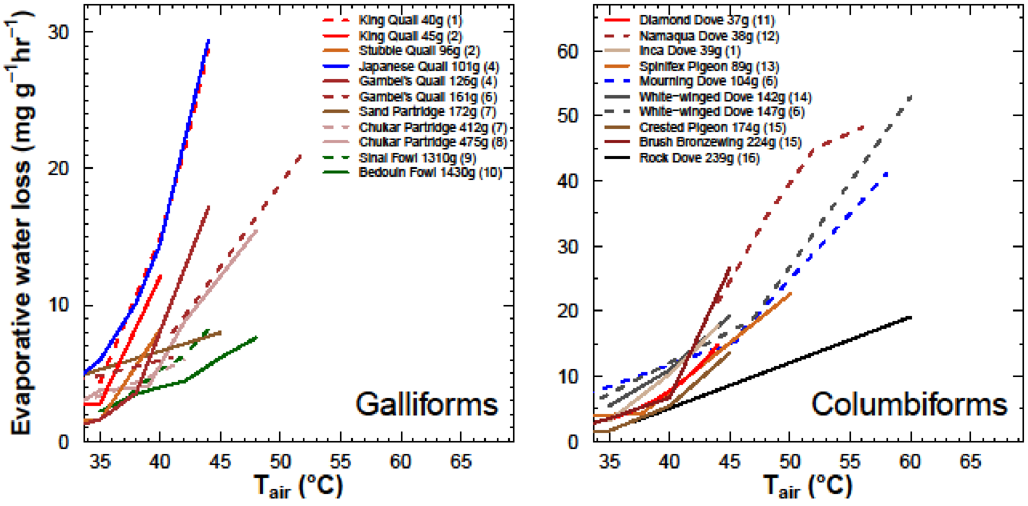


Figure 7.



CHAPTER 2

Avian thermoregulation in the heat:

Resting metabolism, evaporative cooling, and heat tolerance

In Sonoran Desert songbirds

Eric Krabbe Smith[1*], Jacqueline J. O'Neill[1], Alexander R. Gerson[1, 2], Andrew E. McKechnie[3], Blair O. Wolf[1]

3. Department of Biology, University of New Mexico, Albuquerque, NM USA
4. Department of Biology, University of Massachusetts, Amherst, MA USA
5. DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria 0002, South Africa

*Author for correspondence (ericsm@unm.edu)

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Running title

Sonoran Desert passerine bird thermoregulation and heat tolerance

SUMMARY

We examined thermoregulatory performance in seven Sonoran Desert passerine bird species varying in body mass from 10 to 70g – 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 H_2O hr^{-1}. 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 1.39-2.06, 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 (HTL) that did not scale with body mass among species, but were ~50°C for all species except the Pyrrhuloxia and Abert's Towhee (HTL = 48°C). High metabolic costs associated with respiratory evaporation appeared to drive the limited heat tolerance in these desert passeriforms, compared to larger desert columbiforms and galliforms that use metabolically more efficient mechanisms of evaporative heat loss.

KEYWORDS

evaporative water loss; resting metabolic rate; upper critical temperature; body temperature; thermoregulation; heat tolerance limit; Sonoran Desert; passerines

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 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 O_2 values of 0.5% (5000 ppm) or more for best accuracy; achieving this depression in O_2 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 cause “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 evaporate 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; Whitfield et al., 2015; Smith et al., 2015; Noakes et al., 2016; O’Connor et al. 2017; McKechnie et al., 2016a,b). 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 7-fold range in body mass (10-70g). We continuously measured body temperature (T_b, °C), whole animal rates of evaporative water loss (EWL, g H_2O hr^{-1}) and daytime resting metabolism (RMR, W) in response to chamber air temperature (T_{air}, ranging from 30° to 52°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 body mass 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, Arizona, 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 of 2012, daily minimum air temperatures at the Tucson AZMET weather station ranged from 14 to 27°C, daily maximum air temperatures ranged from 31 to 42°C, and the dew point ranged from -15° to 22°C. During June and July of 2013, daily minimum temperatures ranged from 17 to 29°C, daily maximum temperatures ranged from 32 to 43°C, and the dew point ranged from -21° to 23°C.

Animal capture and handling

House Finch (HOFI; *Haemorhous mexicanus*), Pyrrhuloxia (PYRR, *Cardinalis sinuatus*), Northern Cardinal (NOCA; *Cardinalis cardinalis*), Abert's Towhee (ABTO; *Melozone aberti*), and Curve-billed Thrasher (CBTH; *Toxostoma curvirostre*) were captured using standard walk-in traps baited with seed. Lesser Goldfinch (LEGO; *Spinus psaltria*) were caught with a drop-trap hung outside a thistle seed feeder. Cactus Wren (CAWR; *Campylorhynchus brunneicapillus*) 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 hours. Most individuals (141/158 = 89%) were tested within 6 hours 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_2_eq) of 27.8 J (mL CO_2)$^{-1}$ produced (Walsberg and Wolf, 1995; Whitfield et al., 2015). However, Lesser Goldfinch were usually tested within an hour's time of capture; thus we assigned RER/CO_2_eq of 0.76/26.6 to birds tested within 40-60 mins of capture and 0.83/24.9 to birds tested 20-40 mins of capture, in accordance with RER vs. time data from another small granivorous passerine (Zebra Finch, *Taeniopygia guttata*; EKS, unpublished data). Two Pyrrhuloxia and a single House Finch were also similarly assigned RER/CO_2_eq for data points collected within an hour's time 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 cool air stream and T_b was monitored until it returned to resting levels (~40°C). In the summer of 2013, birds were also gavaged with tap water post-exposure to ensure rehydration. Birds were monitored for 1-5 hours 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 metabolism 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 L, 22 cm x 19 cm x 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 ±0.5°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 $CO_{2/}H_2O$ 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, a 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 one to three hour experimental run. In order to keep H_2O 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; H_2O and CO_2 production were monitored and observed to drop to resting levels (typically 30 minutes). T_{air} was then increased to higher trial temperatures and birds were allowed to adjust to each temperature for 10-20 minutes 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 minutes, 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 body mass during a trial (including any fecal losses). Approximately five minutes of baseline data were collected following each temperature trial.

Data analysis

We selected the lowest five-minute average of chamber CO_2 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 equation 10.5 of Lighton (2008), we determined the rate of CO_2 production in mL CO_2 min^{-1} and whole animal RMR in Watts (W), assuming an RER of 0.71 and 27.8 J (mL CO_2)$^{-1}$ for most birds (see Animal capture and handling). Rates of whole animal EWL (g H_2O hr^{-1}) were calculated from the H_2O ppt readings (less baseline values) for the same data points using equation 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 H_2O)$^{-1}$, corresponding to T_{air}=40°C (Tracy et. al, 2010). We defined the ratio EHL/MHP – a dimensionless metric for 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; R Development Core Team, 2015) inside of RStudio (version 0.99.467). We used the linear mixed effects model from the nlme package and individual bird as a random factor (Pinheiro et al., 2014) due 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. Body mass 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

Initial body mass (M_b) averaged 9.7 ± 0.6 g (mean ± SD; N individuals=32) 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 (10-70g), 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 mass as a covariate in all applicable models and presenting mass-independent residuals of these measures when comparing among species (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 (Figure 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 of 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 0.27W in the Lesser Goldfinch to 0.87W in the Curve-billed Thrasher (Table 1). All seven species showed a clear T_{uc} (Figure 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, $P < 0.05$; Figure 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 $T_{air} \leq 36°C$, 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 an interaction of 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 $T_{air} \leq 36$°C varied in six of the species from an average of 0.13 g H_2O hr^{-1} in the House Finch to 0.41 g H_2O hr^{-1} in the Abert's Towhee (Table 1). In the Pyrrhuloxia, minimum EWL was 0.58 g H_2O hr^{-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 ($P < 0.001$; Figure 2); slopes ranged from 0.052 g H_2O hr^{-1}°C^{-1} in the Lesser Goldfinch to 0.270 g H_2O hr^{-1}°C^{-1} in the Curve-billed Thrasher and -- except for a swap in values between the similarly sized Northern Cardinal (39.4g) and Abert's Towhee (41.8g) -- 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 H_2O hr^{-1} in the Lesser Goldfinch to 4.02 g H_2O hr^{-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 $T_{air} \leq 36$°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 $T_{air} \leq 36$°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} x 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 seven species ($P < 0.001$; Figure 3); slopes ranged from 0.177°C per 1°C change in T_{air} in the House Finch to 0.316°C 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 $T_{air} = 52$°C (Table 1). Just below their HTL (heat tolerance limit, see below) at T_{air} of 48°C, all seven species maintained a remarkably consistent $T_{air} – T_b$ gradient of 4.1-4.3°C (Table S2).

