

RESEARCH ARTICLE

Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids

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ABSTRACT

Birds show phylogenetic variation in the relative importance of respiratory versus cutaneous evaporation, but the consequences for heat tolerance and evaporative cooling capacity remain unclear. We measured evaporative water loss (EWL), resting metabolic rate (RMR) and body temperature (T_b) in four arid-zone columbids from southern Africa [Namaqua dove (*Oena capensis*, ~37 g), laughing dove (*Spilopelia senegalensis*, ~89 g) and Cape turtle dove (*Streptopelia capicola*, ~148 g)] and Australia [crested pigeon (*Ocyphaps lophotes*, ~186 g)] at air temperatures (T_a) of up to 62°C. There was no clear relationship between body mass and maximum T_a tolerated during acute heat exposure. Maximum T_b at very high T_a was 43.1±1.0, 43.7±0.8, 44.7±0.3 and 44.3±0.8°C in Namaqua doves, laughing doves, Cape turtle doves and crested pigeons, respectively. In all four species, RMR increased significantly at T_a above thermoneutrality, but the increases were relatively modest with RMR at T_a =56°C being 32, 60, 99 and 11% higher, respectively, than at T_a =35°C. At the highest T_a values reached, evaporative heat loss was equivalent to 466, 227, 230 and 275% of metabolic heat production. The maximum ratio of evaporative heat loss to metabolic production observed in Namaqua doves, 4.66, exceeds by a substantial margin previous values reported for birds. Our results support the notion that cutaneous evaporation provides a highly efficient mechanism of heat dissipation and an enhanced ability to tolerate extremely high T_a .

KEY WORDS: Body temperature, Columbiformes, Cutaneous evaporative water loss, Hyperthermia, Passeriformes, Respiratory evaporative water loss

INTRODUCTION

The defense of a body temperature (T_b) set point below environmental temperature is possible only via evaporative heat dissipation, and animals that regularly experience extremely hot conditions rely heavily on this avenue of heat exchange to avoid lethal hyperthermia. The capacity for evaporative cooling is particularly

pronounced in birds, reflecting their predominantly diurnal activity and limited use of thermally buffered underground microsites, even among species occupying the hottest regions on the planet (Dawson and Bartholomew, 1968; Dawson and Fisher, 1969; Dawson and Schmidt-Nielsen, 1964; Grant, 1982; Williams and Tieleman, 2005, but see also Williams and Tieleman, 2005). A number of studies have shown that birds can maintain T_b 10–20°C below air temperature (T_a) during acute (Dawson and Fisher, 1969; Tieleman et al., 2002b; Whitfield et al., 2015; Wolf and Walsberg, 1996) and chronic (Marder and Arieli, 1988) heat exposure, via rapid increases in the rate of evaporative water loss (EWL) when T_a exceeds normothermic T_b . Under such conditions, a trade-off arises between the avoidance of hyperthermic T_b and the avoidance of dehydration resulting from rapid depletion of body water; at T_a values approaching 50°C, rates of EWL in very small birds may be equivalent to ~7% of body mass per hour (Wolf and Walsberg, 1996).

There are two major physiological mechanisms whereby birds increase rates of evaporative heat loss during acute heat exposure. The first involves accelerating heat dissipation across the surfaces of the respiratory tract via increases in respiration frequency and decreases in tidal volume (panting) and/or rapid vibration of gular membranes (gular flutter; Dawson, 1982). The second involves increases in the rate of trans-cutaneous evaporation (Marder and Arieli, 1988; Webster and Bernstein, 1987), a process regulated over short time scales by adjustments to peripheral microcirculation (Ophir et al., 2002), and over longer time scales by changes in epidermal lipid composition (Haugen et al., 2003; Menon et al., 1989, 1988; Muñoz-García et al., 2008). The relative contributions of respiratory and cutaneous evaporative water loss (REWL and CEWL, respectively) to evaporative heat dissipation at high T_a vary phylogenetically, with the data currently available indicating that REWL predominates in the Passeriformes (Tieleman and Williams, 2002; Wolf and Walsberg, 1996) and Galliformes (Bouverot et al., 1974; Richards, 1976). In contrast, CEWL represents the major avenue of heat dissipation at high T_a in Columbiformes (Hoffman and Walsberg, 1999; Marder and Arieli, 1988; McKechnie and Wolf, 2004; Smith and Suthers, 1969; Webster and Bernstein, 1987; Withers and Williams, 1990). The partitioning of total evaporative water loss into CEWL and REWL in columbids shows some phenotypic flexibility, with CEWL/REWL ratios typically higher in individuals acclimated to hot conditions (Marder and Arieli, 1988; McKechnie and Wolf, 2004; Ophir et al., 2003).

The available data also suggest that birds rely on increases in either REWL or CEWL, but generally not both, as the primary avenue of evaporative heat loss at T_a above normothermic T_b (Wolf and Walsberg, 1996). However, the ecological and evolutionary significance of these different modes of heat dissipation remains unclear. Respiratory evaporation appears to be a less energetically

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List of symbols and abbreviations

CEWL	cutaneous evaporative water loss
EHL	evaporative heat loss
EWL	evaporative water loss
M_b	body mass
MHP	metabolic heat production
RER	respiratory exchange ratio
REWL	respiratory evaporative water loss
RMR	resting metabolic rate
T_a	air temperature
T_b	body temperature
\dot{V}_{CO_2}	carbon dioxide production
\dot{V}_{O_2}	oxygen consumption

efficient mode of heat dissipation compared with cutaneous evaporation, on account of the muscle activity required for panting and consequent metabolic heat production. In dune larks (*Mirafra erythrocephalus*), for example, resting metabolic rate (RMR) increases by 100% between $T_a=35$ and 48°C (Williams, 1999). Experimental evidence for the notion that CEWL is more energetically efficient is provided by heat-acclimated western white-winged doves (*Zenaida asiatica mearnsii*), which increased CEWL compared with conspecifics acclimated to cooler conditions; both T_b and RMR at $T_a=45^\circ\text{C}$ were significantly lower than in cool-acclimated individuals (McKechnie and Wolf, 2004). Similarly, RMR at $T_a>T_b$ was lower in heat-acclimated rock doves (*Columba livia*), with a greater fraction of evaporation occurring cutaneously (Marder and Arieli, 1988). We also note that increased ventilatory rates increase heat gain from the environment when $T_a>T_b$. However, a possible disadvantage of reliance on CEWL was highlighted by a recent study evaluating the effect of humidity on evaporative heat loss in hot conditions. Evaporative cooling at $T_a>T_b$ in the sociable weaver (*Philetairus socius*), a passerine that relies heavily on panting, was less sensitive to elevated humidity compared with the Namaqua dove (*Oena capensis*), a columbid that relies primarily on cutaneous evaporation (Gerson et al., 2014).

To explore further the implications of reliance on either REWL or CEWL as the primary mode of heat dissipation for evaporative cooling and heat tolerance, we determined the upper thermoregulatory limits and maximum evaporative cooling capacities of four species of columbids varying approximately fivefold in body mass (M_b). We predicted that, during acute exposure to $T_a>T_b$, columbids: (1) would exhibit relatively gradual increases in EWL, RMR and T_b with increasing T_a , and (2) are able to tolerate higher maximum T_a before becoming hyperthermic compared with passerines and other taxa that rely primarily on respiratory pathways for evaporative cooling. We did not directly compare thermoregulatory variables between columbids and passerines, because the lack of overlap in the M_b ranges of the members of these two taxa for which data are currently available potentially confounds such comparisons.

