

## RESEARCH ARTICLE

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

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## ABSTRACT

Birds in subtropical deserts face significant thermoregulatory challenges because 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 (HTLs) 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 ( $T_{\text{air}}$ ) from 30°C to 66°C. We found marked increases in resting metabolism at the upper critical temperature ( $T_{\text{uc}}$ ), which was significantly lower in the quail ( $T_{\text{air}}=41.1^{\circ}\text{C}$ ) than in both dove species ( $T_{\text{air}}=45.9\text{--}46.5^{\circ}\text{C}$ ). Gambel's quail maintained low resting metabolic rates and low rates of evaporative water loss at their  $T_{\text{uc}}$  (0.71 W and 1.20 g H<sub>2</sub>O h<sup>-1</sup>, respectively), but were more sensitive to increasing air temperature, reaching their HTL at  $T_{\text{air}}$  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<sub>2</sub>O h<sup>-1</sup>) at their  $T_{\text{uc}}$  and reached their HTL at  $T_{\text{air}}$  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  $T_{\text{air}}$  of 48°C. Higher rates of evaporation and higher  $T_{\text{uc}}$  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).

**KEY WORDS:** Evaporative water loss, Resting metabolic rate, Upper critical temperature, Body temperature, Thermoregulation, Heat tolerance limit

## 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 et al., 2013a,b). 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* Gambel 1843) 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.W., personal observation; 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 through 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* Linnaeus 1758) and white-winged doves (*Zenaida asiatica* Linnaeus 1758) (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,

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Received 15 July 2015; Accepted 7 September 2015

**List of symbols and abbreviations**

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

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 overestimated 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 ( $T_b$ ,  $^{\circ}\text{C}$ ), whole animal rates of evaporative water loss (EWL,  $\text{g H}_2\text{O h}^{-1}$ ) and daytime resting metabolism (RMR, W) in response to chamber air temperature ( $T_{\text{air}}$ , ranging from  $30^{\circ}\text{C}$  to  $66^{\circ}\text{C}$ ) 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  $T_{\text{air}}$ . 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  $T_{\text{air}}$ . We present these species together because of their ecological similarities as large (>100 g), desert-nesting granivores with overlapping distributions, but make no inferences about adaptive differences. Thus, we examine their relative thermoregulatory performance without having 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 on the same day as capture. During June and July of 2012, temperatures at the Tucson AZMET weather station ranged from  $14$  to  $42^{\circ}\text{C}$ , daily maximum temperatures ranged from  $31$  to  $42^{\circ}\text{C}$  and the dew point ranged from  $-15$  to  $22^{\circ}\text{C}$ . During July of 2013, temperatures ranged from  $21$  to  $41^{\circ}\text{C}$ , daily maximum temperatures ranged from  $32$  to  $41^{\circ}\text{C}$ , and the dew point ranged from  $7$  to  $23^{\circ}\text{C}$ .

**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" (30.5 cm) cubed, 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  $20.9 \text{ J ml}^{-1} \text{ CO}_2$  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 (passive integrated transponder) 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 ( $\sim 40^{\circ}\text{C}$ ); Gambel's quail were also gavaged with tap water post-exposure to ensure rehydration. Birds were monitored for 1–5 h 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 litre, 22 cm  $\times$  25 cm  $\times$  12 cm, Rubbermaid, Atlanta, GA, USA) sealed with an opaque lid, modified by addition of inlet and outlet ports, and containing a plastic mesh platform above a 2 cm layer of medium weight mineral oil to trap excreta. The chamber was placed inside a modified ice chest where temperature was controlled to  $\pm 0.5^{\circ}\text{C}$ . Mass-flow controllers (Alicat, Tucson, AZ, USA) provided dry air to the chamber from a pump through columns of silica gel and drierite connected in series (2012) or from a compressor through a membrane dryer (2013: Champion<sup>®</sup> CMD3 air dryer and filter, Champion Pneumatic, Quincy, IL, USA). Excurrent air was sampled at  $250 \text{ ml min}^{-1}$  and directed to a  $\text{CO}_2/\text{H}_2\text{O}$  gas analyzer (model LI-840A, LICOR, Lincoln, NE, USA). Gas analyzer outputs were sampled once per second by Expedata (version 1.4.15, Sable Systems, Las Vegas, NV, USA).

Following PIT tag insertion, 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  $35^{\circ}\text{C}$ ) and one or more higher temperatures ( $40$ – $66^{\circ}\text{C}$  in  $2^{\circ}\text{C}$  increments) in a stepped pattern of temperature trials over the span of the 1–3 h experimental run. In order to keep  $\text{H}_2\text{O}$  content of the respirometry chamber at values that would not impede evaporation (dew point  $< 5^{\circ}\text{C}$ ), flow rates were maintained between 5 and  $40 \text{ litre min}^{-1}$  depending on  $T_{\text{air}}$  and the bird's evaporative rate. The initial thermoneutral temperature trial allowed a bird to calm from handling;  $\text{H}_2\text{O}$  and  $\text{CO}_2$  production were monitored and observed to drop to resting levels (typically within 30 min).  $T_{\text{air}}$  was then increased to higher trial temperatures and birds were allowed to adjust to each temperature for 10–20 min and stabilize before moving to the next temperature. Most birds remained calmer when flow rates were higher and chamber humidity was lower ( $< 5$  ppt water vapor).

As  $T_{\text{air}}$  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 min, (2) showed a  $T_b$  approaching or exceeding  $45^{\circ}\text{C}$ , or (3) showed a loss of balance or righting response (extremely rare). In some trials, birds were exposed to  $T_{\text{air}}$  levels 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 5 min of baseline data were collected following each temperature trial.