Ratio of evaporative heat loss to metabolic heat production

At $T_{air} > 36$°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 of 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 ($P < 0.001$; Figure 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 heat tolerance limit (HTL). The HTL was 48°C for the Pyrrhuloxia and Abert's Towhee and 50°C for the other five species (Figure 4A, includes all but Pyrrhuloxia). The values associated with this limit (Max RMR, Max EWL, Max T_b and Max 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 $T_{air} > 45°C$ (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 critical 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 34.5g – Lesser Goldfinch, House Finch and Cactus Wren – were similar with overlapping 95% CI (Table S3). The slope of RMR in the Northern Cardinal was 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, Figure 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 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*, 610g); 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 to 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 two 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*, 193g) 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 TNZ 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. This observation was not in concordance for all species, however, as the Lesser Goldfinch showed a higher inflection point for EWL than T_{uc}, and we don't 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). Among the six species, T_b increased linearly at $T_{air} > 36°C$ and hyperthermic responses between T_{air} of 35° and 48°C averaged 2.65 ± 0.34°C, quantitatively similar to the hyperthermic responses of 3.02 ± 1.37°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 ± 1.52°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 ± 0.12°C (McKechnie et al., 2016b) and two Sonoran dove species showing increases of 0.75 ± 0.76°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_{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 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°C°C^{-1} 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 (> 100g) 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 $T_{air} – T_b$ 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., 2016). 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); 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 1.4-2.1 at their HTL, which ranged from 48 to 50°C (Table 1). An even smaller Sonoran Desert passerine, the Verdin (*Auriparus flaviceps*, 7g) 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 (Figure 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°C to 54°C and scaled positively with M_b (Whitfield et al., 2015). Working on Australian desert passerines, McKechnie et al. (in press) observed similar maximum EHL/MHP values of 1.2-2.2 with HTL ranging from 46°C 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 (Figure 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 (Figure 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 EWL mechanism. Figure 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_{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*: Zenaida macroura*, 104g) and Gambel's Quail (galliform: *Callipepla gambelii*, 161g). 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 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 where 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 to 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 to larger dove and quail that 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 due to 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 study, for example, lost 5-9% M_b hr^{-1} at their thermal limits (~50°C), which is 2-4 times the 2% M_b hr^{-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 (< 100g) may be in a poor position to persist in hot deserts, relative to other taxa, due to their smaller size and reliance on respiratory EWL, potentially limiting their occupancy of hot dry desert environments during much of the year.

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COMPETING INTERESTS

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

B.O.W. and A.E.M. designed the study. B.O.W., E.K.S. and A.R.G. designed the experimental set up. E.K.S., J.J.O., A.R.G., and B.O.W. collected data. E.K.S., B.O.W. and A.E.M. analyzed the data. E.K.S., A.R.G., J.J.O., A.E.M. and B.O.W. wrote the manuscript.

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SYMBOLS AND ABBREVIATIONS

EHL	whole animal evaporative heat loss rate (Watts or W)
EHL/MHP	evaporative cooling capacity (dimensionless ratio)
EWL	whole animal evaporative water loss rate (g H_2O hr^{-1})
HTL	heat tolerance limit (°C)
M_b	initial body mass (g)
Mya	million years ago
MHP	whole animal metabolic heat production (= RMR)
ppm	parts per million
ppt	parts per thousand
RMR	whole animal resting metabolic rate (Watts or W)
T_{air}	chamber air temperature (°C)
T_b	body temperature (°C)
T_{uc}	upper critical temperature (°C)
95% CI	95% confidence intervals

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TABLES

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

`	**Lesser Goldfinch** LEGO *Spinus psaltria*	**House Finch** HOFI *Haemorhous mexicanus*	**Pyrrhuloxia** PYRR *Cardinalis sinuatus*	**Cactus Wren** CAWR *Campylorhynchus brunneicapillus*	**Northern Cardinal** NOCA *Cardinalis cardinalis*	**Abert's Towhee** ABTO *Melozone aberti*	**Curve-billed Thrasher** CBTH *Toxostoma curvirostre*
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)							
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) 52 (1)	48 (2) 50 (1)	50 (4)	50 (3)	48 (5) 50 (1)	50 (3)
Max RMR (W)	0.38 ± 0.06 (5)	0.62 ± 0.15 (7) 0.71 (1)	0.78 ± 0.14 (2) 0.65 (1)	0.67 ± 0.07 (4)	1.19 ± 0.26 (3)	0.97 ± 0.28 (5) 0.92 (1)	1.62 ± 0.31 (6)
Max RMR / Min RMR	1.43	1.63 1.86 (1)	1.32 1.10 (1)	1.26	1.76	1.37 1.29 (1)	1.86
Metabolic heat production (MHP = RMR) and evaporative water loss (EWL) and heat loss (EHL) rates							
Min EWL (g H_2O hr^{-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_2O hr^{-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_2O hr^{-1} °C^{-1})	0.052	0.098	0.132	0.137	0.180	0.151	0.270
Max EWL (g H_2O hr^{-1})	0.87 ± 0.09 (5)	1.26 ± 0.21 (7) 1.55 (1)	1.70 ± 0.03 (2) 1.90 (1)	2.06 ± 0.33 (4)	2.60 ± 0.03 (3)	2.10 ± 0.31 (5) 2.15 (1)	4.02 ± 0.74 (6)
Max EWL / Min EWL	4.73	9.35 11.52 (1)	2.95 3.29 (1)	8.53	7.86	5.10 5.21 (1)	10.26
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) 1.46 (1)	1.47 ± 0.23 (2) 1.94 (1)	2.06 ± 0.20 (4)	1.50 ± 0.31 (3)	1.48 ± 0.17 (5) 1.57 (1)	1.68 ± 0.30 (6)
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 (°C °C^{-1})	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) 45.3 (1)	43.7 ± 0.1 (2) 43.7 (1)	44.5 ± 0.3 (4)	44.6 ± 0.3 (3)	43.9 ± 0.6 (5) 43.5 (1)	44.3 ± 0.4 (6)
Max T_b - Min T_b (°C)	3.3	4.0 4.4 (1)	3.0	3.5	3.9	2.0 1.6 (1)	3.9

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)		

Notes: Values are means, with 95% confidence intervals in parentheses.
The data for the last 3 species are from Smith et al. (2015).

FIGURE CAPTIONS

Figure 1. Resting metabolic rate as a function of air temperature in Lesser Goldfinch, House Finch, Pyrrhuloxia, Cactus Wren, Northern Cardinal, Abert's Towhee, and Curve-billed Thrasher. RMR was regressed against Tair above (all $P<0.05$) and below the upper critical temperature (Tuc; 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 Tuc using RMR residuals.

Figure 2. Rate of evaporative water loss as a function of air temperature in Lesser Goldfinch, House Finch, Pyrrhuloxia, Cactus Wren, Northern Cardinal, Abert's Towhee, and Curve-billed Thrasher. EWL was regressed against Tair 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.

Figure 3. Body temperature as a function of air temperature in Lesser Goldfinch, House Finch, Pyrrhuloxia, Cactus Wren, Northern Cardinal, Abert's Towhee, and Curve-billed Thrasher. Tb was regressed against Tair 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 Tb=Tair.

Figure 4. Scaling of heat tolerance and evaporative cooling parameters in six Sonoran (AZ), five Australian (data from McKechnie et al., in press) and three southern African passerines (data from Whitfield et al., 2015). (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 (Tair) 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).

Figure 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 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]/Mb (circles, solid lines; all $P<0.001$) and the internal heat load of MHP/Mb (diamonds, dashed lines; all $P<0.05$) were regressed against Tair−Tb for Tair above 36°C. See Table S4 for parameter estimates.

FIGURES

Figure 1.

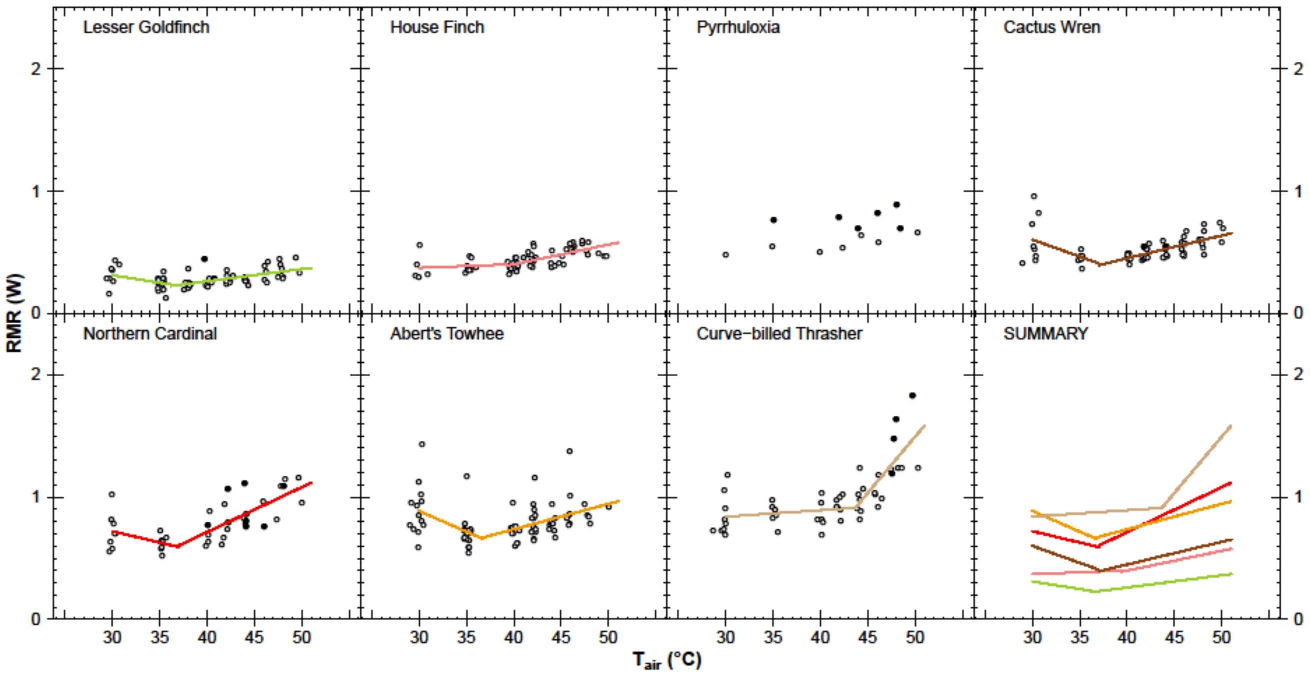


Figure 2.