MATERIALS AND METHODS**Study sites and species**

The southern African component of the study took place at the same study sites and during the same periods as described by Whitfield et al. (2015). We measured EWL, RMR and T_b over a range of T_a in three species from the family Columbidae, namely, Namaqua dove [*Oena capensis* (Linnaeus 1766), ~ 40 g], laughing dove [*Spilopelia senegalensis* (Linnaeus 1766), ~ 100 g; formerly *Streptopelia senegalensis*] and Cape turtle dove [*Streptopelia capicola*

(Sundevall 1857), ~ 153 g] (Hockey et al., 2005). All three species are granivorous, occur widely throughout sub-Saharan Africa in almost all habitats except forests, and are common year-round in the Kalahari Desert, although their numbers decrease during dry periods (Hockey et al., 2005). The Australian component of the study involved data collection for crested pigeons [*Ocyphaps lophotes* (Temminck 1822)] in Gluepot Reserve, South Australia ($33^\circ 46'S$, $140^\circ 07'E$).

Birds were captured using Japanese mist nets at various times of the day, and initially held in cloth bags. All birds used in the study were adults and appeared to be in good condition. The mean body masses of *O. capensis*, *S. senegalensis* and *S. capicola* were 37.1 ± 3.2 g (mean \pm s.d.; $n=29$), 89.4 ± 13.0 g ($n=33$) and 147.5 ± 17.6 g ($n=26$), respectively. The mean body mass of *Ocyphaps lophotes* was 186.5 ± 16.5 g ($n=39$).

All experimental procedures were approved by the Animal Ethics Committees of the University of Pretoria (protocol EC071-11) and the University of Adelaide (S-2013-151A), and the Institutional Animal Care and Use Committee of the University of New Mexico (12-1005370-MCC). Birds were captured under permits issued by the Northern Cape Department of Environmental Affairs (ODB 008/2013) and the Department of Environment, Water and Natural Resources South Australia (E26141-2).

Gas exchange and temperature measurements

Measurements of EWL, carbon dioxide production (\dot{V}_{CO_2}), T_a and T_b were conducted using the same general methods and experimental setup as described by Whitfield et al. (2015). Birds were placed individually in sealable plastic chambers with volumes of 4 litres (*O. capensis*) or 9 litres (*S. senegalensis*, *S. capicola* and *Ocyphaps lophotes*). Depending on T_a and the M_b of the bird, flow rates ranging from 6 to 85 l min^{-1} were used. Birds tended to remain calmer when flow rates were higher and chamber humidities were lower. As was the case in the study by Whitfield et al. (2015), the high flow rates we used meant that fractional depletion of oxygen within the chamber was below the resolution of the oxygen analyzer we used (FC-10A, Sable Systems, Las Vegas, NV, USA), and oxygen consumption (\dot{V}_{O_2}) could therefore not be measured accurately. Core T_b was measured during experiments using a temperature-sensitive passive integrated transponder (PIT) tag injected into the abdominal cavity of each bird, and a PIT tag reader and portable transceiver system, following Whitfield et al. (2015).

Before each dove was placed in a respirometry chamber, we palpated its crop to determine the presence or absence of recently ingested food. We could not be certain whether birds were post-absorptive, and the lack of \dot{V}_{O_2} measurements precluded the calculation of respiratory exchange ratio (i.e. $\dot{V}_{CO_2}/\dot{V}_{O_2}$) and hence inference of the metabolic substrate (Walsberg and Wolf, 1995). For this reason, we converted all measurements of \dot{V}_{CO_2} to metabolic rate (W) assuming RER=0.85 (i.e. a mix of carbohydrate and lipid metabolism; Walsberg and Wolf, 1995), using a thermal equivalence value of $24.4\text{ J ml}^{-1}\text{ CO}_2$ (Withers, 1992).

Experimental protocol and data analyses

We used the same experimental protocol during which birds were exposed to progressively higher T_a in a stepped profile as described by Whitfield et al. (2015) and Smith et al. (2015), and analyzed our data in the same way as in these studies. Birds were exposed to T_a values of $25\text{--}40^\circ\text{C}$ in 5°C increments, and T_a values of $40\text{--}62^\circ\text{C}$ in 2°C increments. Birds were continuously monitored while in the chamber using a video camera and infrared light source. Birds were

removed from chambers when they reached their heat tolerance limit, defined by one of two events: (1) escape behaviour sustained for more than 5–10 s, or (2) thermal endpoint (i.e. extreme heat stress manifested as a loss of coordination or balance, and/or a rapid increase in T_b to $>45^\circ\text{C}$; Whitfield et al., 2015). Data for active birds hence correspond with event 1 and data for calm birds with event 2. Thermal endpoints were taken as T_a values associated with a loss of coordination or balance, sudden decreases in EWL and RMR, and/or uncontrolled increases in T_b to values exceeding 45°C (Whitfield et al., 2015). In the present study, T_b in birds at their heat tolerance limits (i.e. either escape behaviour or thermal endpoint) was generally consistent with values observed in two columbids and a quail by Smith et al. (2015); in all cases, T_b exceeded 45°C and/or increased at a rate of $>0.1^\circ\text{C min}^{-1}$ during the last 5 min of measurements. The T_a associated with the onset of gular flutter for each bird in the chamber was also recorded.

All results are reported as whole-animal values and expressed as means \pm s.d. for calm birds only (i.e. event 2 above), unless otherwise stated. Mean T_b is the average across the last ~ 10 min at a given T_a , whereas $T_{b,\text{max}}$ is the single highest recorded T_b within the same 10 min period. Rates of evaporative water loss were converted to rates of heat loss using a latent heat of vaporisation of $2.41 \text{ J mg}^{-1} \text{ H}_2\text{O}$, corresponding to $T_a=40^\circ\text{C}$ (Tracy et al., 2010). To model relationships between EWL and high T_a , we followed the approach of Whitfield et al. (2015) and fitted both segmented linear and second-order polynomial regression models to EWL versus T_a data, and compared Akaike's information criterion (AIC) values in order to verify the validity of using segmented linear models for

interspecific comparisons (McKechnie and Wolf, 2010). Segmented linear models provided a better fit for *S. senegalensis* (polynomial AIC=592.5; linear segmented AIC=590.7), *O. capensis* (polynomial AIC=664.3; linear segmented AIC=659.9) and *Ocyphaps lophotes* (polynomial AIC=957.0; linear segmented AIC=955.8), whereas a polynomial model provided a better fit for *S. capicola* (polynomial AIC=468.5; linear segmented AIC=472.1). Given the small differences in AIC values, we are confident that our approach of using segmented linear models to describe patterns of EWL and related variables at high T_a is justified, and use such models in all further analyses. We used generalized mixed-effect models with R package 'nlme' (Pinheiro et al., 2009) to determine the coefficients of EWL, RMR, the ratio of evaporative heat loss (EHL) to metabolic heat production (MHP), and T_b as a function of T_a above the respective T_a inflection points identified in the segmented analyses.

RESULTS

Namaqua doves

In Namaqua doves, RMR decreased from $0.39 \pm 0.07 \text{ W}$ at 25°C to $0.27 \pm 0.03 \text{ W}$ at 35°C (Fig. 1). At 56 and 60°C , RMR was 0.35 ± 0.08 and $0.34 \pm 0.11 \text{ W}$, respectively (Fig. 1). An inflection point in RMR occurred at $T_a=35.3^\circ\text{C}$, above which RMR increased significantly with T_a ($t_{1,52}=2.557$, $P=0.014$). Namaqua doves commenced gular fluttering at $T_a=55.1 \pm 3.6^\circ\text{C}$.