**Data analysis**

We selected the lowest 1 min (doves) or 5 min (quail) average of  $\text{CO}_2$  ppm readings less baseline values for each trial temperature. Birds noted as active or failing or having mean  $T_b > 44.7^{\circ}\text{C}$  or slope of  $T_b > 0.1^{\circ}\text{C min}^{-1}$  during a temperature trial were not included in the analysis. Using eqn 10.5 of

Lighton (2008), we estimated the rate of CO<sub>2</sub> production in ml CO<sub>2</sub> min<sup>-1</sup> and whole-animal RMR in watts (W), assuming an RER of 1 (see Animal capture and handling). Rates of whole-animal EWL (g H<sub>2</sub>O h<sup>-1</sup>) were calculated from the H<sub>2</sub>O ppt readings (less baseline values) for the same data points using eqn 10.9 of Lighton (2008).

### Statistical analysis

Statistical analyses and graphs were produced using R (v3.1; R Development Core Team, 2011) inside RStudio (v0.98.932). We used the linear mixed effects model from the nlme package and individual 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  $T_{\text{air}}$  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±s.d.;  $N=19$ ) 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  $T_{\text{air}}$  ( $P<0.001$ ) all significantly predicted RMR and EWL in the species tested.

### Resting metabolism among species

A significant relationship between RMR and body mass was found among species ( $F_{1,107}=52.1$ ,  $P<0.001$ ). Thus, mass-independent RMR residuals were calculated to investigate the mass-independent responses to air temperature among species (Packard and Boardman, 1999). Segmented regressions of these RMR residuals against air temperature allowed us to identify inflection points of 41.1°C in Gambel's quail, 45.9°C in mourning doves and 46.5°C in white-winged doves (Fig. S1). These inflection points represent the upper critical temperatures ( $T_{\text{uc}}$ ) above which daytime RMR increases sharply (Kendeigh, 1969; Table 1). The 95% CI of these  $T_{\text{uc}}$  values overlapped considerably between the two dove species, did not overlap between Gambel's quail and mourning doves, and slightly overlapped between Gambel's quail and white-winged doves – the upper bound of the former being 43.1°C and the lower bound of the latter being 42.8°C (Table 1). A  $z$ -score comparing the mean  $T_{\text{uc}}$  values of Gambel's quail and white-winged doves nonetheless revealed their significant difference ( $z=2.55$ ;  $P<0.01$ ). Thus, while  $T_{\text{uc}}$  values did not differ among dove species,  $T_{\text{uc}}$  values for Gambel's quail were significantly lower than those for both dove species.

### Resting metabolism

For  $T_{\text{air}}$  between 30°C and the  $T_{\text{uc}}$ , RMR decreased as  $T_{\text{air}}$  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  $T_{\text{uc}}$ , RMR increased as  $T_{\text{air}}$  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  $T_{\text{air}}$  and  $M_b$  were assessed for each species independently.

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

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

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

### Evaporative water loss

For  $T_{\text{air}}$  below the  $T_{\text{uc}}$ , there was a significant effect of  $T_{\text{air}}$  ( $F_{1,43}=197.9$ ,  $P<0.001$ ), 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  $T_{\text{air}}$  and species ( $F_{1,43}=22.2$ ,  $P<0.001$ ) – on EWL (g H<sub>2</sub>O h<sup>-1</sup>) indicating differences in the slope of this relationship among species. For  $T_{\text{air}}$  above the  $T_{\text{uc}}$ , EWL was significantly affected by  $T_{\text{air}}$  ( $F_{1,64}=475.6$ ,  $P<0.001$ ), species ( $F_{1,92}=28.8$ ,  $P<0.001$ ),  $M_b$  ( $F_{1,92}=67.9$ ,  $P<0.001$ ) and an interaction of  $T_{\text{air}}$  and species ( $F_{1,64}=30.8$ ,  $P<0.001$ ). Thus, there was a significant difference in the response of EWL to  $T_{\text{air}}$  among species both above and below the respective  $T_{\text{uc}}$ .

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

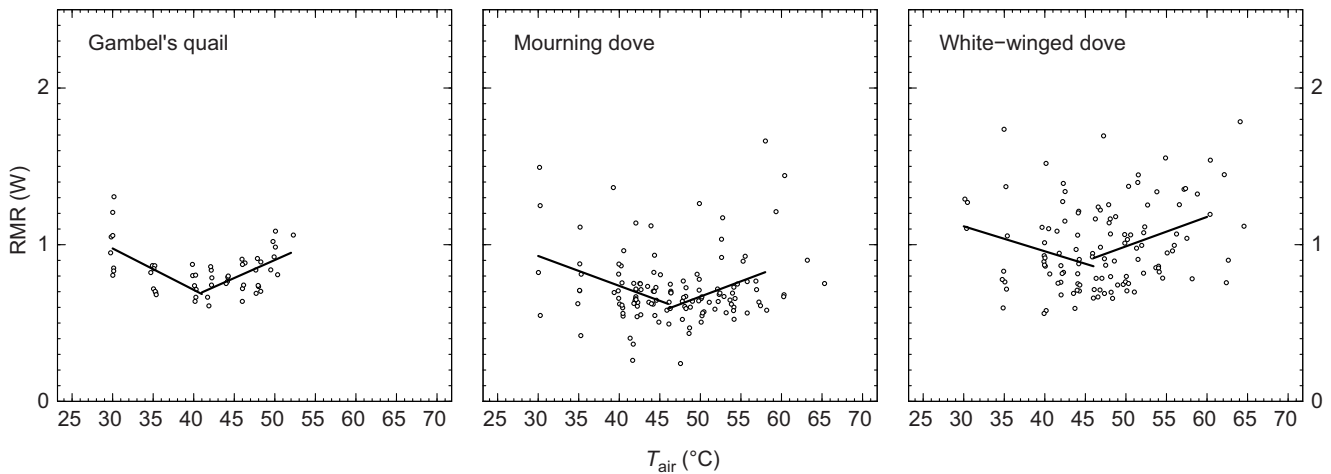
**Table 1. Mean±s.d. values for variables measured in three Sonoran Desert nesting bird species**

Species	Body mass (g)	Normothermic $T_b$ (°C) <sup>a</sup>	$T_{\text{uc}}$ (°C)	RMR (W) <sup>b</sup>	RMR (mW g <sup>-1</sup> ) <sup>b</sup>	EWL (g H <sub>2</sub> O h <sup>-1</sup> ) <sup>b</sup>	HTL (°C)	$T_b$ (°C) <sup>c</sup>	EHL/MHP <sup>c</sup>
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

<sup>a</sup> $T_{\text{air}} \leq 39^\circ\text{C}$ . Sample sizes ( $n$ ) ranged between 11 and 16.