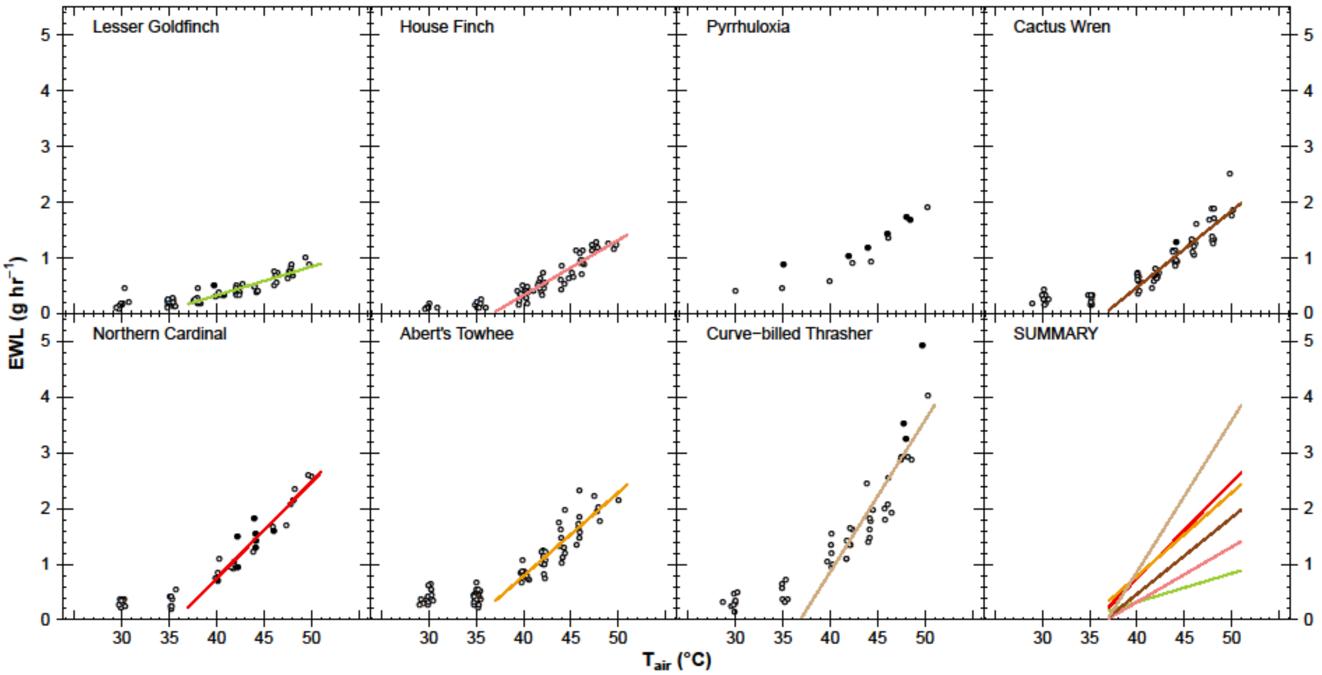
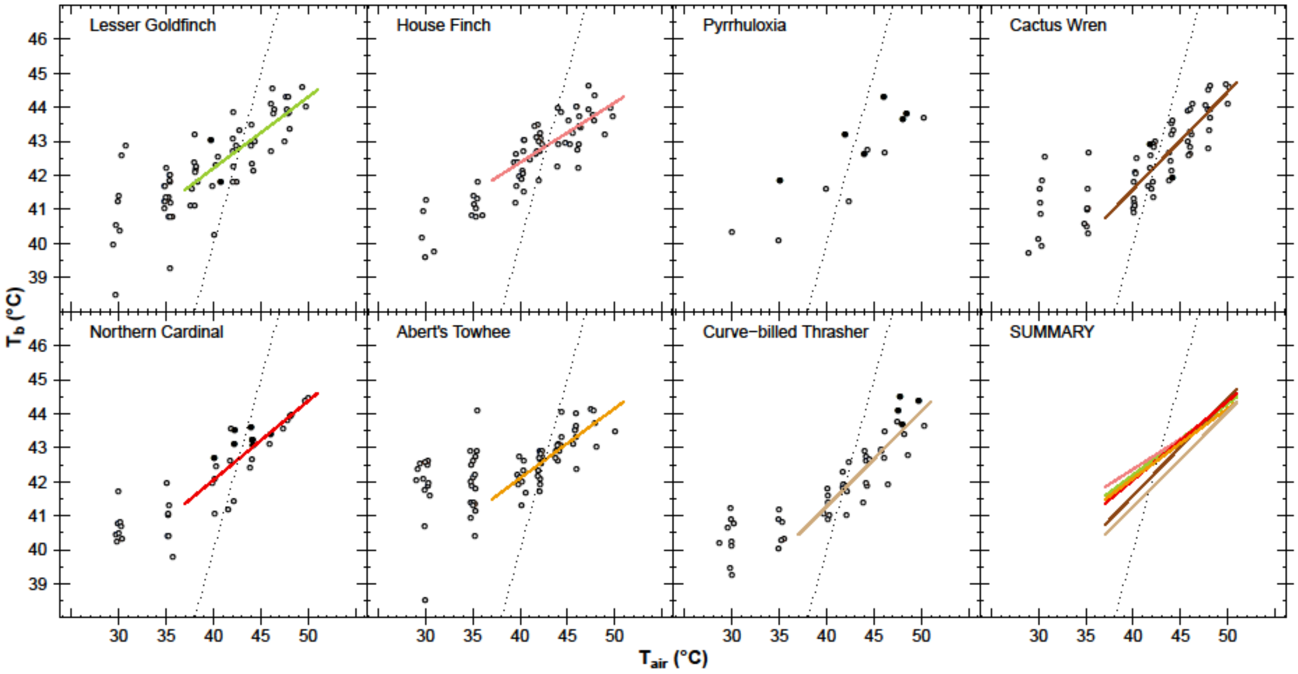
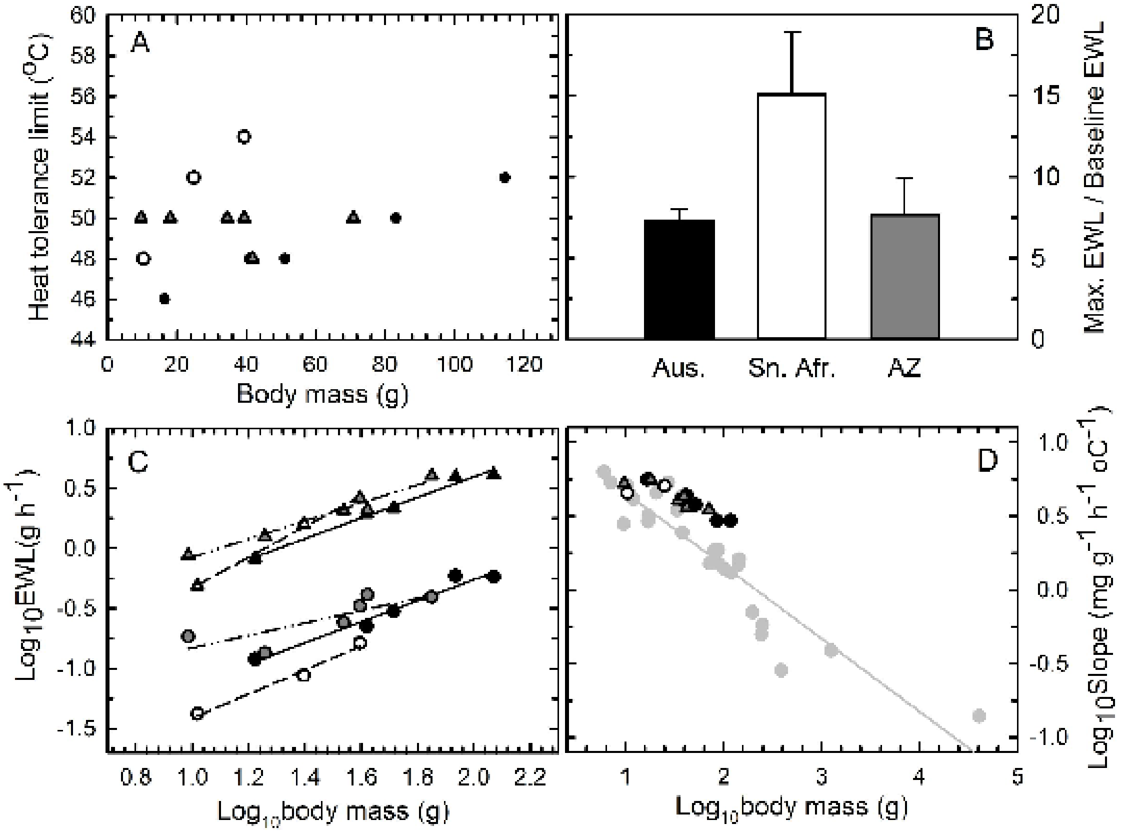