At $T_a < 40^\circ\text{C}$, EWL was consistently low, averaging $0.15 \pm 0.09 \text{ g h}^{-1}$ (Fig. 2). Above the inflection at $T_a=40.9^\circ\text{C}$, EWL increased linearly and significantly ($t_{1,55}=12.140$, $P < 0.001$) by ~ 8 -

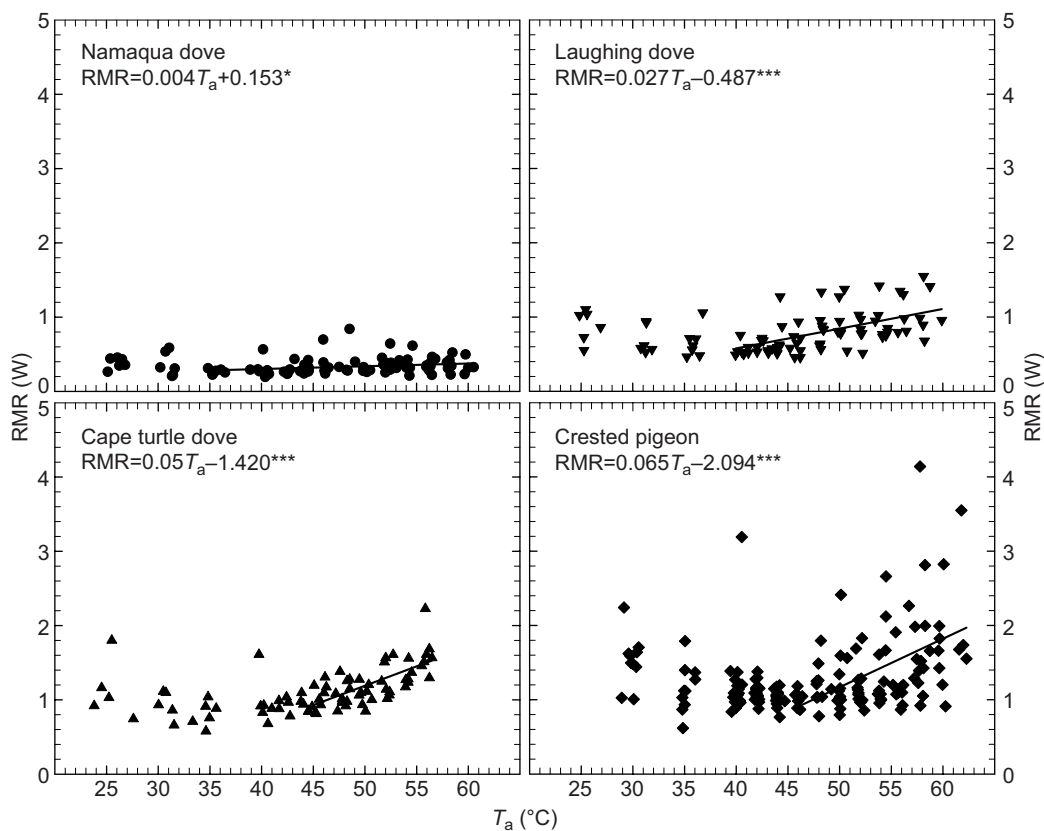


Fig. 1. Resting metabolic rate (RMR) as a function of air temperature (T_a) in calm Namaqua doves (*Oena capensis*; $n=29$), laughing doves (*Spilopelia senegalensis*; $n=33$), Cape turtle doves (*Streptopelia capicola*; $n=26$) and crested pigeons (*Ocyphaps lophotes*; $n=39$). Segmented regressions were used to estimate the inflection point in the relationship between RMR and T_a , and the slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

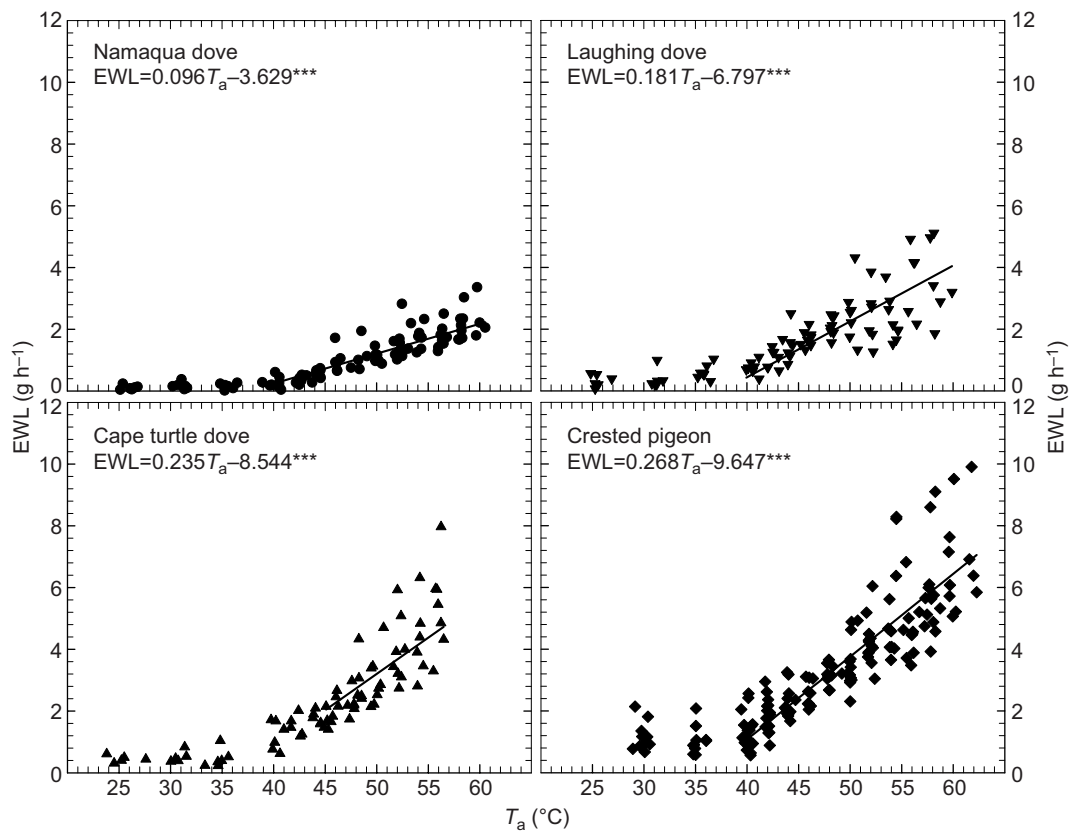


Fig. 2. Evaporative water loss (EWL) as a function of air temperature (T_a) in calm Namaqua doves (*Oena capensis*; $n=29$), laughing doves (*Spilopelia senegalensis*; $n=33$), Cape turtle doves (*Streptopelia capicola*; $n=26$) and crested pigeons (*Ocyphaps lophotes*; $n=39$). Segmented regressions were used to estimate the inflection point in the relationship between EWL and T_a , and the slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

fold to $1.75 \pm 0.38 \text{ g h}^{-1}$ at $T_a=56^\circ\text{C}$ and $2.36 \pm 0.69 \text{ g h}^{-1}$ at 60°C (Fig. 2). At these two T_a values, rates of EWL were equivalent to 5.1–6.3% of M_b per hour. Over the same T_a range, the slope of the relationship between mass-specific EWL and T_a was $2.50 \text{ mg g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. The EHL/MHP ratio increased linearly and significantly from 0.30 ± 0.18 at $T_a < 40^\circ\text{C}$ to 3.41 ± 0.76 and 4.66 ± 0.42 at $T_a=56$ and 60°C , respectively ($t_{1,40}=15.103$, $P<0.001$; Fig. 3, Table 1).

Mean T_b was $40.3 \pm 0.9^\circ\text{C}$ at $25^\circ\text{C} < T_a < 35^\circ\text{C}$, but increased significantly ($t_{1,64}=9.211$, $P<0.001$) at higher T_a (Fig. 4). At $T_a=56$ and 60°C , mean T_b was 42.5 ± 0.6 and $43.1 \pm 1.0^\circ\text{C}$, respectively (Fig. 4). The relationship between T_a and the rate of T_b increase was not significant ($t_{1,61}=-0.40$, $P=0.691$), with T_b either remaining approximately constant (rate of 0°C min^{-1}) or increasing/decreasing slightly (rate typically between -0.1 and $0.1^\circ\text{C min}^{-1}$).

