The Impact of Humidity on Evaporative Cooling in Small Desert Birds Exposed to High Air Temperatures

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ABSTRACT

Environmental temperatures that exceed body temperature (T_b) force endothermic animals to rely solely on evaporative cooling to dissipate heat. However, evaporative heat dissipation can be drastically reduced by environmental humidity, imposing a thermoregulatory challenge. The goal of this study was to investigate the effects of humidity on the thermoregulation of desert birds and to compare the sensitivity of cutaneous and respiratory evaporation to reduced vapor density gradients. Rates of evaporative water loss, metabolic rate, and T_b were measured in birds exposed to humidities ranging from ~2 to 30 g H_2O m^{-3} (0%–100% relative humidity at 30°C) at air temperatures between 44° and 56°C. In sociable weavers, a species that dissipates heat primarily through panting, rates of evaporative water loss were inhibited by as much as 36% by high humidity at 48°C, and these birds showed a high degree of hyperthermia. At lower temperatures (40°–44°C), evaporative water loss was largely unaffected by humidity in this species. In Namaqua doves, which primarily use cutaneous evaporation, increasing humidity reduced rates of evaporative water loss, but overall rates of water loss were lower than those observed in sociable weavers. Our data suggest that cutaneous evaporation is more efficient than panting, requiring less water to maintain T_b at a given temperature, but panting appears less sensitive to humidity over the air temperature range investigated here.

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Introduction

Birds are notable for having the highest body temperatures and mass-specific metabolic rates among endothermic vertebrates while also being primarily diurnal and nonfossorial. This suite of traits dictates that birds living in hot environments are exposed to very high environmental and endogenous heat loads (Bartholomew and Cade 1963; Calder and King 1974). California gulls (*Larus californicus*) nesting on open substrates, for instance, routinely experience operative temperatures (Bakken 1976) up to 60°C during incubation and when tending nestlings (Chappell et al. 1984). Gambel's quail (*Callipepla gambelii*) foraging in sunlit areas often experience operative temperatures of 50°C (Goldstein 1984). Tieleman and Williams (2002) have observed foraging hoopoe larks (*Alaemon alaudipes*) exposed to operative temperatures as high as 47°C, and many species of desert-nesting doves frequently experience operative temperatures of 50°–60°C or more during incubation (Walsberg and Voss-Roberts 1983; Marder and Gavrieli-Levin 1986; B. O. Wolf, personal observation).

In order to avoid lethal hyperthermia while exposed to such high temperatures, birds living in arid environments rely on a suite of behavioral and physiological traits to maintain heat balance by dissipating or reducing heat loads. When ambient temperature exceeds body temperature (T_b), heat flows from the environment to the bird via conduction, convection, and radiation (Calder and King 1974; Schmidt-Nielsen 1997), and the only available avenue for heat dissipation is evaporation (Calder and King 1974; Dawson 1982). The rate of evaporative heat dissipation is directly dependent on the deficit in absolute humidity, measured as water vapor density (WVD), between the evaporating surface of the animal and the environment (Lasiewski et al. 1966; Webster and King 1987; Powers 1992). Thus, high environmental humidity reduces the gradient driving evaporation, limiting the amount of heat an animal can dissipate.

Although subtropical deserts are extremely arid for most of the year, there are discrete and unpredictable rainfall events, yet total annual rainfall remains below 500 mm (Lovegrove 1999). These rainfall events occur over short periods of time, as part of a summer rainfall period (Lovegrove 1999). During these periods, the added moisture in combination with high ambient temperatures can create environmental conditions that can be particularly challenging for endothermic animals

(Calder and King 1974; Weathers 1997). Although many authors have examined the effect of ambient temperature on rates and avenues of evaporation in birds (see, e.g., Bartholomew and Cade 1963; Calder and King 1974; Williams 1996; Williams and Tieleman 2005 and the citations therein), few have investigated the effect of environmental humidity on rates of evaporation and heat balance in birds (Lasiewski et al. 1966; Webster et al. 1985; Webster and King 1987; Powers 1992; Weathers 1997; Hoffman and Walsberg 1999).

Webster and King (1987) and Powers (1992) have shown that at moderate temperatures (up to 37°C), evaporative cooling is impaired as humidity increases. However, the air temperatures in these studies were below or equal to avian T_b, and, consequently, the birds were not dependent solely on evaporation to maintain heat balance. Because of the rapid increase in total evaporative water loss (TEWL) as temperature exceeds T_b in birds, the potential reduction in evaporation due to rising atmospheric humidity could dramatically hinder heat dissipation (Dawson 1982; Marder and Ben-Asher 1983; Wolf and Walsberg 1996; McKechnie and Wolf 2004).