Lesser Goldfinch
House Finch
Pyrrhuloxia
Cactus Wren
Northern Cardinal
Abert's Towhee
Curve−billed Thrasher
SUMMARY
EWL (g hr^{-1})
0
1
2
3
4
5
30
35
40
45
50
T$_{air}$ (°C)

Figure 3.



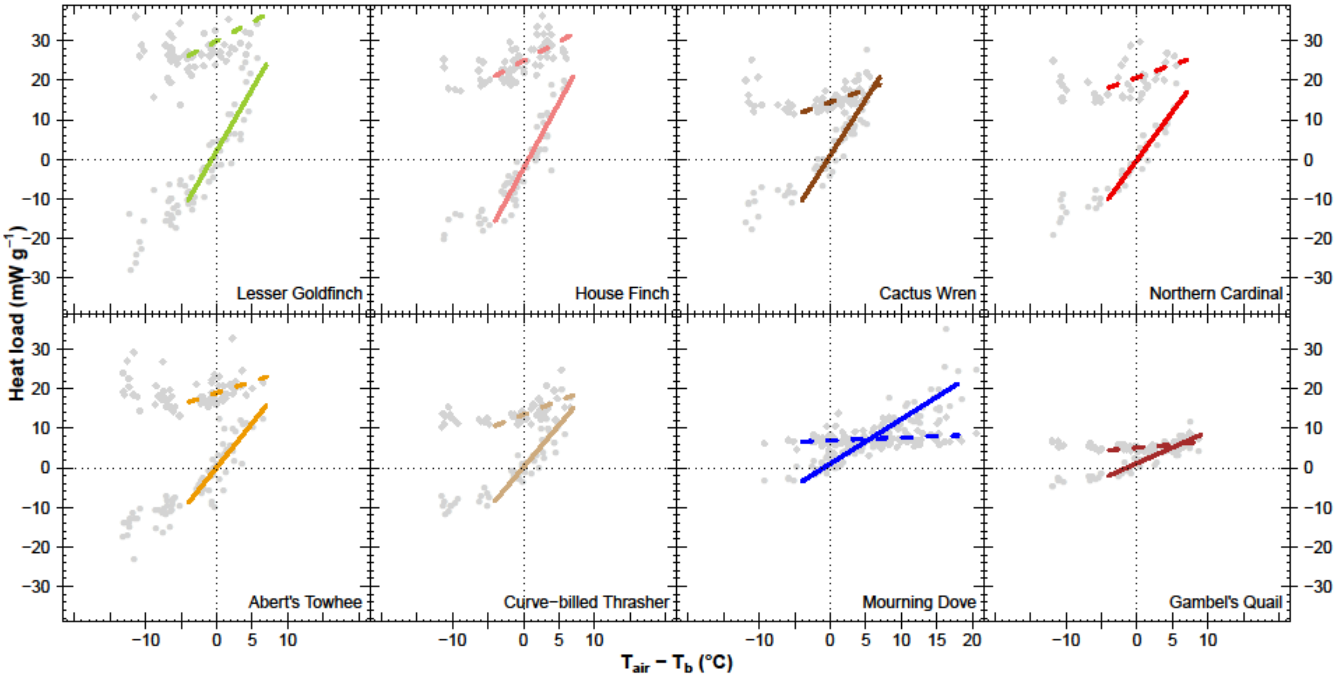
Lesser Goldfinch
House Finch
Pyrrhuloxia
Cactus Wren
Northern Cardinal
Abert's Towhee
Curve−billed Thrasher
SUMMARY
T_b (°C)
T_{air} (°C)
39
40
41
42
43
44
45
46
30
35
40
45
50

Figure 4.



A
Heat tolerance limit (°C)
Body mass (g)
B
Max. EWL / Baseline EWL
Aus.
Sn. Afr.
AZ
C
Log10EWL(g h-1)
Log10body mass (g)
D
Log10Slope (mg g-1 h-1 oC-1)
Log10body mass (g)

Figure 5.


Heat load (mW g^{-1})
Lesser Goldfinch
House Finch
Cactus Wren
Northern Cardinal
Abert's Towhee
Curve−billed Thrasher
Mourning Dove
Gambel's Quail
30
20
10
0
−10
−20
−30
−10
0
5
10
15
20
$T_{air} - T_b$ (°C)

CHAPTER 3

Metabolic efficiency of evaporative heat loss predicts limits of activity in desert birds

Eric Krabbe Smith[1*], Alexander R. Gerson[2], William A. Talbot[1], Todd J. McWhorter[3], Andrew E. McKechnie[4,5], and Blair O. Wolf[1*]

1. *Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA*
2. *Department of Biology, University of Massachusetts, Amherst, MA 01003, USA*
3. *School of Animal & Veterinary Sciences, University of Adelaide, Roseworthy Campus, SA 5371, Australia*
4. *DST-NRF Centre of Excellence at the Percy FitzPatrick Institute, Department of Zoology and Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, South Africa*
5. *South African Research Chair in Conservation Physiology, National Zoological Garden, South African National Biodiversity Institute, P.O. Box 754, Pretoria 0001, South Africa*

*Authors for correspondence: ericsm@unm.edu; wolf@unm.edu

Summary

1. Desert birds reduce their activity during the heat of the day, supporting predictions that daily activities and thus fitness and survival will be increasingly impacted by climate warming. Improving confidence in these predictions requires a detailed, mechanistic understanding of functional limits on activity and variability in these limits across taxa.
2. The Heat Dissipation Limit theory posits that levels of activity are determined by maximal rates of passive heat dissipation. Yet, during periods when environmental temperatures approach and exceed body temperature, animals must dissipate metabolic and environmental heat loads by evaporative processes.
3. We used thermoregulatory data collected during the summer from a suite of 13 species of Sonoran Desert birds, representing five avian orders, to inform a heat balance model and estimate the capacities for work at high air temperatures.
4. We found that the capacity for evaporative heat loss has the potential to strongly limit activity in desert birds at high air temperatures, and that the primary pathway of evaporative cooling and its metabolic efficiency predict variation among species in sustainable metabolic scope.
5. Climate warming will increasingly impact the activities of all desert birds, but our new model suggests that that the impacts to desert songbirds – which depend upon the metabolically costly pathway of panting for evaporative cooling – will be disproportionately high.

Keywords: birds, body temperature, doves, evaporation, heat dissipation limit theory, resting metabolism, nightjars, songbirds, Sonoran Desert, thermoregulation

Introduction

Birds inhabiting hot deserts typically reduce activity to very low levels during the hottest parts of the day, producing potential tradeoffs between reproduction and self-maintenance and between defense of body temperature and water balance (Goldstein 1984; Walsberg 1993; Wolf & Walsberg 1996b). Currently predicted increases in temperatures for deserts of the world and increases in the frequency, severity, duration and geographic extent of heat waves (IPCC 2014) are anticipated to exacerbate these tradeoffs for desert animals. The effects of more frequent severe heat waves may be direct, producing ongoing localized or regional die-offs in birds (McKechnie & Wolf 2010; Albright et al. 2017), or they may be indirect and more difficult to detect, influencing bird populations through reduced fitness and survival (du Plessis et al. 2012; Cunningham et al. 2013b). The latter two studies of songbirds indicate that even modestly warm air temperatures of 33-35°C can reduce the body condition of adult birds and/or nestling growth rates. Here, we use thermoregulatory data from birds measured in the field to: 1) model the functional limits on workloads of birds in the heat, and 2) examine how heat exposure may differentially limit the capacities for work among avian orders. We hypothesized that birds that differ in their pathways of evaporative heat loss (EHL) would show distinct differences in their capacities for exercise in the heat.