The maximum T_a tolerated by Namaqua doves was 60°C . All Namaqua doves at their heat tolerance limits were active (i.e. measurements were terminated because of activity), and were therefore not included in the results above. The percentage of individuals that reached heat tolerance limits increased from zero at $T_a=54^\circ\text{C}$ to 39% at $T_a=60^\circ\text{C}$ (Fig. 5). In two of the birds that had reached their heat tolerance limits at 60°C , mean T_b was 44.2°C and 44.5°C and $T_{b,\text{max}}$ was 45.1°C in both individuals.

Laughing doves

Calm laughing doves that reached their thermal endpoints at high T_a values were included in the results below. There was a decrease in RMR from $0.89 \pm 0.21 \text{ W}$ at $T_a=25^\circ\text{C}$ to $0.56 \pm 0.11 \text{ W}$ at $T_a=40^\circ\text{C}$

(Fig. 1). An inflection point in RMR occurred at $T_a=40.0^\circ\text{C}$, above which RMR increased linearly and significantly ($t_{1,38}=6.637$, $P<0.001$; Fig. 1), with RMR averaging $1.05 \pm 0.27 \text{ W}$ (Table 1) and $1.11 \pm 0.36 \text{ W}$ (Fig. 1) at 56 and 58°C , respectively. Laughing doves began to gular flutter at $T_a=43.5 \pm 2.3^\circ\text{C}$.

At $T_a < 40^\circ\text{C}$, EWL was stable and low, averaging $0.46 \pm 0.27 \text{ g h}^{-1}$ (Fig. 2). Above 40°C , EWL increased linearly and significantly ($t_{1,38}=13.642$, $P<0.001$) with increasing T_a by ~ 8 -fold to $3.60 \pm 1.17 \text{ g h}^{-1}$ (Table 1) and $3.65 \pm 1.39 \text{ g h}^{-1}$ (Fig. 2) at $T_a=56$ and 58°C , respectively. At these higher T_a values, however, a large amount of scatter in the EWL data was observed. The slope of the relationship between mass-specific EWL and T_a was $1.87 \text{ mg g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$. Above 35°C , EHL/MHP increased approximately linearly ($t_{1,38}=8.247$, $P<0.001$) from 0.62 ± 0.11 at 35°C to 2.28 ± 0.39 at 56°C and 2.27 ± 0.76 at 58°C (Fig. 3). Though a linear regression was fitted for comparative purposes, the EHL/MHP ratio appeared to reach a plateau at higher T_a values (Fig. 3), suggesting that the relationship may be a nonlinear one.

Mean T_b averaged $40.8 \pm 0.8^\circ\text{C}$ at $T_a < 40^\circ\text{C}$, and increased linearly ($t_{1,28}=8.14$, $P<0.001$) above this T_a (Fig. 4). At $T_a=56$ and 58°C , mean T_b was 43.6 ± 1.0 and $43.7 \pm 0.8^\circ\text{C}$ (Fig. 4), respectively. There was no significant relationship between T_a and the rate of T_b increase ($t_{1,15}=1.67$, $P=0.12$), and considerable variation was observed above $T_a=56^\circ\text{C}$.

The maximum T_a tolerated by laughing doves was 58°C , although one individual reached $T_a=60^\circ\text{C}$. The T_a at which individuals reached their heat tolerance limits was more variable than in the other three species, varying from 44 to 58°C (Fig. 5).

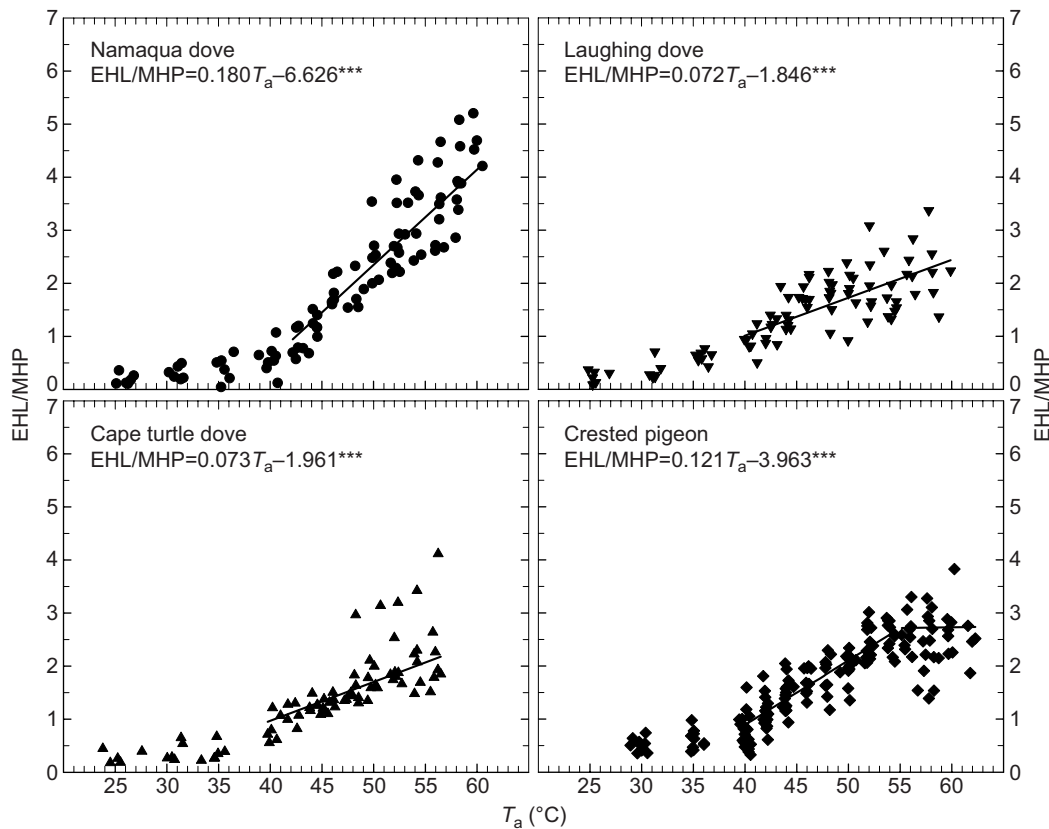


Fig. 3. Ratio of evaporative heat loss (EHL) to metabolic heat production (MHP) as a function of air temperature (T_a) in calm Namaqua doves (*Oena capensis*; $n=29$), laughing doves (*Spilopelia senegalensis*; $n=33$), Cape turtle doves (*Streptopelia capicola*; $n=26$) and crested pigeons (*Ocyphaps lophotes*; $n=39$). Segmented regressions were used to estimate the inflection point in the relationship between EHL/MHP and T_a , and the slopes and intercepts were calculated using linear mixed-effects models. For crested pigeons, the regression model for EHL/MHP versus T_a between 40°C and 55.1°C is provided in the figure; the solid line at $T_a > 55^\circ\text{C}$ shows the non-significant model fitted above the inflection point at higher T_a values. Significant relationships are represented by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Cape turtle doves

In calm Cape turtle doves, RMR decreased from 1.23 ± 0.39 W at $T_a = 25^\circ\text{C}$ to 0.81 ± 0.16 W at $T_a = 35^\circ\text{C}$ (Fig. 1). An inflection point occurred at $T_a = 44.56^\circ\text{C}$, above which RMR increased linearly and significantly ($t_{1,26} = 7.219$, $P < 0.001$) to a maximum of 1.62 ± 0.29 W at $T_a = 56^\circ\text{C}$ (Table 1, Fig. 1). Cape turtle doves began to gular flutter at $40.8 \pm 3.4^\circ\text{C}$.