Evaporative cooling in birds typically involves a combination of cutaneous and respiratory water loss pathways. The reliance on cutaneous evaporation varies among taxa (Bernstein 1971; Dawson 1982; Marder and Ben-Asher 1983; Webster and Bernstein 1987; Ro and Williams 2010), as does the specific mechanism of respiratory evaporation (Calder and King 1974; Wolf and Walsberg 1996; Hoffman and Walsberg 1999; McKechnie and Wolf 2004). Rates of cutaneous water loss (CEWL) in birds are regulated in part by adrenergic control of venous blood flow to the skin in response to heat stress (Ophir et al. 2002) and as such are not completely passive, but the metabolic costs of modulating CEWL seem to be negligible (Marder and Ben-Asher 1983; Marder and Gavrieli-Levin 1987). The permeability of the skin to water is directly related to the relative quantity and structure of the lipids in the stratum corneum, which varies with environmental aridity and among phylogenetic classes of birds (Haugen et al. 2003; Ro and Williams 2010; Muñoz-Garcia and Williams 2011; Champagne et al. 2012). The specific mechanisms that columbiforme birds use to greatly enhance cutaneous evaporation at high temperatures have not received as much attention (Wolf and Walsberg 1996; Hoffman and Walsberg 1999; McKechnie and Wolf 2004). Respiratory water loss in birds can be augmented via panting, where high ventilation rates result in the movement of large volumes of air across the evaporative surfaces of the lung and nasal mucosa, or gular fluttering, where high-frequency vibrations of the gular pouch result in high rates of evaporation (Calder and King 1974; Dawson and Wittow 2000; Robertshaw 2006).

These pathways of evaporative water loss differ substantially in their phylogenetic distribution among birds. For instance, passerines (Passeriformes) rely on a combination of panting and CEWL at air temperatures below T_b, but as temperatures rise above T_b, there is a dramatic increase in respiratory evaporative water loss (REWL) but only a modest increase in CEWL (Wolf and Walsberg 1996). Thus, at high temperatures, up to 80% of TEWL occurs as REWL. Columbiformes, on the other hand, rely to a greater extent on cutaneous water, with the latter accounting for up to 80% of TEWL when air temperature exceeds T_b. In these birds, once cutaneous evaporation is no longer adequate for the maintenance of heat balance, gular fluttering is utilized (Bartholomew et al. 1968; Weathers and Schoenbaechler 1976; Marder and Ben-Asher 1983; Arad et al. 1987; Marder and Arieli 1988; Hoffman and Walsberg 1999; McKechnie and Wolf 2004).

Despite our knowledge of the pathways of evaporative water loss, their phylogenetic distribution, and the acknowledgement of the potential role of ambient humidity on the rate of evaporation, few studies have quantified the influence of ambient humidity on rates of evaporation. The objective of this study was to characterize the impact of humidity on the efficiency of evaporative heat dissipation in birds exposed to high temperatures and to compare sensitivity to humidity in birds using divergent evaporative heat dissipation pathways. We chose to investigate evaporative water loss in two species: the sociable weaver (*Philetairus socius*; Passeriformes), and the Namaqua dove (*Oena capensis*; Columbiformes). We predicted increased thermoregulatory costs and reduced evaporative efficiency at high humidity for both species. However, because of the largely passive nature of cutaneous evaporation as well as the high evaporative surface area, we predicted that high humidity would inhibit cutaneous evaporation to a greater degree than respiratory evaporation.

Material and Methods

Field Site and Bird Capture and Care

The study was conducted in the southern Kalahari Desert at Leeupan Farm (26°57′03.8S, 021°52′20.0E), South Africa, during February 2013. During the experimental period, temperature at the field site ranged from 8.6° to 42.3°C. Daily maximum temperature ranged from 32.9° to 42.3°C, and humidity ranged from 1.5 to 12.9 g m^{-3} (dew points of −9.0° to 16.0°C).

Sociable weavers leave their colonial roost en masse at sunrise. A mist net was opened each morning between 0530 and 0545 hours, just before sunrise near a roost colony, and 5–10 birds were caught immediately as birds left the nest, thus ensuring birds were postabsorptive, allowing a respiratory quotient (RQ) of 0.71 to be assumed for these birds. These birds were held in soft-sided cages (1.0 m × 1.0 m × 1.0 m) for up to 10 h with free access to water and were observed drinking throughout the day. Birds were returned to the location of capture after measurements were complete each day.

Namaqua doves were caught at a nearby farm using mist nets set around cattle water troughs as the doves arrived to drink at midday. Birds were held outdoors in soft-sided cages (1.0 m × 1.0 m × 1.0 m) sheltered from the sun and wind for up to 72 h. While in captivity, millet seed and water were provided ad lib. Birds habituated to captivity quickly, and all birds were observed eating and drinking the same day as

captured. All measurements on Namaqua doves were completed within 72 h of capture. Birds were weighed daily and maintained weight while in captivity. The crop was checked just before each respirometry trial. All birds had full crops, so RQ was assumed to be 0.93 for all measurements on this species, a value that has been shown to be accurate for birds digesting millet (Nagy 1983, pp. 1–44; Walsberg and Wolf 1995). All procedures were approved by the University of Pretoria's Animal Ethics Committee (approval EC071-11), and all bird capture was permitted by the Department of Environment and Nature Conservation, Northern Cape Province.