Drent and Daan (1980) examined trade-offs between workload, fitness and survival in breeding birds and estimated a “maximum sustained working level,” defined as the ratio of active to resting metabolism. These authors found that for birds tending nestlings, this ratio, also called sustained metabolic scope, was approximately ~ 4 X basal metabolic rate (BMR) – not unlike that of humans engaged in intense physical labor. Peterson, Nagy and Diamond (1990) and Hammond and Diamond (1997) found sustained metabolic scopes typically ranged from 1.5 to 5 X resting metabolic rate (RMR) among 45 species of mammals and birds, whereas Butler

(1991) observed that metabolic scopes for sustained flight in birds were 4 - 10 X RMR. Although several hypotheses have been proposed to explain ceilings on metabolic scope (Hammond & Diamond 1997; Nilsson & Nord 2018), the Heat Dissipation Limit (HDL) theory (Speakman & Król 2010) could potentially account for limits on avian performance in the heat. Building on the work of Hammond et al. (1994) who observed increased metabolic ceilings and food intake in mice kept in the cold, Johnson and Speakman (2001) and Król, Murphy and Speakman (2007) observed increases in food intake, milk production, and pup size in animals with higher heat loss rates facilitated experimentally by cold exposure or reduced insulation. In light of these results, Speakman and Król (2010) proposed that limits to energy expenditure in endotherms are set by limits on heat dissipation and developed a model predicting that the capacity for heat dissipation in endotherms decreases with increasing ambient temperature and scales with body mass to the 0.63 power.

The HDL model proposed by Speakman and Król has important limitations – especially for animals living in warm environments where air temperature (T_{air}) regularly approaches or exceeds body temperature (T_b). In the formulation of the HDL model, all heat dissipation is passive (i.e. the model does not include evaporative heat dissipation), and T_b is assumed to be constant and always above T_{air}. However, for animals living in hot environments, when $T_{air} > T_b$, the metabolic heat produced by the animal and any additional environmental heat load must be dissipated by evaporating water from the skin and/or respiratory surfaces. In addition, a common response to heat exposure in birds and mammals is facultative increases in T_b of 1 - 5°C. This reversible hyperthermic response minimizes the thermal gradient between the animal and its environment, reducing environmental heat gain and minimizing rates of evaporative water loss.

Here, we seek to extend the central idea of the HDL theory – that capacities for heat dissipation limit levels of activity in animals – to avian activity in the heat.

Materials and methods

MEASUREMENTS OF EVAPORATIVE WATER LOSS, RESTING METABOLISM, AND BODY TEMPERATURE

We continuously measured active phase whole animal rates of evaporative water loss (EWL, g H_2O hr^{-1}) and resting metabolism (RMR, W) and body temperature (T_b, °C) using open flow respirometry, in response to chamber air temperature (T_{air}, ranging from 30° to 66°C), in 13 species of Sonoran Desert birds caught from the wild near Tucson, AZ, USA, during the summers of 2012 and 2013 (Smith et al. 2015, 2017; Talbot et al. 2017, 2018). Experimental conditions mimicked the temperatures and humidities of hot, dry desert environments and provided a sufficient vapor pressure gradient for evaporation (Lasiewski, Acosta & Bernstein 1966; Gerson et al. 2014). Here we assumed respiratory exchange ratios (RER) of 0.71 in the songbirds, nightjars, and owls and 0.93 in the doves and quail. Data from active birds or birds having mean $T_b > 44.7$°C or slope of $T_b > 0.1$°C min^{-1} were excluded from analyses, eliminating any artifact of heat storage in these animals. 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 H_2O)$^{-1}$, corresponding to T_{air}=40°C (Tracy et al. 2010). We defined evaporative cooling capacity as a dimensionless ratio (EHL/RMR).

OUR MODEL OF SUSTAINABLE METABOLIC SCOPE

We use the above thermoregulatory data to inform a basic heat balance equation (Box 1). For steady state conditions with heat flux = 0, the internal heat load (RMR) and the external heat load, due to the temperature gradient between an animal and its environment ($T_{air} – T_b$), must be balanced by EHL (Equation 1). We rearrange Equation 1 to solve for a maximum RMR which balances the equation, populating the equation with sustainable maximum responses for EHL and T_b at air temperatures 2°C below the heat tolerance limit for each species (Equation 2). Heat tolerance limits (HTL) were previously determined for each species (Smith et al. 2015, 2017; Talbot et al. 2017, 2018); we assumed sustainable maximum values occurred in the 2°C air temperature bin ($T_{air\text{-}susmax}$) below the HTL. In our model, evaporative heat loss (EHL_{susmax}) at $T_{air\text{-}susmax}$ acts as a benchmark value for sustainable evaporative potential; and hyperthermic responses ($T_{b\text{-}susmax}$) at $T_{air\text{-}susmax}$ model savings in evaporative water loss due to a reduced thermal gradient ($T_{air} – T_b$) associated with elevated T_b (Table 1). We solve for the sustainable maximum multiples of RMR, using RMR at T_{air} of 35°, 42°, 48° and 54°C (Equation 3). Equation 3 represents the model of sustainable metabolic scope for birds in the heat shown in Fig. 1.

ESTIMATES OF CONDUCTANCE

In order to estimate conductances (C, W $°C^{-1}$) for each species, we rearranged Equation 1:

$$C = (EHL – RMR) / (T_{air} – T_b) \qquad \text{(Eq. 4)}$$

At $T_{air} < T_b$, passive heat loss represented a significant part of overall heat balance; we used Equation 4 to estimate dry thermal conductance (McNab 1980), which reached a minimum in these birds at T_{air} =35°C (C_{dry}; Table 1). For $T_{air} > T_b$, EHL dominated heat balance and we used

Equation 4 to estimate evaporative conductance over a range of $T_{air} > 36°C$ in each species (C_{evap}; Table 1).

LIMITATIONS OF THE MODEL

Our model relies on two important assumptions. First, although it is informed by empirical data, our use of EHL_{susmax} may overestimate total evaporative capacity at lower T_{air} (35-42°C) because the atmospheric gradient for evaporation is smaller at lower T_{air} than at $T_{air\text{-}susmax}$. This may be most important in doves, which rely directly on the vapor pressure deficit for cutaneous evaporation; for birds that use gular flutter or panting, air in the respiratory passages becomes saturated with water vapor at pressures associated with T_b and thus T_{air} is less important (Gerson et al. 2014). Our use of $T_{b\text{-}susmax}$ at lower T_{air} is supported, as flying and provisioning birds readily increase T_b to near maximum levels (Torre-Bueno 1976; Hirth, Biesel & Nachtigall 1987; Nilsson & Nord 2018), probably to also maximize passive heat loss. Second, we assume that conductance values derived from studies of animals resting in a standard metabolic chamber accurately reflect conductance values of birds in natural environments. We expect that movement associated with foraging and flight can disrupt the boundary layer around an animal and increase dry thermal conductance and heat flow, thus potentially under-estimating heat loads for foraging animals when $T_{air} > T_b$. Flying birds have high conductance values, which increase passive heat flow and potentially reduce the need for evaporative heat dissipation as T_{air} decreases with increasing altitude.

Results

Our model (Fig. 1) predicts a striking decrease in metabolic scope with increasing T_{air} among all species irrespective of body mass, indicating potential constraints on current activities in birds and confirming that global warming will increasingly constrain the activities of birds in future climates.

This model also shows that the magnitude of decreases in metabolic scope with increasing T_{air} will vary across avian orders. The differences in metabolic scope among orders are functionally related to the primary pathway of evaporation – respiratory panting, gular flutter or cutaneous evaporation – and, particularly, to the differing metabolic efficiency of these evaporative mechanisms whose occurrence varies across avian orders (Table 1). At greatest risk are taxa that rely on panting for evaporative cooling, such as songbirds, which must forcibly ventilate their respiratory surfaces to evaporate water. Songbirds have the lowest heat tolerance limits (48-50°C, maximum tolerable T_{air} during acute heat exposure) among birds investigated to date, driven by the high metabolic costs of panting (Smith et al. 2017). Here, evaporative cooling capacities (EHL/RMR ratios) incorporate the metabolic costs of evaporative cooling, and larger values predict which species will have the highest sustained metabolic scopes in the heat. Although songbirds showed the capacity to increase EHL to an average of 476% of minimal levels when exposed to high T_{air} (Table 1), much of this increase is offset by the increases in RMR associated with panting, such that their maximum evaporative cooling capacities are limited to values below two at $T_{air\text{-}susmax}$ (Figs 2a-2b).

In contrast, nightjars have the highest metabolic scope and potential for activity at high T_{air} among species measured to date (Fig. 1). They also exhibit very high heat tolerance limits, withstanding T_{air} = 60-62°C for short periods (Talbot et al. 2017). Gular flutter, used by nightjars, owls, doves, and quail (Bartholomew, Lasiewski & Crawford 1968), varies in its metabolic efficiency. In nightjars, the area of the buccal surfaces may equal 15% of the total skin surface area and thus provides a large evaporative surface for cooling (Cowles & Dawson 1951). When the lower wetted surface is oscillated at a high frequency, rates of evaporative water loss can increase by 100%, but with a concomitant increase in RMR of <10%. The greater heat tolerance of nightjars is thus facilitated by a metabolically efficient gular flutter apparatus, which produces increases in EHL at $T_{air\text{-}susmax}$ averaging 815%, compared to 476% in songbirds (Table 1), but with low RMR and evaporative cooling capacities (EHL/RMR) above three (Figs 2a-2b).