<sup>b</sup> $T_{\text{air}} (\pm 1^\circ\text{C}) = T_{\text{uc}}$  (upper critical temperature). Sample sizes ( $n$ ) ranged between 7 and 15.

<sup>c</sup> $T_{\text{air}} (\pm 1^\circ\text{C}) = \text{HTL}$  (heat tolerance limit)  $-2^\circ\text{C}$ . Sample sizes ( $n$ ) ranged between 5 and 6.



**Fig. 1. Resting metabolic rate as a function of air temperature in Gambel's quail, mourning doves and white-winged doves.** RMR was regressed against  $T_{\text{air}}$  below (all  $P < 0.05$ ) and above the  $T_{\text{uc}}$  (all  $P < 0.01$ ).  $T_{\text{uc}}$  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 2 for parameter estimates and Fig. S1 for determination of  $T_{\text{uc}}$  using RMR residuals.

For mourning doves at  $T_{\text{air}}$  below their  $T_{\text{uc}}$  of 45.9°C, EWL increased with  $T_{\text{air}}$  ( $F_{1,16}=63.6$ ,  $P < 0.001$ ; Fig. 2) with a slope of 0.069 g H<sub>2</sub>O h<sup>-1</sup> °C<sup>-1</sup> (Table 2) and  $M_b$  was a significant covariate ( $F_{1,40}=14.2$ ,  $P < 0.001$ ). EWL increased more steeply with  $T_{\text{air}}$  above the  $T_{\text{uc}}$  ( $F_{1,27}=286.2$ ,  $P < 0.001$ ; 0.210 g H<sub>2</sub>O h<sup>-1</sup> °C<sup>-1</sup>; Fig. 2; Table 2) and  $M_b$  was a significant covariate ( $F_{1,37}=11.6$ ,  $P < 0.01$ ). EWL averaged 0.74 g H<sub>2</sub>O h<sup>-1</sup> at  $T_{\text{air}}$  of 35°C, 1.27 g H<sub>2</sub>O h<sup>-1</sup> at 42°C and 1.96 g H<sub>2</sub>O h<sup>-1</sup> at 48°C (Table 3).

For white-winged doves at  $T_{\text{air}}$  below their  $T_{\text{uc}}$  of 46.5°C, EWL increased with  $T_{\text{air}}$  ( $F_{1,21}=87.9$ ,  $P < 0.001$ ; Fig. 2) with a slope of 0.140 g H<sub>2</sub>O h<sup>-1</sup> °C<sup>-1</sup> (Table 2) and  $M_b$  was a significant covariate ( $F_{1,30}=12.9$ ,  $P < 0.01$ ). EWL increased more steeply with  $T_{\text{air}}$  above the  $T_{\text{uc}}$  ( $F_{1,25}=174.5$ ,  $P < 0.001$ ; 0.383 g H<sub>2</sub>O h<sup>-1</sup> °C<sup>-1</sup>; Fig. 2; Table 2). EWL averaged 0.99 g H<sub>2</sub>O h<sup>-1</sup> at  $T_{\text{air}}$  of 35°C, 1.95 g H<sub>2</sub>O h<sup>-1</sup> at 42°C and 3.41 g H<sub>2</sub>O h<sup>-1</sup> at 48°C (Table 3).

### 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<sub>2</sub>O)<sup>-1</sup> and define the ratio EHL/MHP – a dimensionless metric for evaporative cooling capacity – as EHL relative to metabolic heat production (MHP=RMR). For  $T_{\text{air}}$  below the  $T_{\text{uc}}$ , there was a significant effect of  $T_{\text{air}}$  ( $F_{1,43}=374.7$ ,  $P < 0.001$ ) and species ( $F_{1,89}=6.50$ ,  $P < 0.05$ ), as well as a significant interaction of  $T_{\text{air}}$  and species ( $F_{1,43}=14.9$ ,  $P < 0.001$ ) on EHL/MHP. For  $T_{\text{air}}$  above the

$T_{\text{uc}}$ , EHL/MHP showed a significant effect of  $T_{\text{air}}$  ( $F_{1,64}=282.6$ ,  $P < 0.001$ ) and species ( $F_{1,93}=6.01$ ,  $P < 0.05$ ) and a significant interaction of  $T_{\text{air}}$  and species ( $F_{1,64}=10.6$ ,  $P < 0.01$ ). Thus, there was a significant difference in the response to  $T_{\text{air}}$  among species both above and below the respective  $T_{\text{uc}}$ . There were no significant effects of  $M_b$  on EHL/MHP ( $P > 0.05$ ), either above or below the  $T_{\text{uc}}$ .