Gas Exchange and Body Temperature Measurements

Rates of CO_2 production and evaporative water loss were measured using a flow-through respirometry system optimized for high flow rates. Birds were placed individually in clear 1.6-L plastic respirometry chambers (Lock & Lock) within a temperature-controlled incubator. The latter consisted of a large insulated ice chest, in which air temperature was controlled using a 162-W Peltier device (model AC-162, TE Technology, Traverse City, MI) and a custom-built controller that incorporated a TE Technology digital display (MP-2986) and control card (TC-36-25-RS486). In order to precisely control humidity within the respirometry chamber and minimize equilibration time while adjusting humidity, we mixed two air streams, one consisting of humid air (dew point ≈ 27°C) pumped into the chamber at a fixed flow rate of 1.0 or 2.0 L min^{-1} and the second consisting of dry air at flow rates between 0.5 and 20 L min^{-1}.

High flow rates of dry air were generated using compressed air that was pushed through a membrane air dryer (Champion CMD3 air dryer and filter, Champion Pneumatic, Princeton, IL). Flow of air into the chamber was controlled using mass flow controllers (Alicat Scientific, Tucson, AZ). Humid air was generated by pumping air through a custom-built dew point generator where ambient air was bubbled through water held in two 2.0-L Nalgene bottles housed in an insulated box followed by a water condensation trap to prevent liquid water from reaching the mass flow controllers. Although the temperature of this dew point generator was not independent of ambient temperature, the insulation prevented rapid fluctuations in temperature, and evaporative cooling maintained the temperature below ambient, preventing condensation from occurring within the system. Because of the slight fluctuations in temperature of the dew point generator, incurrent humidity was measured before and after each humidity treatment.

Dry and humid air streams were combined downstream of the incurrent flow controllers and were passed through a copper coil to equilibrate incurrent air temperature with chamber temperature. Downstream of the chamber, air was subsampled at a rate of 300 mL min^{-1}. CO_2 (ppm) and H_2O (ppt) were measured using a CO_2 and water vapor analyzer (LI-COR model LI-840A, Lincoln, NE).

Temperature-sensitive passive integrated transponder (PIT) tags were injected intraperitoneally into each bird using an implanter needle (MK7, Biomark), with a small amount of cyanoacrylate adhesive used to seal the abdominal wall. During measurements, PIT tags were scanned using a portable transceiver system (FS2001, Biomark, Boise, ID) with an 8-inch antenna every 5 s. Before the experiment, it was determined that these PIT tags were accurate to within 0.15°C across the measurement range. Chamber temperature was measured using a TC-2000 thermocouple reader (Sable Systems International) and standard type-T (Cu-Cn) thermocouples.

All instruments were connected to an analog-digital converter (UI-II, Sable Systems International) connected to a laptop computer. Data were logged every second using Expedata (Sable Systems International). Chamber temperature, CO_2, H_2O, flow rates, T_b, and change in T_b over time were extracted using the lowest 90 s of CO_2 measurements from each 5-min interval at each humidity level.

Experimental Design

Temperature treatments were determined based on upper limits of thermoneutrality previously determined for both species (Whitfield 2014). Birds were exposed to humidity ranging from 2 to 26 g H_2O m^{-3} at each of four temperatures. Sociable weavers were exposed to 40°, 44°, 48°, and 52°C, whereas Namaqua doves were exposed to 44°, 48°, 52°, and 56°C. For the 40° and 44°C trials for the sociable weavers and the 44° and 48°C trials for the Namaqua doves, birds were placed directly into a chamber preheated to the desired air temperature set point. For higher temperatures, birds were placed into the chamber at 44°C (weavers) or 48°C (doves), and the temperature was then ramped to the experimental temperature over the course of 10–20 min. By following this protocol, birds remained calm throughout the experimental trials. During each respirometry trial, birds were constantly monitored using a live video feed from within the incubator. This, combined with real-time T_b measurements, allowed constant assessment of the experimental animal. Data from birds that were active (e.g., sustained jumping or fluttering) were not included in the analyses, and body temperatures were monitored to ensure that 45.5°C was not exceeded. This value is lower than the published lower lethal limit of similar-sized birds of 46.0°C (Dawson 1954).

Initially, flow rate was adjusted to maintain chamber humidity below 3.0 g H_2O m^{-3}. After a 10-min habituation period, once T_b had stabilized, 5 min of stable measurements was recorded, followed by a 5-min baseline period to record incurrent WVD (g H_2O m^{-3}) and [CO_2]. Thereafter, humidity was increased within the chamber, by introducing a humid flow of air (~30 g H_2O m^{-3}) at 1 or 2 L min^{-1}. Then, to control humidity, the dry flow rate of air was adjusted to between 0.5 and 20 L min^{-1} to achieve stable humidity levels of approximately 6.0, 13.0, 19.0, or 26.0 g H_2O m^{-3}. Once humidity stabilized for each treatment, 5–10 min of stable measurements was recorded, followed by a 5-min baseline period to record incurrent WVD and CO_2. Upon completion of the

run, birds were removed and immediately weighed. Birds were then placed in a cooled area to help reduce T_b if high T_b was reached during measurements. Birds were gavaged with 0.5–2.0 mL H_2O and returned to a cage, where they were monitored until release. All birds completely regained body mass before release.

Calculations

Flow rates of humid air were corrected using equation (8.6) from Lighton (2008). CO_2 was calculated using equation (10.5) from (Lighton 2008). Metabolic heat production (mW) was calculated as in Walsberg and Wolf (1995), assuming an RQ of 0.71 for weavers and an RQ of 0.93 for doves. H_2O was calculated using equation (10.9) from Lighton (2008), assuming 0.803 mg H_2O per mL of water vapor (Lighton 2008). Evaporative heat loss (mW) was calculated using a latent heat of vaporization of 2.26 J mg^{-1} H_2O. Effective heat dissipation (EHD) ratio is simply evaporative heat loss relative to metabolic heat gain.