Compared to songbirds, doves also show large metabolic scopes and potential for activity in the heat (Fig. 1). Doves rely primarily on cutaneous evaporation to dissipate large heat loads with essentially no metabolic cost (McKechnie & Wolf 2004). Cutaneous evaporation is therefore not subject to the additional heat load associated with panting in songbirds; and doves' heat tolerance limits (T_{air} = 58-60°C) (Smith et al. 2015) and evaporative cooling capacities (EHL/RMR) are commensurate with those of nightjars (Fig. 2b).

Discussion

Our analysis predicts that pathways of EHL have a profound impact on the potential metabolic scope and thus the range of activities in which birds can engage in during hotter periods of the day. When T_{air} approaches and exceeds T_b activity may be strongly constrained in songbirds (Walsberg 1993; Wolf & Walsberg 1996b). The activities of nocturnal species such as owls and nightjars may be less affected, but many nightjars nest in exposed sites on the ground and thus experience very high heat loads during the day, e.g. surface temperatures of 60-70°C (Walsberg 2000). Birds and other desert animals suppress activity on hot days and our data reveal that heat constrains activity to differing extents across avian taxa. Although each species in this study shows significant hyperthermic responses with increasing heat stress, these responses vary among orders and are smallest in the doves and greatest in the nocturnal species – owls and nightjars (Fig. 2c). The passerines show intermediate increases in T_b when exposed to hot conditions, but have T_b values that most closely approach the known lethal limits for birds; doves, nightjars and owls all maintained lower T_b values at $T_{air\text{-}susmax}$, indicating that the mechanism of evaporative heat dissipation is the primary determinant of differences in potential metabolic scope.

More importantly, our model results show that increases in global temperatures have the potential to greatly reduce the periods that birds can safely pursue activities that determine survival and fitness (Fig. 1), as well as to substantially increase the metabolic and water costs of existence (Table 1 and Fig. 2), especially in the hotter, drier regions of the globe. Projected increases in the frequency, intensity, duration and geographic extent of short-term events such as heat waves (IPCC 2014) will cause direct mortality through mass die-offs, as have been observed in a number of regions globally (McKechnie & Wolf 2010; Albright et al. 2017). An emerging body of literature also suggests that temperature-driven reductions in body condition and reproductive success among arid-zone passerines are best predicted by the number of days on which maximum T_{air} exceeds some threshold value (du Plessis et al. 2012; Cunningham et al. 2013a, 2013b; Gardner et al. 2016). Although the critical T_{air} values identified in these studies (33-35°C) are likely well within the thermoneutral zones of the species concerned, water loss rates may double between 25° and 35°C, which could impose additional demands on adults reliant on vegetation or insect prey to maintain water balance. High workloads in temperate species during periods of warm weather may also produce thermal challenges and extreme hyperthermia with uncertain costs (Nilsson & Nord 2018).

Nightjars (Caprimulgiformes) and doves (Columbiformes) have heat dissipation capacities that far exceed those of songbirds (Passeriformes) (Wolf & Walsberg 1996a; McKechnie & Wolf 2004; Smith et al. 2015, 2017; Talbot et al. 2017). Yet, even highly heat tolerant species such as doves and nightjars may be negatively affected by greater limits on activity and increased water demands with higher T_{air}. During the Sonoran Desert summer, Mourning Doves often nest in sites exposed to high T_{air} and high solar heat loads, conditions under which birds must actively cool their eggs during the day to maintain egg viability, with consequent high water loss rates (Walsberg & Voss-Roberts 1983). To satisfy their evaporative cooling requirements, doves must often fly long distances to water each day, suggesting that, in addition to heat dissipation limits on activity, the costs of obtaining additional water to balance water budgets may place increasingly large demands on activity budgets. Rates of evaporation can increase 6 to 10-fold as T_{air} increases from thermoneutral values to maximum tolerable limits (~48-50°C for songbirds) and can exceed 5% of M_b per hour (Wolf & Walsberg 1996a; Smith et al. 2017). Thus, relative rates of evaporation or resting metabolism may define threshold temperatures, in turn affecting the activity levels and body condition of adult birds.

In sum, our analysis provides a mechanistic explanation for constraints on activity in warmer environments and importantly notes that these constraints are not equal across avian orders; songbirds, for example, which represent nearly 50% of avian diversity, appear to be most sensitive to increases in global temperatures. Hotter climates will be potentially catastrophic to bird communities; limits on activity during heat waves will cause direct mortality and local to regional extirpation of some species. Higher temperatures and associated drought will decrease reproductive success through diminished food availability and foraging activity – and will reduce adult survival over longer periods through chronic challenges that affect body condition.

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Author contributions

E.K.S., A.R.G. and B.O.W. designed the study. B.O.W., E.K.S. and A.R.G. designed the experimental set up. E.K.S., W.A.T., A.R.G., and B.O.W. collected data. E.K.S., A.R.G. and B.O.W. analyzed the data. E.K.S., A.R.G., W.A.T., A.E.M., T.J.M. and B.O.W. wrote the manuscript. The authors of this paper declare no conflict of interest.

Data accessibility

Data will be made available via Dryad Digital Repository upon acceptance.

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BOX AND TABLE

Box 1. Estimating metabolic scope in the heat

Equation 1: Heat flux = $0 = RMR + C * (T_{air} - T_b) - EHL$

Equation 2: $RMR_{susmax} = EHL_{susmax} - C * (T_{air} - T_{b\text{-}susmax})$

Equation 3: Multiples of RMR = $\mathbf{(EHL_{susmax} - C * (T_{air} - T_{b\text{-}susmax}))/RMR}$

In order to estimate the maximum sustained metabolic scope, we rely on a basic heat transfer equation.

Eq 1: For steady state conditions with heat flux = 0, 1) the internal heat load due to RMR; and 2) the external heat load, due to the temperature gradient between an animal and its environment -- must be balanced by EHL.

Eq 2: We rearrange this equation to solve for a maximum RMR which balances the equation, populating the equation with sustainable maximum responses for EHL and T_b at air temperatures 2°C below the heat tolerance limit (HTL) for each species. Conductances (C) were estimated for each species at T_{air} below and above T_b. See Methods and Table 1 for determinations of HTL, C and susmax values.

Eq 3: Then we solve for the maximum sustainable multiples of RMR, using RMR at differing T_{air} This is our model of sustained metabolic scope for birds in the heat. RMR and T_{air} were plotted at T_{air} of 35°, 42°, 48° and 54°C in Figure 1.

Table 1. Mean values of select variables related to the model of sustained metabolic scope in 13 Sonoran Desert bird species

common name	order	1° evap pathway at high T_{air} [1]		$T_{air\text{-}susmax}$ [2]	C_{dry} [2]	C_{evap} [2]	M_b [3]	HTL [3]		RMR (W) [3]		Δ RMR (%)	EHL (W) [3]		Δ EHL (%)	T_b (°C) [3]		Δ T_b (°C)
		pathway	mechanism	(°C)	(W / °C)	(W / °C)	(g)	(°C)	T_{air} -->	35°C	$T_{air\text{-}susmax}$		35°C	$T_{air\text{-}susmax}$		35°C	$T_{air\text{-}susmax}$	
Lesser Goldfinch	Passeriformes	respiratory	panting	48	0.02	0.03	9.7	50		0.26	0.34	33	0.13	0.49	292	41.3	43.8	2.5
House Finch	Passeriformes	respiratory	panting	48	0.05	0.06	18.1	50		0.38	0.54	40	0.10	0.80	677	41.1	43.9	2.8
Cactus Wren	Passeriformes	respiratory	panting	48	0.05	0.10	34.5	50		0.45	0.59	31	0.15	1.03	573	41.1	43.8	2.8
Northern Cardinal	Passeriformes	respiratory	panting	48	0.07	0.11	39.4	50		0.62	1.03	66	0.23	1.38	497	40.8	43.8	3.0
Elf Owl	Strigiformes	respiratory	gular flutter	46	0.04	0.08	39.7	48		0.42	0.53	26	0.25	0.80	222	39.5	42.8	3.3
Abert's Towhee	Passeriformes	respiratory	panting	46	0.06	0.10	41.8	48		0.71	0.93	30	0.28	1.14	308	42.0	43.4	1.4
Common Poorwill	Caprimulgiformes	respiratory	gular flutter	60	0.03	0.09	44.3	62		0.32	0.50	57	0.20	1.98	866	38.5	42.4	3.9
Lesser Nighthawk	Caprimulgiformes	respiratory	gular flutter	58	0.04	0.08	50.6	60		0.35	0.54	52	0.19	1.67	764	39.6	43.0	3.3
Curve-billed Thrasher	Passeriformes	respiratory	panting	48	0.10	0.17	70.9	50		0.86	1.34	54	0.33	2.04	513	40.6	43.7	3.1
Western Screech-Owl	Strigiformes	respiratory	gular flutter	50	0.11	0.14	102.5	52		0.79	1.05	33	0.38	2.16	471	39.0	43.0	4.0
Mourning Dove	Columbiformes	cutaneous	n/a	56	0.05	0.11	104.0	58		0.81	0.83	3	0.49	2.50	407	41.0	41.8	0.8
White-winged Dove	Columbiformes	cutaneous	n/a	58	0.06	0.21	147.3	60		1.06	1.30	23	0.66	4.54	584	41.3	42.7	1.4
Gambel's Quail	Galliformes	respiratory	gular flutter	50	0.06	0.13	160.7	52		0.84	1.02	22	0.45	2.14	376	41.1	43.6	2.5

NOTES:

1. At $T_{air} \geq 40$°C, the evaporative pathway is primarily respiratory in Passeriformes (≥75%, Wolf and Walsberg 1996a) and Galliformes (75%, Richards 1976), and cutaneous in Columbiformes (≥70%, McKechnie and Wolf 2004).
The respiratory evaporative mechanism is panting only in Passeriformes and panting supplemented by gular flutter in Caprimulgiformes, Strigiformes, and Galliformes (Bartholomew et al. 1968).