At $T_a < 40^\circ\text{C}$, EWL was stable and low, averaging 0.48 ± 0.21 g h⁻¹ (Fig. 2). Above 40°C , EWL increased approximately linearly with increasing T_a ($t_{1,26} = 9.379$, $P < 0.001$). Water loss rates increased ~10-fold, averaging 5.40 ± 1.48 g h⁻¹ at $T_a = 56^\circ\text{C}$ (Table 1). The slope of the relationship between mass-specific EWL and T_a was 1.62 mg g⁻¹ h⁻¹ °C⁻¹. Above $T_a = 35^\circ\text{C}$, EHL/MHP increased linearly ($t_{1,25} = 8.552$, $P < 0.001$) from 0.36 ± 0.16 at $T_a = 35^\circ\text{C}$ to 2.30 ± 0.88 at $T_a = 56^\circ\text{C}$ (Fig. 3). Average EHL/MHP increased only slightly at the higher T_a values, but more linearly than in the other two southern African species (Fig. 3).

Mean T_b averaged $41.1 \pm 0.9^\circ\text{C}$ at $T_a < 40^\circ\text{C}$, and increased linearly ($t_{1,25} = 13.63$, $P < 0.001$) above this T_a (Fig. 4). At $T_a = 56^\circ\text{C}$, mean T_b was $44.7 \pm 0.3^\circ\text{C}$ (Table 1, Fig. 4). The rate of T_b increase increased linearly ($t_{1,25} = 2.81$, $P < 0.01$) with increasing T_a , though considerable variation was observed.

The maximum T_a tolerated by Cape turtle doves was 56°C . In most cases, measurements were terminated on account of activity, with just one individual reaching its thermal endpoint at $T_a = 56^\circ\text{C}$ and included in the results above. The single individual that reached

its thermal endpoint at 56°C exhibited a mean T_b , mean $T_{b,\text{max}}$, rate of T_b increase and EHL/MHP of 44.7°C , 45.5°C , $1.27^\circ\text{C min}^{-1}$ and 1.62, respectively (Table 1).

Crested pigeons

Crested pigeons generally remained calm with little sign of agitation, and data from almost all individuals are included in the results below. Mass-specific RMR decreased from 1.52 ± 0.35 W at 30°C to a minimum of 1.00 ± 0.11 W at 46°C , with an inflection point at $T_a = 46.6^\circ\text{C}$ (Fig. 1). At T_a above the inflection point, RMR increased to 1.28 ± 0.45 W at $T_a = 56^\circ\text{C}$ and a maximum of 2.13 ± 0.95 W in four individuals that reached $T_a = 62^\circ\text{C}$ (Fig. 1). The mixed model revealed a significant linear increase in RMR above the inflection point ($t_{1,46} = 4.36$, $P < 0.001$). Crested pigeons commenced gular fluttering at $T_a = 48.0 \pm 5.7^\circ\text{C}$.

EWL remained low and stable at $T_a < 40^\circ\text{C}$, averaging 1.12 ± 0.46 g h⁻¹ (Fig. 2). Above $T_a = 40.3^\circ\text{C}$, EWL increased linearly and significantly ($t_{1,89} = 19.211$, $P < 0.001$) by ~6-fold to 4.63 ± 1.59 g h⁻¹ at $T_a = 56^\circ\text{C}$, and reached a maximum of 7.26 ± 1.82 g h⁻¹ at $T_a = 62^\circ\text{C}$ (Fig. 2). The slope of the relationship between mass-specific EWL and T_a was 1.39 mg g⁻¹ h⁻¹ °C⁻¹. Minimum EHL/MHP was 0.51 ± 0.12 at $T_a = 38^\circ\text{C}$. EHL/MHP then increased linearly and significantly ($t_{1,70} = 23.032$, $P < 0.001$; Fig. 3, Table 1) above a lower inflection point at $T_a = 38.8^\circ\text{C}$ to 2.57 ± 0.28 at $T_a = 54^\circ\text{C}$. A second inflection point then occurred at $T_a = 55.1^\circ\text{C}$, above which

Table 1. Mean (\pm s.d.) maximum body temperature ($T_{b,max}$), rate of T_b increase (~ 10 min period), evaporative water loss (EWL), resting metabolic rate (RMR) and ratio of evaporative heat loss to metabolic heat production (EHL/MHP) in Namaqua doves, laughing doves, Cape turtle doves and crested pigeons at the highest air temperature (T_a) at which all species were tested ($\sim 56^\circ\text{C}$)

	Namaqua dove ($n=8$)	Laughing dove ($n=5$)	Cape turtle dove ($n=7$)	Crested pigeon ($n=10$)
T_b ($^\circ\text{C}$)	42.5 \pm 0.6	43.6 \pm 1.0	44.7 \pm 0.3	41.7 \pm 1.3
$T_{b,max}$ ($^\circ\text{C}$)	42.7 \pm 0.7	43.8 \pm 1.0	45.0 \pm 0.3	43.2 \pm 1.1
Rate of T_b increase ($^\circ\text{C min}^{-1}$)	0.02 \pm 0.05	0.03 \pm 0.01	0.06 \pm 0.04	0.02 \pm 0.02
EWL (g h^{-1})	1.75 \pm 0.38	3.60 \pm 1.17	5.40 \pm 1.48	4.63 \pm 1.59
RMR (W)	0.35 \pm 0.08	1.05 \pm 0.27	1.62 \pm 0.29	1.28 \pm 0.45
EHL/MHP	3.41 \pm 0.76	2.28 \pm 0.39	2.30 \pm 0.88	2.53 \pm 0.49

Only data from inactive birds were included.

EHL/MHP was not significantly related to T_a ($P=0.95$; Fig. 3). Values for EHL/MHP were 2.75 \pm 0.54 and 2.40 \pm 0.38 at $T_a=60$ and 62 $^\circ\text{C}$, respectively.

Mean T_b was 40.6 \pm 0.8 $^\circ\text{C}$ at $T_a < 40^\circ\text{C}$, but increased significantly ($t_{1,17}=6.93$, $P<0.001$) at higher T_a (Fig. 4). At $T_a=60$ and 62 $^\circ\text{C}$, mean T_b was 44.3 \pm 1.2 and 44.3 \pm 0.8 $^\circ\text{C}$, respectively (Fig. 4). The relationship between T_a and the rate of T_b increase was not significant ($t_{1,22}=1.51$, $P=0.15$), with T_b either remaining approximately constant (rate of 0 $^\circ\text{C min}^{-1}$) or increasing/decreasing slightly (rates typically between -0.1 and 0.1 $^\circ\text{C min}^{-1}$). In the three birds that had reached their thermal endpoints at 62 $^\circ\text{C}$, mean T_b values were 44.8, 43.2 and 44.6 $^\circ\text{C}$.

DISCUSSION

The picture that emerges from our data for four columbids is a lack of a clear relationship between M_b and the maximum T_a value

tolerated during acute heat exposure. Although the three southern African species showed negative scaling, with the maximum T_a tolerated during acute heat exposure being highest in the smallest species and vice versa, the larger Australian crested pigeon tolerated the highest T_a values (60–62 $^\circ\text{C}$) of any species in this study. A pattern of negative scaling would be expected if evaporative heat dissipation is limited by surface area/volume ratios, as would be predicted for birds that rely primarily on cutaneous evaporation at very high T_a .