Statistics

Each individual bird was exposed to a single air temperature but experienced one to five humidity treatments at that air temperature. Since multiple measurements were made on a single individual, general linear mixed models were used with individual identity included as a random factor. Initial models included temperature, humidity, initial mass, and the interaction between temperature and humidity. Backward-stepwise model selection was used, where the least significant term was removed until only significant terms remained (Crawley 2005). In the case of a significant interaction, the data set was split by temperature treatment or species (as appropriate), and the effect of humidity was further assessed. Body mass was not a significant covariate and was removed from the models. Consequently, CO_2 and H_2O were standardized by initial body mass. All post hoc comparisons were performed using Tukey's honest significant difference (HSD) test. All statistics were performed using R with the nlme package for mixed models (Pinheiro et al. 2001; R Development Core Team 2011).

Results

Overall, 26 sociable weavers and 25 Namaqua doves were used for measurements. Initial mass was 23.6 ± 1.1 g (mean ± SD) for sociable weavers and 39.4 ± 3.4 g for Namaqua doves.

Sociable Weavers

The relationship between TEWL and humidity differed depending on temperature (humidity × temperature: $F_{3,67} = 16.98$, $P < 0.001$; fig. 1*A*), and there was a significant relationship between TEWL and temperature (temperature: $F_{3,22} = 254.00$, $P < 0.001$) and between TEWL and humidity (humidity: $F_{1,67} = 102.57$, $P < 0.001$). At 40° and 44°C, there was not a significant relationship between TEWL and humidity (40°C: $F_{1,24} = 0.30$, $P = 0.588$; 44°C: $F_{1,23} = 0.41$, $P = 0.531$), but at 48°C, there was a significant negative relationship between TEWL and humidity ($F_{1,20} = 42.90$, $P < 0.001$). At 52°C, birds could not tolerate humidity above 2.5 g m^{-3}, and as a result the response to humidity could not be determined.

Because the response of TEWL to humidity differed among temperatures, the response to temperature was assessed within each humidity treatment. Within each humidity treatment, TEWL increased with increasing temperature (humidity, 3.3 g m^{-3}: $F_{3,40} = 179$, $P < 0.001$; humidity, 11.9 g m^{-3}: $F_{2,17} = 128.3$, $P < 0.001$; humidity, 17.9 g m^{-3}: $F_{2,15} = 84.17$, $P < 0.001$; humidity, 26.6 g m^{-3}: $F_{2,15} = 84.17$, $P < 0.001$), but the magnitude of this response decreased at higher humidities (fig. 1*A*).

As temperature increased, there was a significant increase in metabolic rate (MR; fig. 1*C*; $F_{3,22} = 11.58$, $P < 0.001$), but there was no effect of humidity ($F_{1,70} = 2.82$, $P = 0.097$). Pairwise comparisons (Tukey's HSD multiple comparison of means) among temperature treatments revealed no significant difference in MR between 40° and 44°C ($P = 0.382$) or between 44° and 48°C ($P = 0.320$) but a significant increase in MR when temperature increased from 40° to 48°C ($P = 0.004$).

Much like evaporative water loss, EHD ratio responded to humidity differently depending on temperature (fig. 1*E*; humidity × temperature: $F_{3,67} = 8.428$, $P < 0.001$). There was also an overall effect of ambient temperature ($F_{3,22} = 39.33$, $P < 0.001$) and humidity ($F_{1,67} = 19.12$, $P < 0.001$). There was no significant relationship between EHD and humidity at 40° or 44°C (40°C: $F_{1,24} = 0.23$, $P = 0.63$; 44°C: $F_{1,23} = 0.00$, $P = 0.99$; table 1). There was a significant negative relationship between EHD ratio and WVD only in the 48°C temperature reatment ($F_{1,20} = 18.80$, $P < 0.001$). Again, this could not be assessed within the 52°C treatment. Much like TEWL, EHD increased with increasing temperature, but the magnitude of this response decreased as humidity increased (humidity, 3.3 g m^{-3}: $F_{3,40} = 42.86$, $P < 0.001$; humidity, 11.9 g m^{-3}: $F_{2,17} = 36.74$, $P < 0.001$; humidity, 17.9 g m^{-3}: $F_{2,15} = 11.53$, $P < 0.001$; humidity, 26.6 g m^{-3}: $F_{2,15} = 6.38$, $P = 0.012$; fig. 1*E*). Within each humidity treatment, EHD increased significantly with each temperature treatment (Tukey's HSD multiple comparison of means within humidity treatment; $P < 0.001$), except there was no significant increase in EHD between 44° and 48°C above 17.9 g m^{-3} ($P > 0.050$; fig. 1*E*).