In Gambel's quail EHL/MHP increased with  $T_{\text{air}}$  both below and above the  $T_{\text{uc}}$  (below:  $F_{1,5}=57.4$ ,  $P < 0.001$ ; above:  $F_{1,11}=33.9$ ,  $P < 0.001$ ; Fig. 3). EHL/MHP averaged 0.55 at  $T_{\text{air}}$  of 35°C, 1.42 at 42°C and 1.97 at 48°C, increasing 3.6-fold between 35 and 48°C (Table 3). At  $T_{\text{air}}$  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  $T_{\text{air}}$  both below and above the  $T_{\text{uc}}$  (below:  $F_{1,16}=123.8$ ,  $P < 0.001$ ; above:  $F_{1,27}=159.1$ ,  $P < 0.001$ ; Fig. 3). EHL/MHP averaged 0.65 at  $T_{\text{air}}$  of 35°C, 1.26 at 42°C and 2.19 at 48°C, increasing 3.4-fold between 35 and 48°C (Table 3). At  $T_{\text{air}}$  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  $T_{\text{air}}$  both below and above the  $T_{\text{uc}}$  (below:  $F_{1,21}=122.9$ ,  $P < 0.001$ ; above:  $F_{1,25}=84.5$ ,  $P < 0.001$ ; Fig. 3). EHL/MHP averaged 0.62 at  $T_{\text{air}}$  of 35°C, 1.22 at 42°C and 2.27 at 48°C, increasing 3.7-fold between 35 and 48°C (Table 3). At  $T_{\text{air}}$  of 58°C, just below the HTL, white-winged doves reached a maximum EHL/MHP of 3.69 (Table 1).

**Table 2. Slope ( $m$ ) and intercept ( $b$ ) for the relationships of metabolic variables in response to air temperature ( $T_{\text{air}}$ ) below and above the upper critical temperature ( $T_{\text{uc}}$ ) in Gambel's quail, mourning doves and white-winged doves**

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

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

**Table 3.** Mean±s.d. values for metabolic variables in Gambel's quail, mourning doves and white-winged doves at three air temperatures ( $T_{\text{air}}\pm 1^\circ\text{C}$ )

$T_{\text{air}}$ ( $^\circ\text{C}$ )	Gambel's quail			Mourning dove			White-winged dove		
	35 $^\circ\text{C}$ (n=8)	42 $^\circ\text{C}$ (n=6)	48 $^\circ\text{C}$ (n=7)	35 $^\circ\text{C}$ (n=7)	42 $^\circ\text{C}$ (n=19)	48 $^\circ\text{C}$ (n=12)	35 $^\circ\text{C}$ (n=8)	42 $^\circ\text{C}$ (n=12)	48 $^\circ\text{C}$ (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 ( $\text{mW g}^{-1}$ )	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 ( $\text{g H}_2\text{O h}^{-1}$ )	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 $\text{Mb h}^{-1}$ )	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
$T_b$ ( $^\circ\text{C}$ )	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

### Body temperature

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

$T_{\text{air}}$  below 39 $^\circ\text{C}$  did not affect  $T_b$  in Gambel's quail ( $F_{1,14}=0.08$ ,  $P=0.78$ ) and normothermic  $T_b$  averaged 41.1 $^\circ\text{C}$  (Table 1).  $T_b$  increased with  $T_{\text{air}}$  above 39 $^\circ\text{C}$  ( $F_{1,17}=67.8$ ,  $P<0.001$ ; Fig. 4) with a fairly steep slope of 0.170 $^\circ\text{C }^\circ\text{C}^{-1}$  (Table 2).  $T_b$  averaged 41.8 and 42.5 $^\circ\text{C}$  at  $T_{\text{air}}$  of 42 and 48 $^\circ\text{C}$ , respectively (Table 3) and 43.6 $^\circ\text{C}$  at  $T_{\text{air}}$  of 50 $^\circ\text{C}$  (Table 1). Thus at  $T_{\text{air}}$  of 50 $^\circ\text{C}$ , just below the HTL, Gambel's quail maintained a  $T_a-T_b$  gradient of 6.4 $^\circ\text{C}$ .

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

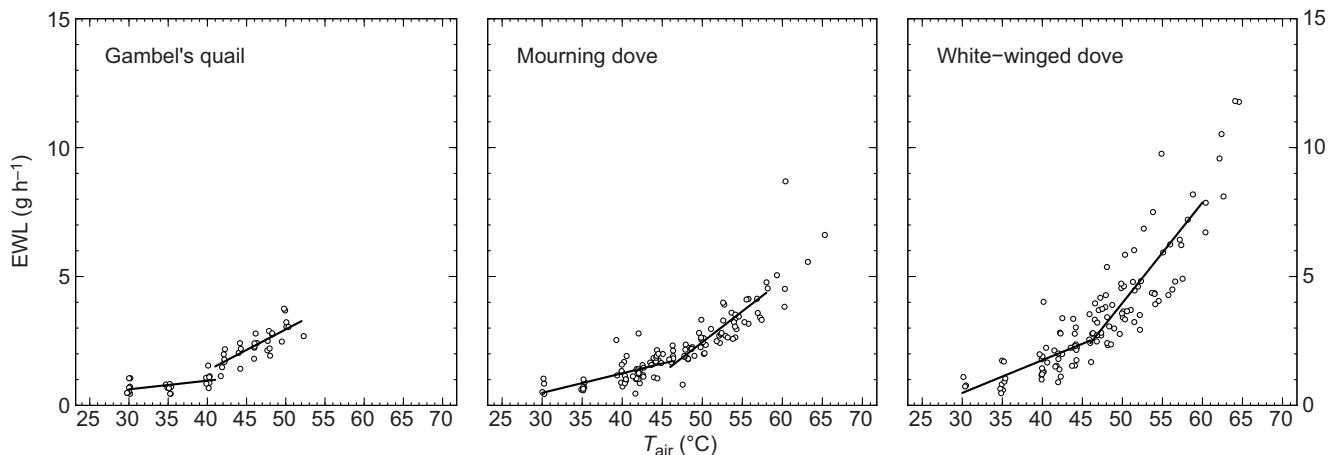
$T_{\text{air}}$  below 39 $^\circ\text{C}$  did not affect  $T_b$  in white-winged doves ( $F_{1,9}=0.40$ ,  $P=0.54$ ) and normothermic  $T_b$  averaged 41.4 $^\circ\text{C}$  (Table 1).  $T_b$  increased with  $T_{\text{air}}$  above 39 $^\circ\text{C}$  ( $F_{1,62}=25$ ,  $P<0.001$ ; Fig. 4) with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