The lack of a relationship between M_b and maximum T_a tolerated among these four columbids contrasts with the pattern among three ploceid passerines, where maximum T_a reached scaled positively with M_b , ranging from $\sim 48^\circ\text{C}$ in the 10-g scaly-feathered weaver to $\sim 54^\circ\text{C}$ in the 40-g white-browed sparrow-weaver (Whitfield et al., 2015). Notwithstanding the small sample sizes involved (three to four species per study) and the limited overlap in M_b ranges, these

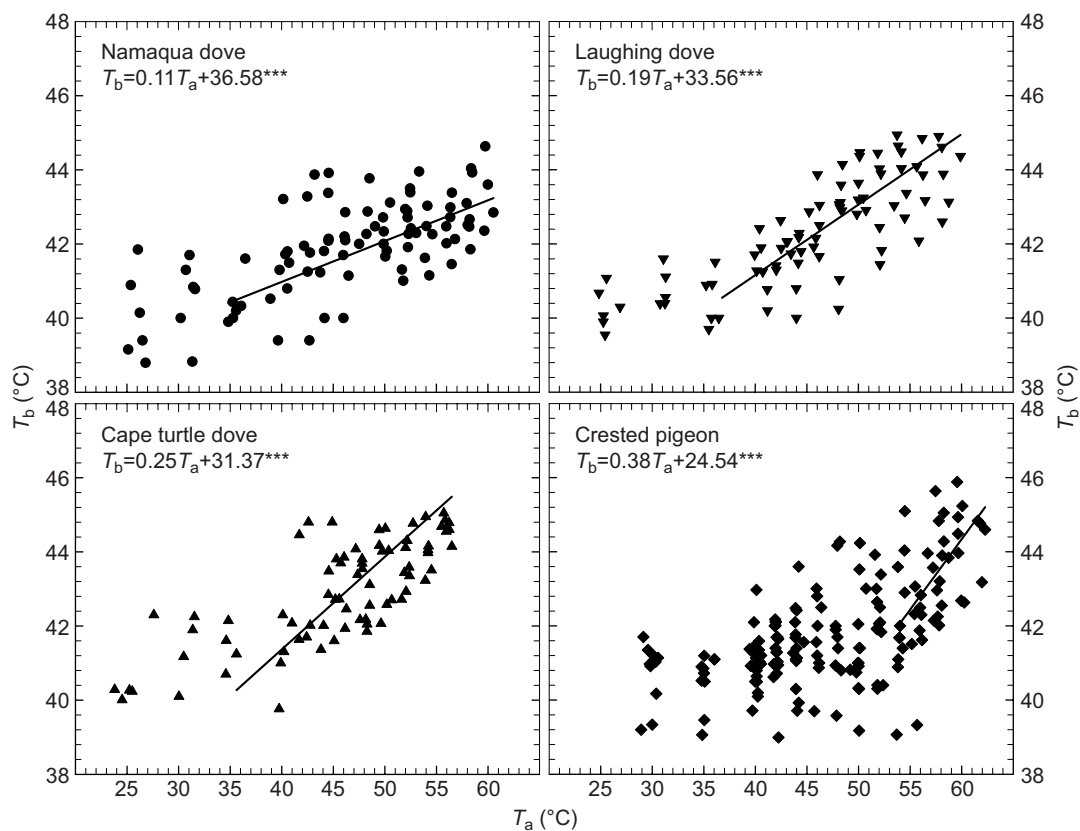


Fig. 4. Body temperature (T_b) as a function of air temperature (T_a) in Namaqua doves (*Oena capensis*; $n=29$), laughing doves (*Spilopelia senegalensis*; $n=33$), Cape turtle doves (*Streptopelia capicola*; $n=26$) and crested pigeons (*Ocyphaps lophotes*; $n=39$). Segmented regressions were used to estimate the inflection point in the relationship between mean T_b and T_a , and the slopes and intercepts were calculated using linear mixed-effects models. Significant relationships are represented by asterisks: * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

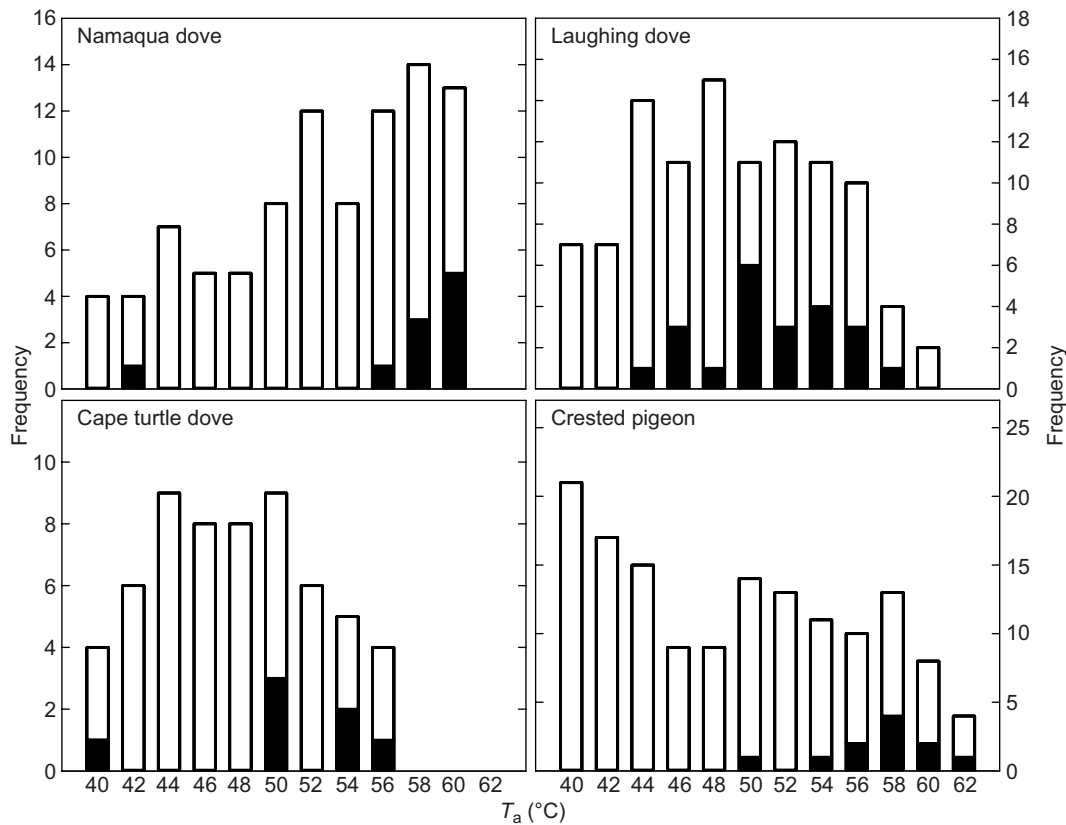


Fig. 5. Frequency of individuals that reached (black bars) and did not reach (white bars) heat tolerance limits (i.e. showed escape behaviour or reached thermal endpoints) during measurements at air temperatures $\geq 40^{\circ}\text{C}$ for Namaqua doves (*Oena capensis*), laughing doves (*Spilopelia senegalensis*), Cape turtle doves (*Streptopelia capicola*) and crested pigeons (*Ocyphaps lophotes*).

data raise the possibility that the scaling of avian heat tolerance and evaporative cooling capacity during acute heat exposure may differ fundamentally depending on the primary mode of evaporative heat dissipation.

Body temperatures and thermal endpoints

The columbids investigated here were able to maintain T_b at sub-lethal levels even at $T_a \approx 56\text{--}62^{\circ}\text{C}$ during acute heat exposure, and showed more gradual increases in T_b at high T_a than were observed in the ploceids (Whitfield et al., 2015). The maximum T_b values we recorded (both at $T_a = 60^{\circ}\text{C}$) were 45.8°C in a Namaqua dove and 45.9°C in a crested pigeon, values within the known avian lethal T_b range ($45.7\text{--}47.8^{\circ}\text{C}$; Arad and Marder, 1982; Brush, 1965; Dmi'el and Tel-Tzur, 1985; Randall, 1943). We did not, however, observe a loss of coordinated movement associated with high T_b in the doves, which contrasts with the passerines in our previous study (Whitfield et al., 2015). The latter observation suggests that lethal T_b values in these four columbids are nearer the upper end of the range reported in the literature.