Rising humidity resulted in increased body temperatures at higher temperatures but had no effect at lower temperatures (fig. 2*A*; temperature × humidity $F_{3,67} = 6.06$, $P = 0.001$). There was a significant increase in T_b with temperature ($F_{3,22} = 42.63$, $P < 0.001$) and a significant increase in T_b with increasing humidity overall ($F_{1,67} = 52.09$, $P < 0.001$). Within the 40°C treatment, there was no significant relationship between T_b and humidity ($F_{1,24} = 2.31$, $P < 0.142$), but there was a significant increase in T_b with humidity within the 44° and 48°C treatments (44°C: $F_{1,23} = 42.92$, $P < 0.001$; 48°C: $F_{1,20} =$

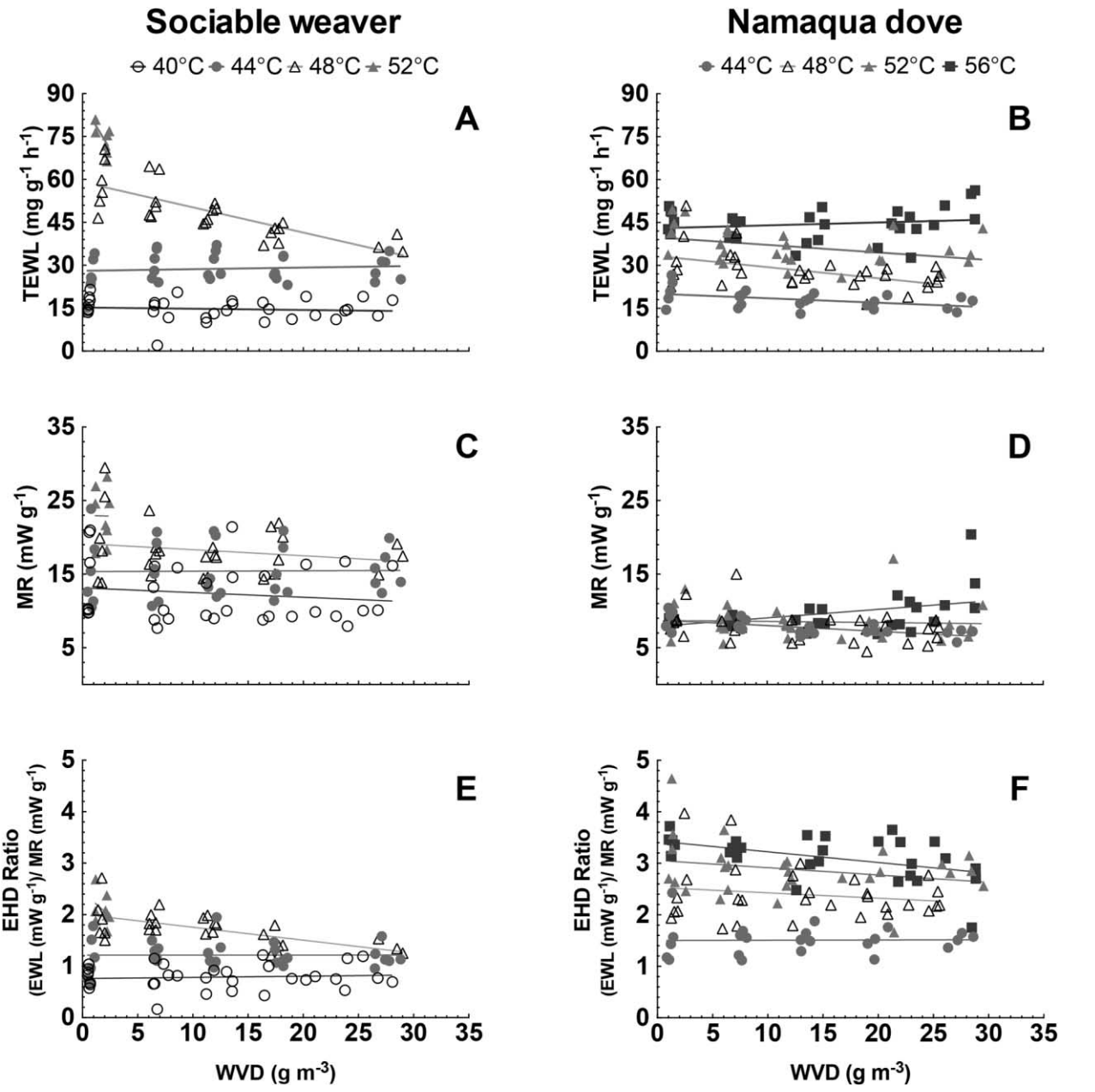

Figure 1. Response of total evaporative water loss (TEWL; *A*, *B*), metabolic rate (MR; *C*, *D*), and effective heat dissipation ratio (EHD ratio; *E*, *F*) to increasing humidity over a range of temperatures that exceed body temperature in Namaqua doves (*Oena capensis*) and sociable weavers (*Philetairus socius*). See text for statistical details and table 1 for parameter estimates.

179.16, $P < 0.001$; table 1; fig. 2). Again, this relationship could not be assessed within the 52°C treatment.