2. See Materials and methods for estimations of $T_{air\text{-}susmax}$, C_{dry}, and C_{evap}.

3. M_b, HTL (heat tolerance limit), RMR (resting metabolic rate), EHL (evaporative heat loss), and T_b data are from Talbot et al. (2017, 2018) and Smith et al. (2015, 2017).

FIGURES AND LEGENDS

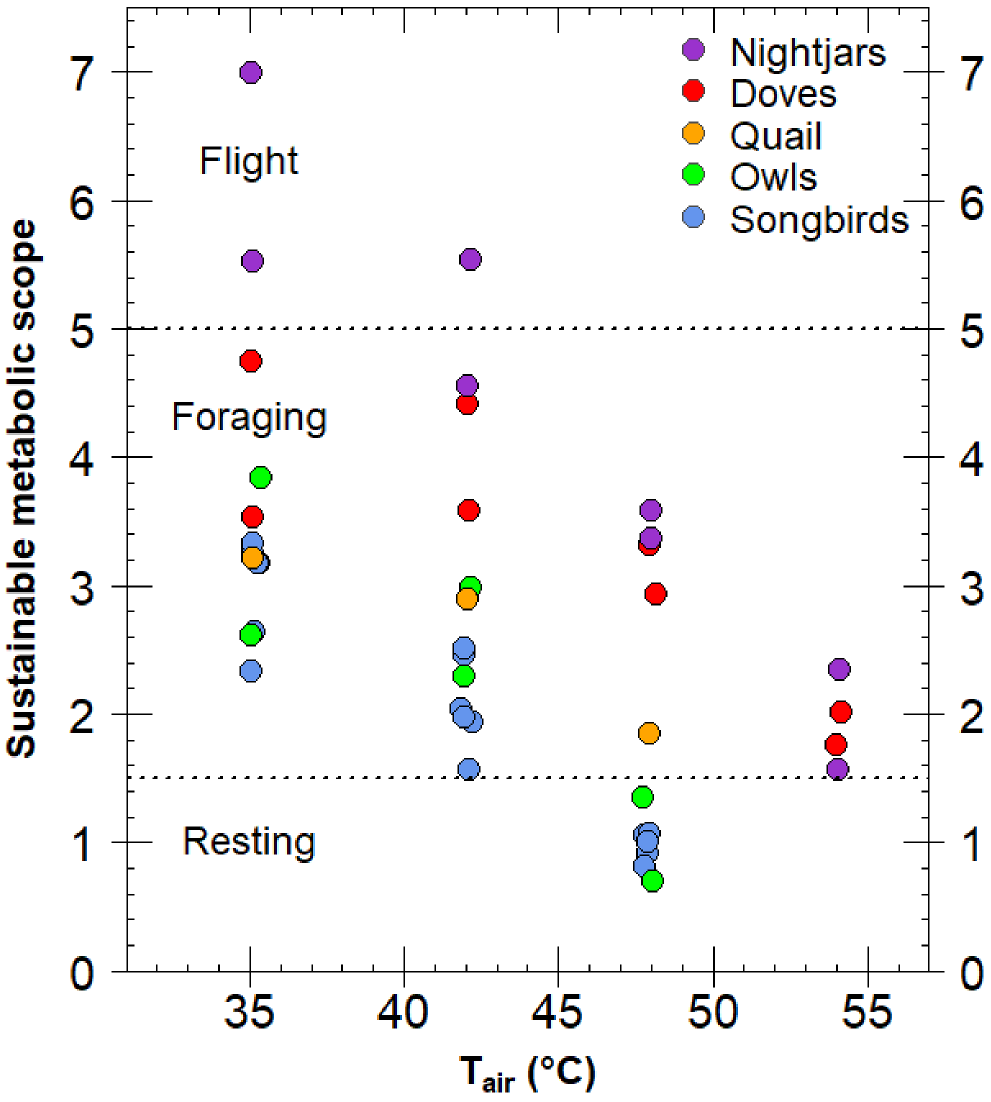

Fig. 1. Sustainable metabolic scope (available multiples of RMR) as a function of T_{air} in five orders of Sonoran Desert birds. Dotted lines represent boundaries between multiples of RMR for different activities in birds (resting, foraging, and flight). Each data point represents a species value calculated from Equation 3 (Box 1), using average whole-animal values (n = 3 to 18 samples) at T_{air} = 35°, 42°, 48° and 54°C.

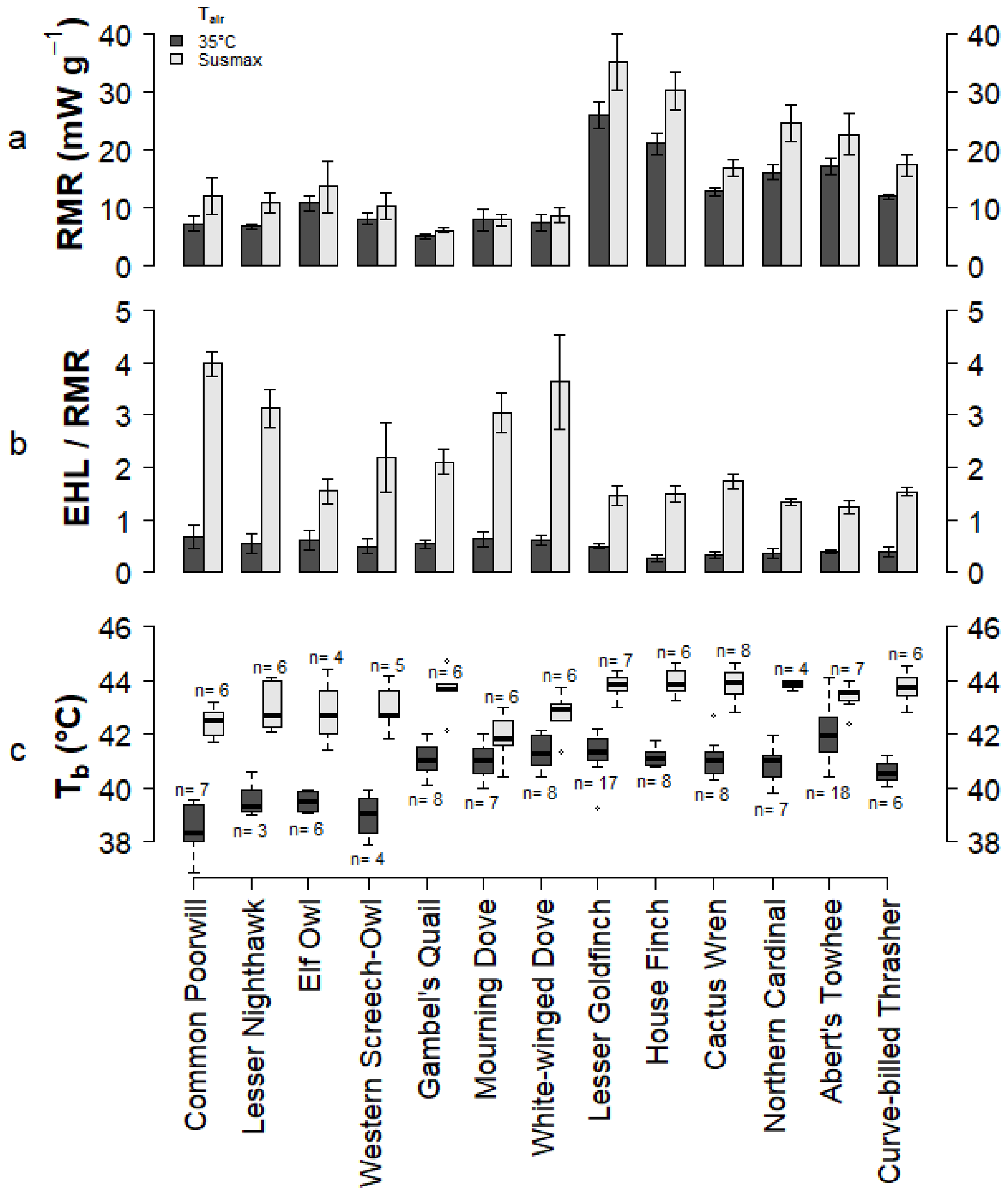

Fig. 2. Resting metabolic rate (RMR), evaporative cooling capacity (EHL/RMR) and body temperature (T_b) measured at two air temperatures (T_{air} = 35°C and $T_{air\text{-}susmax}$) in 13 Sonoran Desert bird species. RMR (a) and EHL/RMR (b) represent means of n samples per species +/- 2SE. T_b (c) shows the distribution of n samples per species. Sample sizes (n) shown in the latter panel apply to all 3 panels. See Table 1 for the $T_{air\text{-}susmax}$ values of each species.