Thermal endpoints (i.e. T_b and T_a values associated with thermoregulatory failure in birds not displaying escape behaviour) were not as clear in the columbids investigated here as in the ploceid passerines Whitfield et al. (2015) examined previously. Whereas in the latter study, 100% of white-browed sparrow-weaver and sociable weaver individuals and 60% of scaly-feathered weaver individuals reached thermal endpoints, in the present study, at no T_a did $>50\%$ of individuals of any species reach thermal endpoints. The fact that we could not determine clear thermal endpoints in the present study reflected the tendency of the doves to become agitated

and show prolonged escape behaviour at high T_a to a greater degree than was the case for the passerines in Whitfield et al.'s (2015) study, with the result that we often had to remove birds from the chambers before their thermal endpoints in the absence of activity could be elicited.

At $T_a \approx 56^{\circ}\text{C}$ (the highest T_a reached by all four species), hyperthermia was more pronounced in Cape turtle doves (mean $T_b = 44.7^{\circ}\text{C}$) than laughing doves (mean $T_b = 43.6^{\circ}\text{C}$) or Namaqua doves (mean $T_b = 42.5^{\circ}\text{C}$), and least pronounced in crested pigeons (mean $T_b = 41.7^{\circ}\text{C}$; Table 1). This positive scaling relationship between the extent of hyperthermia and M_b among the three southern African species, but a much lower value for the larger Australian crested pigeon, approximately mirrors the pattern we found for overall heat tolerance, as quantified by the highest T_a tolerated. These observations also raise the possibility that the evolution of crested pigeons' thermal physiology has taken place under a qualitatively and/or quantitatively different set of selection pressures compared with those experienced by the three African species. One climatic factor that may be relevant is the lower maximum T_a values typical of the Kalahari Desert compared with those that occur in many parts of the Australian arid zone.

Among the five of seven Cape turtle doves that exhibited hyperthermic T_b at $T_a = 56^{\circ}\text{C}$, rates of T_b increase remained fairly low, which we interpret as indicative of facultative, regulated hyperthermia rather than thermoregulatory breakdown and lethal heat stroke (Leon, 2006). Laughing and Namaqua doves showed similar patterns of hyperthermic T_b combined with modest rates of T_b increase at $T_a = 58^{\circ}\text{C}$ (mean $T_b = 43.6^{\circ}\text{C}$) and 60°C (mean

$T_b=43.8^\circ\text{C}$), respectively. The hyperthermic T_b values in these columbids are within the range for avian facultative hyperthermia (reviewed by Tieleman and Williams, 1999), with water conservation thought to be the primary function of this physiological response. The latter authors noted that during acute exposure to heat (1 h), birds ranging in M_b from 10 to 1000 g may reduce their total evaporative water loss by as much as 50% by becoming hyperthermic, whereas during chronic exposure (5 h), only small birds ($M_b<100$ g) benefit (Tieleman and Williams, 1999). Whereas ploceid passerines exposed to high T_a values exhibited rapid increases in T_b combined very high mean T_b values ($\sim 45^\circ\text{C}$) (Whitfield et al., 2015), hyperthermia in the columbids was characterized by a generally stable T_b somewhat elevated above normothermic levels, with little or no change in rate of T_b increase with increasing T_a .

In general, columbids appear to show shallower increases in T_b at high T_a compared with passerines: an examination of changes in T_b between $T_a=35$ and 48°C among six passerine species reveals a mean T_b increase of $3.02\pm 1.37^\circ\text{C}$ (Tieleman et al., 2002a; Whitfield et al., 2015; Wolf and Walsberg, 1996; B.S., M.C.W., A.E.M. and B.O.W., unpublished data), whereas the corresponding value for seven columbids is just $1.46\pm 0.19^\circ\text{C}$ (Hoffman and Walsberg, 1999; McKechnie and Wolf, 2004; Withers and Williams, 1990; present study). The smaller increase among columbids supports the notion that the CEWL-predominated evaporative cooling of the former group provides the physiological basis for more effective maintenance of T_b below T_a compared with the REWL-predominated evaporative cooling of the latter group, although the larger M_b of the columbids compared with passerines potentially confounds this comparison.

Evaporative water loss

As expected on the basis of allometric scaling predictions (Bartholomew and Cade, 1963; Dawson, 1982; Williams, 1996), EWL at $T_a=56^\circ\text{C}$ (highest T_a reached by all three species) generally increased with increasing M_b , although the value for crested pigeons was lower than that for the smaller Cape turtle dove (Table 1). The slope of mass-specific EWL versus T_a was steepest in Namaqua doves and shallowest in crested pigeons, as expected on the basis of the scaling of this variable (McKechnie and Wolf, 2010). The slope for Namaqua doves was very similar to the value predicted by the allometric relationship reported by the latter authors, whereas the slopes for laughing doves, Cape turtle doves and crested pigeons were 20, 33 and 30% higher, respectively, than the predicted values.

At the highest T_a values to which birds were exposed in this study ($56\text{--}62^\circ\text{C}$), Namaqua doves dissipated heat more than twice as rapidly than the three larger species. Namaqua doves were dissipating $\sim 470\%$ of their metabolic heat load at $T_a=60^\circ\text{C}$, a percentage higher than those recorded for other columbids at the same T_a (~ 286 , 369 and 308% in heat-acclimated rock doves, white-winged doves and mourning doves, respectively; Marder and Arieli, 1988; Smith et al., 2015). We hence conclude that, among columbids, Namaqua doves have an unusually pronounced capacity for evaporative cooling. The EHL/MHP value we observed in this species also exceeds by a substantial margin those reported for other species with pronounced heat tolerance (e.g. spotted nightjar *Eurostopus argus*; Dawson and Fisher, 1969). The skin surface area/mass ratio for Namaqua doves is 25–42% greater than those of the columbids examined by Marder and Arieli (1988) and Smith et al. (2015), raising the possibility that the greater surface area/volume ratio of this species may be a factor contributing to the very rapid rates of cutaneous evaporative heat dissipation and consequently high EHL/MHP ratio. Despite the comparatively large volumes of

water necessary for this mechanism of heat dissipation, water storage within the crop (Williams and Koenig, 1980) may make it sustainable over short periods.

Once acute dehydration limits are better understood, assessing the period over which a bird can defend T_b before the onset of lethal dehydration will be important, particularly in the context of extrapolating laboratory data to free-ranging birds. Studies of dehydration tolerance in the past have typically involved withholding water at T_a well below body temperature ($\sim 25^\circ\text{C}$) and measuring M_b loss over time scales of days to weeks (e.g. Williams and Koenig, 1980), an approach that does not permit the separation of water versus tissue loss. Rock doves, for example, have been shown to tolerate M_b loss equivalent to 16–18% after being deprived of water for 48 h, as well as food for 24 h of that period (Arad et al., 1989), conditions very different to rapid EWL during acute heat stress.

Resting metabolic rate

All four columbids examined showed only small increases in RMR at T_a above thermoneutrality, and even when defending T_b more than 15°C below T_a , the mean RMR of inactive birds never increased to more than $\sim 2\times$ RMR (Fig. 1). This observation is qualitatively similar to those made for other columbids during acute heat exposure (Marder and Arieli, 1988; Withers and Williams, 1990), as well as for houbara bustards, *Chlamydotis macqueenii* (Tieleman et al., 2002b). Marder and Arieli's (1988) data for heat-acclimated rock doves are particularly striking in this regard, with RMR at $T_a\sim 60^\circ\text{C}$ virtually identical to that at $30^\circ\text{C}<T_a<40^\circ\text{C}$. The general absence of large increases in RMR at $T_a>T_b$ in columbids contrasts with the pattern typical of passerines (Dawson, 1954; Hinds and Calder, 1973; Tieleman et al., 2002a; Weathers and Greene, 1998; Whitfield et al., 2015; Wolf and Walsberg, 1996) and other avian orders (Hinsley et al., 1993; Lasiewski et al., 1970; Marder and Bernstein, 1983; Weathers and Caccamise, 1975), and indeed the classic Scholander–Irving model of endothermic homeothermy (Scholander et al., 1950).