### Heat tolerance limit

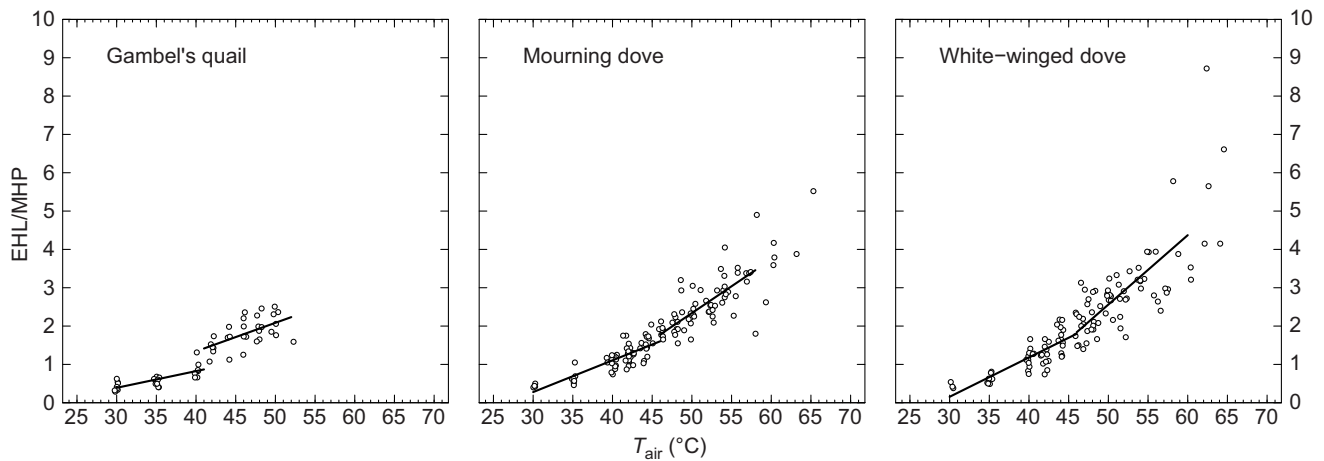
The results presented thus far pertained to data collected from birds that were inactive and maintaining stable  $T_b$  (see Materials and methods). To investigate heat tolerance, we examined the final 5 min of all temperature trials above 39 $^\circ\text{C}$  with regard to  $T_b$  maximum and  $T_b$  slope (Fig. 5). The  $T_b$  (maximum, slope) for Gambel's quail (45.1 $^\circ\text{C}$ , 0.27 $^\circ\text{C min}^{-1}$ ) and mourning doves (46.1 $^\circ\text{C}$ , 0.24 $^\circ\text{C min}^{-1}$ ) resulted from individuals in 52 and 54 $^\circ\text{C}$  temperature trials, respectively; the values for white-winged doves (46.0 $^\circ\text{C}$ , 0.39 $^\circ\text{C min}^{-1}$ ) were recorded by different individuals in trials of 54 $^\circ\text{C}$  and above. Individual birds passed a given trial if  $T_b$  and slope of  $T_b$  remained less than or equal to 44.7 $^\circ\text{C}$  and 0.1 $^\circ\text{C min}^{-1}$ , 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  $T_{\text{air}}$ , a species was considered to have reached its HTL. Thus, the HTL of Gambel's quail was 52 $^\circ\text{C}$  (1/9 pass), of mourning doves was 58 $^\circ\text{C}$  (3/8 pass) and of white-winged doves was 60 $^\circ\text{C}$  (1/4 pass; Fig. 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 $^\circ\text{C}$ ) 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  $T_{\text{air}}$  as high as 60 $^\circ\text{C}$ , while Gambel's quail did so successfully up to 50 $^\circ\text{C}$ .



**Fig. 2.** Rate of evaporative water loss as a function of air temperature in Gambel's quail, mourning doves and white-winged doves. EWL was regressed against  $T_{\text{air}}$  below (all  $P<0.01$ ) and above the  $T_{\text{uc}}$  (all  $P<0.001$ ).  $T_{\text{uc}}$  in Gambel's quail, mourning doves and white-winged doves are 41.1, 45.9 and 46.5 $^\circ\text{C}$ , respectively. See text for statistical details of linear regressions, Table 2 for parameter estimates and Fig. S1 for determination of  $T_{\text{uc}}$  using RMR residuals.



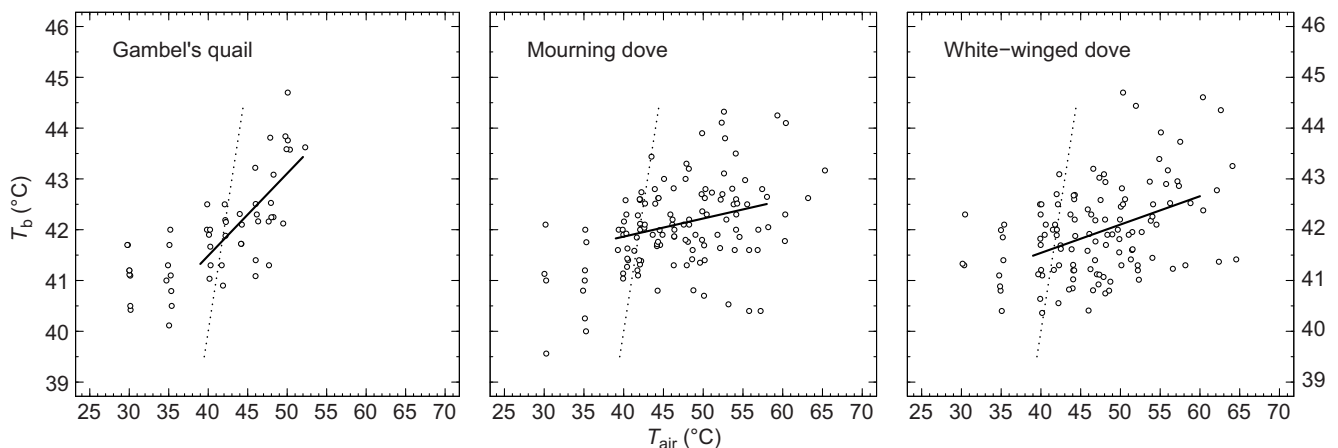
**Fig. 3. Evaporative cooling capacity (EHL/MHP) as a function of air temperature in Gambel's quail, mourning doves and white-winged doves.** EHL/MHP was regressed against  $T_{\text{air}}$  below and above the  $T_{\text{uc}}$  (all  $P < 0.001$ ).  $T_{\text{uc}}$  in Gambel's quail, mourning doves and white-winged doves are 41.1, 45.9 and 46.5°C, respectively. See text for statistical details of linear regressions, Table 2 for parameter estimates, and Fig. S1 for determination of  $T_{\text{uc}}$  using RMR residuals.