CONCLUSIONS

In Chapters 1 and 2 of this dissertation, we found that thermoregulatory performance and water balance of Sonoran Desert songbirds, doves and quail differed greatly. The quail showed lower resting metabolic rates and lower mass-specific rates of evaporative water loss at air temperatures above body temperature, which serves to conserve water and energy, but also potentially makes them vulnerable to increasing temperatures, especially during heat waves. Desert birds require the capacity to increase evaporative water loss during periods of extreme heat in order to maintain sub-lethal body temperatures -- while minimizing dehydration over the long term (Williams et al., 2012). Doves and songbirds showed greater rates of mass-specific evaporative water, which could reduce abundances if water were unavailable, such as during longer or more intense droughts. However, the greater rates of evaporative water loss and low metabolic rates associated with cutaneous evaporation enables doves to survive at temperatures of 60°C or more, maintaining body temperatures as much as 15°C below air temperature.

What accounts for these differing responses to high air temperatures among songbirds, doves, and quail? Desert birds will reduce activity and seek shaded microsites during the heat of the day. However, once environmental temperature exceeds body temperature, their only avenue for balancing internal and external heat loads is through evaporative cooling (Calder and King, 1974). Songbirds increase evaporative water loss by panting, where high ventilation rates move air across the evaporative surfaces of the lungs. Panting increases metabolic rates is therefore costly with respect to both metabolism and water loss. Quail and nightjars elevate evaporative water loss by gular flutter, where the gular pouch on the throat is vibrated at high frequencies. Gular flutter varies in its metabolic efficiency and is extremely efficient in nightjars. At high air temperatures, doves use non-glandular, cutaneous evaporation, where blood flow to the skin is elevated under adrenergic control. Cutaneous evaporation in doves shows very low metabolic costs. Thus the metabolic efficiency of cooling mechanisms varies with phylogeny.

As air temperature exceeds body temperatures, an animal becomes highly dependent on evaporative cooling. Previous avenues for cooling -- conduction, convection, and radiation -- add to the heat load and evaporative heat loss becomes the only avenue for balancing internal and external heat loads. In Chapter 2, we showed how the internal metabolic heat loads of six songbird species increased steeply in response to air temperatures above 36°C, contributing a significant portion of the total heat load. These responses contrasted with those of the dove and quail, where the internal heat load was more similar to the external heat load and its trajectory was nearly flat, contributing a much smaller portion of the total heat load. In Chapter 3 we further examined the metabolic efficiency of evaporation as part of overall heat balance in Sonoran Desert birds. We relied on a basic heat transfer equation, where the internal metabolic heat load and the external heat load, due to the temperature gradient between an animal and its environment, were balanced by sustainable evaporative heat loss. We solved for the maximum sustainable multiples of RMR at air temperatures between 35° and 54°C, assuming sustainable maximum values of evaporative heat loss and body temperature from our data.

Applying this model to 13 species of Sonoran Desert birds from 5 orders, we found wide variation in sustainable maximum metabolic scope. In the summer in the Sonoran Desert, nightjars mostly roost and nest on bare, hot ground with little shade, relying for evaporative heat loss on metabolically and hygrically efficient gular flutter. Because they maintain low metabolic rates and are efficient evaporators they can sustain activity at a wide range of temperatures. Desert doves nest in exposed locations during the summer heat and must evaporatively cool (rather than warm) their eggs to maintain viability. This adds to the evaporative costs of defending a relatively low body temperature. Because doves use cutaneous evaporation at high air temperatures with negligible metabolic costs, they can forage in the heat of the day. Songbirds have relatively high metabolic rates and because panting is metabolically and hygrically expensive they have limited ability to remain active in the heat.

Ecological aspects of thermoregulatory performance in desert birds

How good is our model from Chapter 3? Very few ecological studies describe on-the-ground responses of birds to air temperatures above 36°C. Recent studies suggest that maximum air temperatures above moderately high threshold values (i.e. 33°-35°C) may reduce the body condition and reproductive success among desert songbirds. Cunningham et al. (2013) found that young Common Fiscals, a small predatory songbird, showed lower fledging masses when air temperatures exceeded 33°C and delayed fledging when temperatures exceeded 35°C. Duplessis et al. (2012) found that adult Southern Pied Babblers, communally nesting songbirds of the Kalahari Desert, were unable to maintain body mass when air temperatures exceeded 35.5°C. Gardner et al. (2016) found among a semiarid population of White-plumed Honeyeaters in Australia that repeated exposure over a 26-year period to conditions of low-rainfall and air temperatures exceeding 35°C reduced body condition and survival. But these are all relatively low temperature thresholds, probably well within the thermoneutral zones of these species and below temperatures for which our model applies (> 36°C). A recent paper examining nine species South African birds from three orders is suggestive with regard to the effects of higher air temperatures. Using open aviaries in the Kalahari Desert, Thompson et al. (2018) found that two species of songbird reduced activity while one dove species increased activity with increasing aviary temperatures approaching 45°C.

Our model of sustainable maximum metabolic scope essentially assumes unlimited supplies of water to provide the sustainable maximum EHL values utilized, but desert birds will become dehydrated even using these "sustainable" values after some time (hours to days). This dissertation showed that songbirds have the highest rates of evaporative water loss at high air temperatures relative to other orders of birds that live in hot deserts. This observation suggests that songbirds should be more reliant on free water resources in hot deserts then other taxa which use more efficient evaporative mechanisms, such as doves (which rely on cutaneous water loss) and nightjars and quail (which rely on gular flutter). Studies of visitation to human made desert water holes, however, provide mixed support for this hypothesis. In her isotope labeling study of avian visitors to three Sonoran Desert water holes over three springs / summers, Hyde (2011) found that doves, nightjars and quail were among the highest apparent users of these water developments (180 users / 230 total captures = 78% apparent usage). Consequently, as we noted in Chapter 3, even highly heat tolerant species such as doves and nightjars may be negatively affected by greater limits on activity and increased water demands with higher air temperatures.

Interestingly, many resident Sonoran Desert songbird species showed very low rates of free water use in Hyde's study. The Verdin, Black-tailed Gnatcatcher, Black-throated Sparrow, Ash-throated Flycatcher, Cactus Wren and Curve-Billed Thrasher are primarily insectivorous species and less than 2% (6/377) of individuals captured within 1km of the water hole showed a deuterium label in the blood indicating use of these water resources. However, the first three of these insectivorous species showed significant ($P < 0.05$) positive relationships between winter season rainfall and reproductive success in a recent study of drought-caused delays in nesting among Sonoran Desert birds (McCreedy and van Riper, 2015). Why do these insectivores, which are not dependent on water for drinking, show reduced reproductive success with delayed precipitation? As insectivores, their livelihoods are indirectly linked to precipitation because insects act as both sources of energy and water for these species. In contrast, granivorous songbirds such as the Lesser Goldfinch and House Finch showed much higher usage rates of the Sonoran Desert water holes than the insectivores, with 48% (100/207) of the individuals showing water use from these catchments. Thus the House Finch and Lesser Goldfinch appear tied to free water resources – or the human civilization that provides them. At their thermal limits, the other songbird species in Chapter 2 lost 5-6% M_b hr^{-1}, while the House Finch lost 7% M_b hr^{-1} and the Lesser Goldfinch 9% of M_b hr^{-1}. The latter smaller-bodied species lose water at a proportionally higher rate and are thus more vulnerable than the larger to dehydration resulting from evaporative cooling. With increasing warmer temperatures predicted across deserts of the southwestern United States, the Lesser Goldfinch and House Finch will endure increased risk of dehydration, reductions in daily activity, and changes in geographic distribution and possible local extirpation (Albright et al., 2017). Overall, songbirds (< 100g) may be in a poor position to persist in hot deserts, relative to other taxa, due to their smaller size and reliance on respiratory evaporative cooling, potentially limiting their occupancy of hot dry desert environments during the hottest parts of the year.

It is critical that we understand the thermoregulatory and water balance challenges that birds face in a rapidly warming world. Such understanding might allow us predict and perhaps mitigate such events; it is a prerequisite for understanding avian distributions now and in a warmer future. These studies are a first step in examining the relative responses of birds to higher temperatures, providing a baseline measure and new model of their ecological performance in the heat. Given the apparent differences among species in physiological responses to heat stress, examining tolerances of naturally occurring avian communities in similar ways will be critical for understanding their composition and persistence.

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