There was a significant increase in T_b with increasing temperature within each humidity treatment (humidity, 3.3 g m^{-3}: $F_{3, 40} = 35.72$, $P < 0.001$; humidity, 11.9 g m^{-3}: $F_{2, 17} = 22.58$, $P < 0.001$; humidity, 17.9 g m^{-3}: $F_{2, 15} = 25.74$, $P < 0.001$; humidity, 26.6 g m^{-3}: $F_{2, 12} = 20.13$, $P < 0.001$). Within each humidity treatment, there was a significant increase in T_b with each increase in temperature (Tukey's HSD multiple comparison of means within humidity treatment, $P < 0.001$), except at the lowest humidity between 40° and 44°C, where there was no difference in T_b ($P > 0.05$; fig. 2*A*).

Namaqua Doves

The response of evaporative water loss to increasing humidity depended on temperature (fig. 1*B*; temperature × humidity: $F_{3, 84} = 4.08$, $P = 0.009$; temperature: $F_{3, 19} = 64.12$, $P < 0.001$; humidity: $F_{1, 84} = 7.67$, $P = 0.007$). There was a negative relationship between TEWL and humidity at 44°C ($F_{1, 17} =$

Table 1: Slope (m) and intercept (b) for the relationship of metabolic rate (MR), total evaporative water loss (TEWL), and body temperature (T_b) in response to absolute humidity (g m^{-3}) at each temperature exposure in sociable weavers

	MR		TEWL		T_b	
Temperature (°C)	m	b	m	b	m	b
40	−.063 (−.02, .11)	13.13 (10.59, 15.66)	−.043 (−.20, .12)	15.24 (12.85, 17.64)	.02 (−.03, .06)	40.90 (40.22, 41.58)
44	.006 (−.15, .16)	15.34 (12.90, 17.78)	.056 (−.15, .27)	28.07 (24.76, 31.38)	.06 (.02, .10)	41.75 (41.05, 42.45)
48	−.083 (−.27, .10)	19.15 (16.58, 21.71)	−.88 (−1.19, −.58)	59.06 (54.80, 63.32)	.09 (.07, .11)	43.34 (43.06, 43.62)
52	−.039 (NA)	22.98 (9.77, 36.20)	−6.36 (−13.39, .66)	86.48 (73.07, 99.89)	.47 (−.08, 1.03)	44.41 (43.35, 45.48)

Note. Values are means, with 95% confidence intervals in parentheses. NA = confidence interval could not be accurately computed.

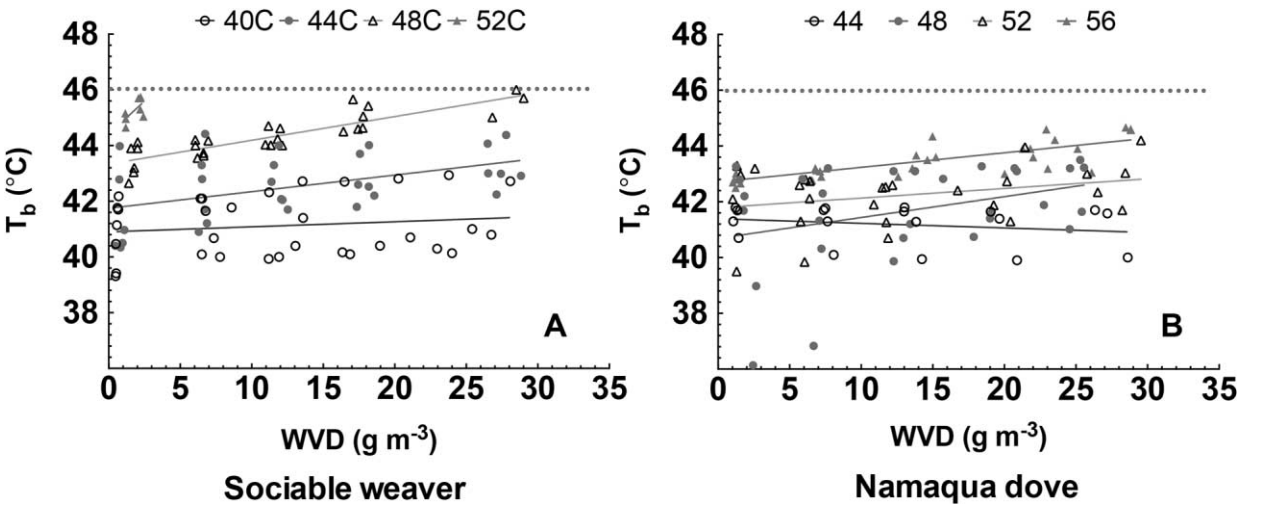

Figure 2. Response of body temperature (T_b) to increasing humidity over a range of temperatures that exceed T_b in Namaqua doves (*Oena capensis*) and sociable weavers (*Philetairus socius*). Dotted lines correspond to the lower limit of published values for lethal T_b in birds (46°C). See text for statistical details and table 1 for parameter estimates.