Contrary to expectations based on literature on the scaling of RMR in heat-stressed birds (Bartholomew and Cade, 1963; Weathers, 1981), Namaqua doves in our study exhibited a shallower slope of mass-specific RMR versus T_a (when accounting for individual responses in a mixed model) than the three larger species. We suspect this result reflects the fact that panting/gular fluttering was delayed until much higher T_a values ($\sim 55^\circ\text{C}$) in Namaqua doves compared with the other two species (~ 44 , 41 and 48°C in laughing doves, Cape turtle doves and crested pigeons, respectively). Earlier work suggested that, in columbids, panting and/or gular fluttering commences at $T_b=42\text{--}43^\circ\text{C}$ (Bartholomew and Dawson, 1954; Randall, 1943), observations that are supported by our data, with $T_b=42^\circ\text{C}$ corresponding to $T_a\sim 55$, 44 and 42°C in Namaqua, laughing and Cape turtle doves, respectively. The observation that larger doves apparently needed to supplement CEWL with panting and/or gular fluttering at lower T_a than smaller species likely reflects decreasing surface area/volume ratios with increasing M_b , although Marder and Arieli (1988) noted the absence of panting or gular flutter in some rock doves exposed to $T_a=60\text{--}65^\circ\text{C}$ and low humidity. This observation might hold for other species that were habituated to human disturbance, as were the rock doves.

As is the case for increases in T_b , columbids also appear to generally show smaller fractional increases in RMR at high T_a compared with passerines. Among seven passerines, the mean ratio of RMR at $T_a=48^\circ\text{C}$ compared with $T_a=35^\circ\text{C}$ is 1.38 ± 0.22 (Tieleman et al., 2002a; Whitfield et al., 2015; Wolf and Walsberg, 1996; B.S.,

M.C.W., A.E.M. and B.O.W., unpublished data), whereas the corresponding value for seven columbids is 1.07 ± 0.09 (Hoffman and Walsberg, 1999; McKechnie and Wolf, 2004; Withers and Williams, 1990; present study). The smaller fractional increases in RMR among columbids compared with passerines between $T_a = 35$ and 48°C support the notion that evaporative cooling predominated by CEWL is more energetically efficient than REWL-predominated cooling. Although M_b is again a confounding factor in this comparison, we argue that these differences likely reflect the metabolic cost of muscle contractions involved in panting (Dawson, 1982; Richards, 1970), and the concomitant rapid increases in RMR that typically occur with increasing T_a above the thermoneutral zone in passerines (e.g. Ambrose et al., 1996; Trost, 1972; Williams, 1999). A recent demonstration that the metabolic cost of lung ventilation in running birds is very low (<2% of total metabolic rate; Markley and Carrier, 2010) reiterates the need to better understand the costs involved in respiratory evaporative heat dissipation, particularly in the context of how variation in these costs might contribute to inter- and intraspecific variation in the efficiency of evaporative cooling (Noakes et al., 2016).

Cutaneous versus respiratory evaporation: ecological and evolutionary implications

Our data suggest that variation in the primary avenue of avian evaporative heat loss may have important consequences for birds' capacity to tolerate acute heat exposure under both laboratory and natural conditions. For instance, data for columbids (present study) and ploceid passerines (Whitfield et al., 2015) suggest that the scaling of thermal limits during acute heat exposure may depend on the primary avenue of evaporative heat dissipation.

To understand the ecological significance of phylogenetic variation in avian evaporative cooling pathways, we need to extrapolate laboratory data on acute heat stress to natural conditions. The goal of the present study, like those of Whitfield et al. (2015) and Smith et al. (2015), was to quantify upper limits to heat tolerance and evaporative cooling capacity in a manner facilitating direct comparisons of standardized variables among species. The conditions birds experienced during our experimental protocol (rapid increases in T_a combined with very low humidity values maintained via high flow rates) are unlikely to directly mirror conditions they routinely experience in natural habitats, although humidity values in desert habitats are often similar to those experienced by birds in our study (see e.g. <http://www.bom.gov.au/> for data for Australia). Nevertheless, we would argue that the broad patterns identified here concerning the very efficient evaporative cooling and tolerance of high environmental temperatures by columbids reflect ecologically important differences. In hot desert environments in southern Africa and North America, for instance, columbids are often more active at higher T_a compared with passerines (B.S., B.O.W. and A.E.M., personal observations). Moreover, the onset of panting/gular flutter in columbids typically occurs at considerably higher T_a than in similarly sized passerines (B.S., N. Pattinson, M. Thompson, S. J. Cunningham and A.E.M., unpublished data).

One factor crucial in extrapolating the responses of arid-zone birds to acute heat stress under laboratory conditions to natural environments concerns the availability of drinking water. Most arid-zone columbids are strongly water-dependent and are regular drinkers (Fisher et al., 1972; Maclean, 1996; Wolf et al., 2002), and the greater overall heat tolerance of columbids we have documented in the present study is probably tightly linked to the availability of water for rapid evaporative heat dissipation. In the absence of drinking

water, heat tolerance in columbids may be compromised relatively quickly; for instance, our data suggest that at an environmental temperature of 48°C and with no access to water, Namaqua, laughing and Cape turtle doves would experience EWL equivalent to 11% of body mass after 4.6, 4.6 and 6.4 h, respectively. Dehydration equivalent to 11–15% of body mass is likely near the upper limit of avian dehydration tolerance (Wolf, 2000).

The data currently available on the relative roles of respiratory and cutaneous evaporation in avian thermoregulation at very high T_a are largely restricted to two orders, Columbiformes and Passeriformes (Tieleman and Williams, 2002; Wolf and Walsberg, 1996), and patterns of EWL partitioning in other orders remain less clear. One reason behind the paucity of data for many orders is that measuring REWL and CEWL is more technically challenging than measuring total evaporation, and requires either a partitioned chamber in which REWL and CEWL are measured in separate compartments (e.g. Hoffman and Walsberg, 1999; Lasiewski et al., 1971; Wolf and Walsberg, 1996) or a mask system (e.g. Tieleman and Williams, 2002). Both these approaches require that birds be habituated to the experimental setup, and that chambers and/or masks be custom-built for particular study species. However, the pronounced differences in heat tolerance and evaporative cooling capacity between the only two orders that are relatively well studied in this regard highlight the need for quantitative data on the contributions of REWL and CEWL to total evaporation in many more avian taxa. Such data are a prerequisite for fully understanding phylogenetic variation among birds in heat tolerance and evaporative cooling capacity.

Finally, data on avian thermoregulatory responses to acute heat stress and dehydration tolerance are relevant to modelling the impacts of more frequent and intense heat waves on arid-zone avifaunas. Absolute maximum air temperatures and the frequency of intense heat events are predicted to increase substantially in the coming decades (IPCC, 2011), and catastrophic avian mortality events similar to those documented historically, particularly in the Australian arid zones (Finlayson, 1932; Serventy, 1971; Towie, 2009, 2010), are likely to occur much more frequently than they have in the past (McKechnie and Wolf, 2010). Developing models that use data collected under laboratory conditions to predict the heat tolerance and hydration status of free-ranging birds in natural habitats is vital for predicting where and when these die-offs are likely to occur.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

B.O.W. and A.E.M. designed the study. M.C.W., B.S., A.R.G., E.K.S., W.A.T. and B.O.W. collected data. M.C.W., A.E.M. and A.R.G. analyzed the data. M.C.W., A.E.M., B.S. and B.O.W. wrote the manuscript.

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