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  $T_{\text{air}}$  above 41°C and that California quail (*Callipepla californica*) could not survive  $T_{\text{air}}$  above 44°C. Birds exposed to very high environmental temperatures in nature are typically subject to very low atmospheric humidity. High chamber humidity impeded the 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).

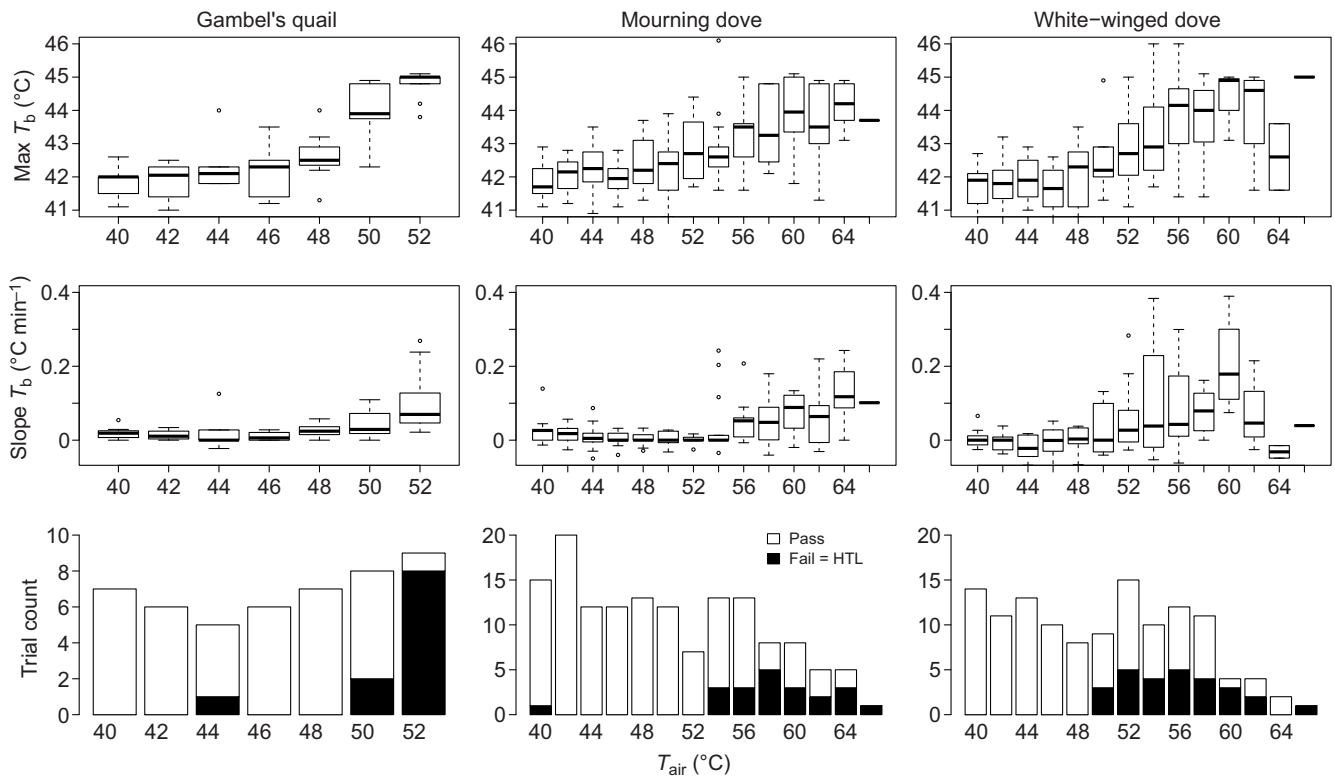
In addition, most studies of thermoregulation in these taxa have focused on responses to  $T_{\text{air}}$  below normothermic  $T_{\text{b}}$ . Prior to this study, thermoregulatory performance at  $T_{\text{air}}$  above 40°C had only been quantified in 9 of the 300+ species of columbiform birds and 7 of the 170+ species of galliform birds (see Figs 6 and 7). Of these, only 4 columbiform and 3 galliform species were exposed to  $T_{\text{air}}$  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  $T_{\text{air}}$  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  $T_{\text{air}}$  above the  $T_{\text{uc}}$  (Table 2, Table S1). However, the  $T_{\text{uc}} - T_{\text{air}}$  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) (Table 1). These differences in the  $T_{\text{uc}}$  among doves and quail are importantly related to pathways of evaporative heat dissipation. At a  $T_{\text{air}}$  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  $T_{\text{air}} \geq 40^\circ\text{C}$ , the primary evaporative pathway is respiratory in passerines ( $\geq 75\%$ , Wolf and Walsberg, 1996) and galliforms (75%, Richards, 1976) and cutaneous in doves ( $\geq 70\%$ , 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.



**Fig. 4. Body temperature as a function of air temperature 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 2 for parameter estimates. The dotted lines represent  $T_{\text{b}} = T_{\text{air}}$ .