6.04, $P = 0.025$), 48°C ($F_{1,23} = 10.88$, $P = 0.003$), and 52°C ($F_{1,21} = 4.68$, $P = 0.042$), although as temperature increased, the slope of this relationship increased toward 0, until at 56°C, there was no relationship between humidity and TEWL ($F_{1,23} = 0.99$, $P = 0.33$; fig. 1*B*; table 2). This may correspond to an increase in the use of gular flutter, which was observed at 52° and 56°C in this species (A. R. Gerson, personal observation). Within each humidity treatment, there was a significant increase in TEWL with increasing temperature (humidity, 3.3 g m^{-3}: $F_{3,37} = 24.87$, $P < 0.001$; humidity, 11.9 g m^{-3}: $F_{3,22} = 43.31$, $P < 0.001$; humidity, 17.9 g m^{-3}: $F_{3,17} = 24.68$, $P < 0.001$; humidity, 26.6 g m^{-3}: $F_{3,19} = 32.08$, $P < 0.001$), and in all cases there was a significant increase in TEWL with each increase in temperature (Tukey's HSD post hoc within each humidity treatment, $P < 0.05$), except between 52° and 56°C, where there was not a significant increase in TEWL at the lowest humidity treatment ($P > 0.05$; fig. 1*B*).

The response of MR to increasing humidity depended on temperature (temperature × humidity: fig. 1*D*; $F_{3,84} = 5.82$, $P = 0.001$) but no overall effect of either independent variable alone. At 44° and 48°C, increasing humidity resulted in a reduction in MR (44°C: $F_{1,17} = 20.908$, $P < 0.001$; 48°C: $F_{1,23} = 5.64$, $P = 0.026$), whereas there was no effect of humidity on MR at 52°C ($F_{1,21} = 0.013$, $P = 0.908$). At 56°C, there was a significant increase in MR with increasing humidity ($F_{1,23} = 6.39$, $P = 0.019$; table 2). Within each humidity treatment, there was a significant increase in MR with temperature only at the highest humidity ($F_{3,19} = 4.69$, $P = 0.013$).

For EHD ratio, there was a significant relationship with both temperature (fig. 1*F*; $F_{3,19} = 24.16$, $P < 0.001$) and humidity ($F_{1,87} = 10.65$, $P = 0.001$), where the EHD ratio decreased with increasing humidity within each temperature and the magnitude of the EHD ratio increased among increasing temperatures. Pairwise comparisons indicate a significant increase in EHD ratio between 44° and 48°C ($P < 0.001$) but not between 48° and 52°C ($P = 0.089$) or between 52° and 56°C ($P = 0.402$).

The response of T_b to increasing humidity depended on temperature (humidity × temperature: fig. 2*B*; $F_{3,84} = 5.96$, $P = 0.001$), and there was a significant relationship between humidity and T_b ($F_{1,84} = 45.38$, $P < 0.001$) as well as a significant relationship between temperature and T_b ($F_{3,19} = 4.64$, $P = 0.013$). There was no relationship between T_b and humidity at 44°C ($F_{1,17} = 1.155$, $P = 0.297$), but at 48°, 52°, and 56°C, there was a positive relationship between T_b and humidity (48°C: $F_{1,23} = 13.594$, $P = 0.001$; 52°C; $F_{1,21} = 10.99$, $P = 0.003$; 56°C: $F_{1,23} = 46.91$, $P < 0.001$). Within each humidity treatment, there was a significant increase in T_b with increasing temperature (humidity, 3.3 g m^{-3}: $F_{3,37} = 4.009$, $P < 0.013$; humidity, 11.9 g m^{-3}: $F_{3,22} = 8.03$, $P < 0.001$; humidity, 17.9 g m^{-3}: $F_{3,17} = 6.47$, $P < 0.001$; humidity, 26.6 g m^{-3}: $F_{3,19} = 11.84$, $P < 0.001$).

Comparisons between Species

Comparisons of MR, TEWL, and T_b between species were conducted only for temperatures of 44° and 48°C because these temperatures were common to both species and the effect of humidity could be assessed over the entire range tested for both species. Given that data could be collected on only two species in this study and the response to humidity at high temperature has not been broadly investigated, phylogenetically informed comparisons could not be made; therefore, interpretations of this comparison must be made cautiously (Garland and Adolph 1994; Garland et al. 2005). That being stated, it is still pertinent to report the differences between these two species in their response to high temperature and

Table 2: Slope (m) and intercept (b) for the relationship of metabolic rate (MR), total evaporative water loss (TEWL), and body temperature (T_b) in response to absolute humidity (g m^{-3}) at each temperature exposure in Namaqua doves

	MR		TEWL		T_b	
Temperature (°C)	m	b	m	b	m	b
44	−.08 (−.12, −.03)	8.57 (7.90, 9.26)	−.16 (−.30, −.01)	20.08 (17.78, 22.39)	−.01 (−.04, .02)	41.36 (40.88, 41.84)
48	−.08 (−.17, .01)	8.62 (7.24, 9.99)	−.39 (−.66, −.11)	33.29 (29.01, 37.56)	.07 (−.01, .15)	40.69 (39.45, 41.93)
52	−.01 (−.12, .09)	8.42 (6.84, 10.01)	−.27 (−.51, −.01)	39.82 (35.90, 43.74)	.03 (−.01, .08)	41.79 (41.11, 42.47)
56	.11 (.02, .20)	7.57 (6.03, 9.09)	.10 (−.13, .33)	42.99 (39.12, 46.86)	.05 (.04, .07)	42.7 (42.43, 42.99)

Note. Values are means, with 95% confidence intervals in parentheses.