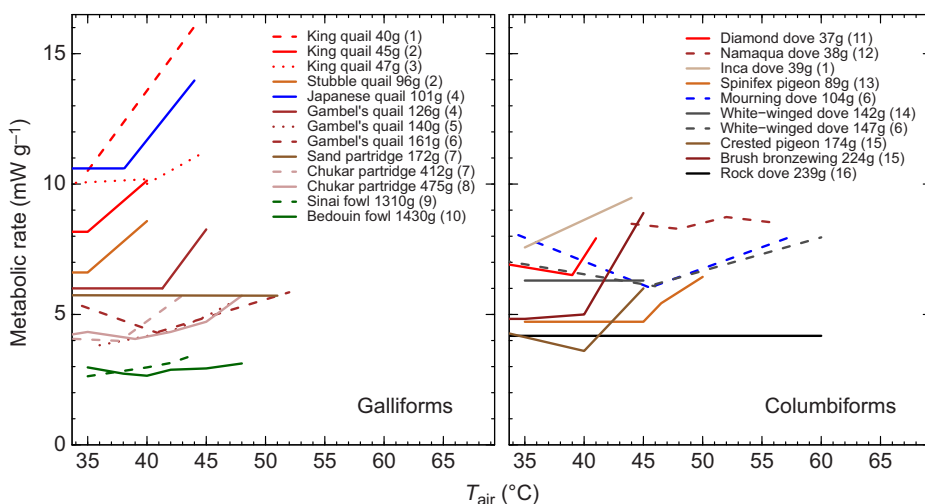


**Fig. 5. Maximum body temperature and slope of body temperature during temperature trials at air temperatures  $\geq 40^{\circ}\text{C}$  in Gambel's quail, mourning doves and white-winged doves.** In temperature trials, a bird passed until reaching its heat tolerance limit (fail=HTL, coded in black), when maximum body temperature exceeded  $44.7^{\circ}\text{C}$  or slope of body temperature exceeded  $0.1^{\circ}\text{C min}^{-1}$  during the last 5 min of a trial.

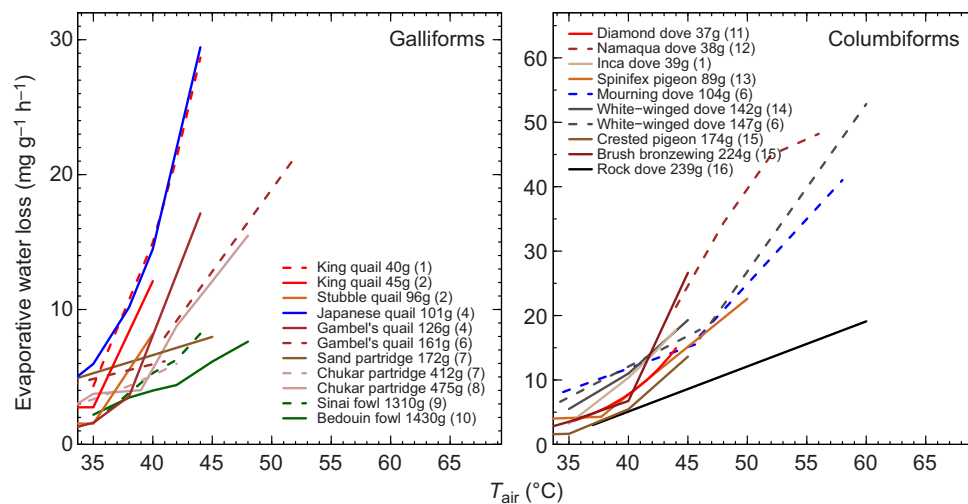
Other studies of columbiforms have reported responses of metabolic rate to temperature similar to those reported in the current study (Fig. 6). In rock doves acclimated to very high  $T_{\text{air}}$  (up to  $62^{\circ}\text{C}$ ) metabolic rate remained constant from 30 to  $60^{\circ}\text{C}$  and no  $T_{\text{uc}}$  is apparent (Marder and Arieli, 1988). White-winged doves acclimated to  $43^{\circ}\text{C}$  showed no significant difference in RMR between 35 and  $45^{\circ}\text{C}$  (McKechnie and Wolf, 2004), but these  $T_{\text{air}}$  were below the  $T_{\text{uc}}$  found in this study. Spinifex Pigeons (89 g, *Geophaps plumifera*; Withers and Williams, 1990) and Crested Pigeons (186 g, *Ocyphaps lophotes*; B.O.W., unpublished results), like the two species of dove tested here, show  $T_{\text{uc}}$  of  $46^{\circ}\text{C}$ . However, three columbiforms, including the diamond dove ( $\sim 40$  g, *Geopelia*

*cuneata*), crested pigeon (174 g) and brush bronzewing (224 g, *Phaps elegans*), show  $T_{\text{uc}}$  close to normothermic  $T_{\text{b}}$ , 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  $T_{\text{air}}$  below  $25^{\circ}\text{C}$ , suggesting a seasonal adjustment of  $T_{\text{uc}}$  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  $T_{\text{uc}}$  where metabolic rate increases



**Fig. 6. Metabolic rate as a function of air temperature in galliform and columbiform birds.** Data obtained from a range of authors: <sup>1</sup>Lasiewski and Seymour, 1972; <sup>2</sup>Roberts and Baudinette, 1986; <sup>3</sup>Pis, 2010; <sup>4</sup>Weathers, 1981; <sup>5</sup>Goldstein and Nagy, 1985 (data from summer of 1981); <sup>6</sup>This study; <sup>7</sup>Frumkin et al., 1986; <sup>8</sup>Marder and Bernstein, 1983; <sup>9</sup>Arad and Marder, 1982; <sup>10</sup>Marder, 1973; <sup>11</sup>Schleucher, 1999; <sup>12</sup>Gerson et al., 2014; <sup>13</sup>Withers and Williams, 1990; <sup>14</sup>McKechnie and Wolf, 2004; <sup>15</sup>Larcombe et al., 2003; <sup>16</sup>Marder and Arieli, 1988.



**Fig. 7. Rate of evaporative water loss as a function of air temperature in galliform and columbiform birds.** Note difference in scale of ordinate between the two graphs. Numbers refer to references as listed in Fig. 6.

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 (Fig. 6). Data from eight studies encompassing six species show that  $T_{uc}$  range from 35 to 42°C with only the sand partridge (*Ammoperdix heyi*) showing no increase in metabolic rate with  $T_{air}$  ranging from 35 to 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<sup>-1</sup> at the  $T_{uc}$  (Table 1), which is less than the BMR of 6.0 mW g<sup>-1</sup> found for birds acclimated to 25°C (Weathers, 1981) and comparable with an RMR of 5.0±1.7 mW g<sup>-1</sup> ( $n=24$ ; 33°C≤ $T_{air}$ ≤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<sup>-1</sup> at the  $T_{uc}$ , which is less than the BMR of 7.1 mW g<sup>-1</sup> 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<sup>-1</sup> at the  $T_{uc}$ , which compares favorably with the metabolic rate (6.3±0.8 mW g<sup>-1</sup>;  $n=15$ ; 35°C≤ $T_{air}$ ≤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 2, Fig. 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 2, Table S1). However, as a percentage of  $M_b$ , EWL was 30%

greater in mourning doves (2.1%  $M_b$  h<sup>-1</sup>) and 45% greater in white-winged doves (2.3%  $M_b$  h<sup>-1</sup>) than that observed in Gambel's quail (1.6%  $M_b$  h<sup>-1</sup>) at a  $T_{air}$  of 48°C (Table 3). White-winged doves increased their EWL with  $T_{air}$  more steeply than the other two species, both above and below  $T_{uc}$  (Table 2, Table S1). Compared with similarly sized Gambel's quail, white-winged doves evaporated water at higher rates 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 (Fig. 7). At the highest  $T_{air}$  measured among columbiforms, ~55–60°C, EWL ranges from 2–3%  $M_b$  h<sup>-1</sup> in rock doves to 4–5%  $M_b$  h<sup>-1</sup> in the smaller dove species (39–147 g). At the highest  $T_{air}$  frequently measured among galliforms, ~44–45°C, EWL ranges from 0.7%  $M_b$  h<sup>-1</sup> in the large bedouin fowl (~1400 g, *Gallus domesticus*) to 3%  $M_b$  h<sup>-1</sup> in the small king quail (40 g, *Coturnix chinensis*). In this study EWL in Gambel's quail at  $T_{air}$  of 50°C measured about 2%  $M_b$  h<sup>-1</sup>.

### 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 (~40 g) 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- to 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 to 1400 g have not been shown to produce EHL/MHP ratios >2.0 or tolerate  $T_{\text{air}}$  above 48°C. Large Sinai and bedouin fowls (~1300–1400 g) produce a maximum EHL/MHP of 1.65 at 44°C and apparently tolerate maximum  $T_{\text{air}}$  of 48°C (Marder, 1973; Arad and Marder, 1982). Chukar partridge (475 g, *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 (~100 g, *Coturnix japonica*) produce a maximum EHL/MHP of 1.12 at a  $T_{\text{air}}$  of 43°C. The smallest galliform that has been studied, king quail (~40 g), 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  $T_{\text{air}}$  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  $T_{\text{air}}$ .

### 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  $T_{\text{air}}$  above this range, staying well below lethal temperatures and reaching a value of 41.9°C for  $T_{\text{air}}$  of 56°C in mourning doves and 42.7°C for  $T_{\text{air}}$  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  $T_{\text{air}}$  of 44–45°C (Lasiewski and Seymour, 1972; MacMillen and Trost, 1967; Schleucher, 1999; Withers and Williams, 1990; Larcombe et al., 2003), although it exceeds the 0.8°C variation in  $T_b$  found for heat-acclimated rock doves exposed to  $T_{\text{air}}$  of 30–60°C (Marder and Arieli, 1988). At ~41°C, the normothermic  $T_b$  of Gambel's quail and the dove species were very similar. As  $T_{\text{air}}$  increased, however,  $T_b$  of Gambel's quail had a significantly steeper slope and lower intercept than that of both dove species (Fig. 4, Table 2), reaching 43.6°C at  $T_{\text{air}}$  of 50°C (Table 1). Thus, just below the HTL, Gambel's quail maintained a  $T_{\text{air}}-T_b$  gradient of just 6.4°C, compared with 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  $T_{\text{air}}$ . 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  $T_{\text{air}}$  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  $T_{\text{air}}$  of 48°C maintained a stable  $T_b$  for 2–4.5 h, but could not maintain  $T_b$  below lethal levels at  $T_{\text{air}}$  of 52°C. Thus, like the quail observed in our study, this large galliform (475 g) reached its limit of heat tolerance at a  $T_{\text{air}}$  of 52°C. Our findings and those of others provide strong evidence that desert-dwelling columbiform birds, primarily

because of 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  $T_{\text{air}}$  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  $T_{\text{air}}$  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 doves could reduce their abundance if water were unavailable, for example, because of 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  $T_{\text{air}}$ , 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.W., personal observation; 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 h can drink 17% of their  $M_b$  in water in 10 min (Bartholomew and Dawson, 1954). Gambel's quail are much less mobile and typically range about 0.5 km 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 the tolerances of naturally occurring avian communities in similar ways will be critical for understanding their composition and persistence.

#### Acknowledgements

We thank the Cadden and Wolf families for allowing us to conduct this research on their properties. Matt Baumann, Corrie Borgman, Jennifer Clark, Mateo Garcia, Michael Griego, Chuck Hayes, Alex Kusarov, Ben Smit and Bill Talbot provided invaluable assistance in the field and laboratory. We thank Christian Giardina and Andrew McKechnie for helpful comments on the manuscript.

#### Competing interests

The authors declare no competing or 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.

#### Funding

This research was supported by the National Science Foundation [grant number IOS-1122228 to B.O.W.]. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

#### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.128645/-DC1>

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