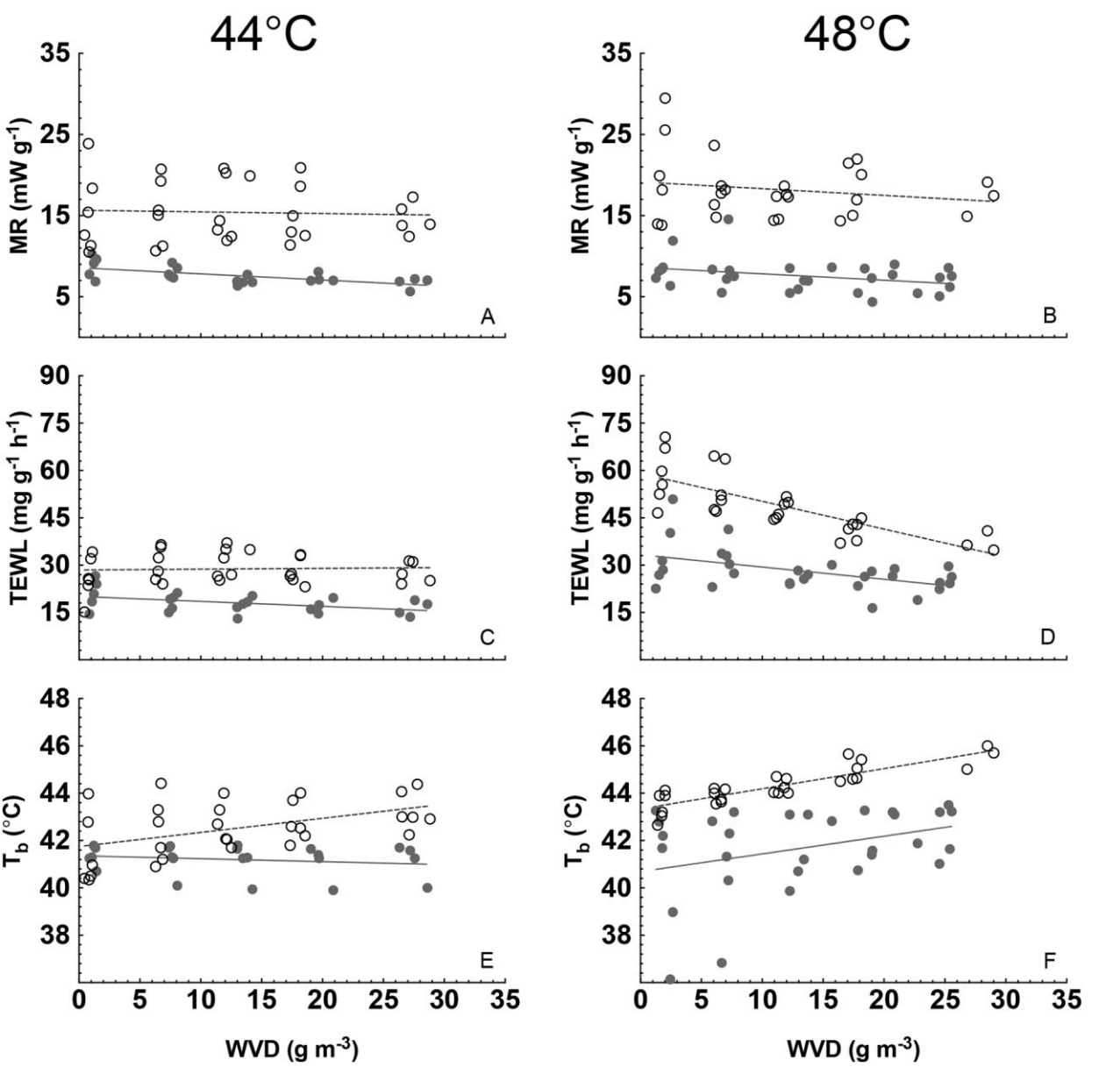

Figure 3. Comparison of the response of metabolic rate (*A*, *B*), evaporative water loss (*C*, *D*), and body temperature (*E*, *F*) to increasing humidity at common temperatures between sociable weavers (dashed lines) and Namaqua doves (solid lines). The left column corresponds to 44°C and the right column to 48°C, the two common exposure temperatures for the species studied. See text for statistical details and table 1 for parameter estimates.

humidity, as that is currently of interest in understanding how these separate species will respond to high-temperature, high-humidity challenges. Since these birds occupy the same habitat but utilize different evaporative pathways at high temperatures, understanding the effectiveness of the evaporative response is essential to understanding how populations of these birds may respond to thermal challenges.

Mass-specific MR was not different between the two temperatures ($F_{1,20} = 2.40$, $P = 0.137$; fig. 3*A*, 3*B*), and overall mass-specific MR was 158% higher in sociable weavers compared to Namaqua doves (weavers: 17.79 ± 2.29 mW g^{-1}, doves: 6.89 ± 1.37 mW g^{-1}; $F_{1,21} = 71.25$, $P < 0.001$). As humidity increased, Namaqua doves reduced MR, while sociable weavers did not (see above).

At 44°C, the TEWL of sociable weavers (28.79 ± 5.06 mg g^{-1} h^{-1}) was 59.7% higher than that of Namaqua doves (18.03 ± 3.28 mg g^{-1} h^{-1}; $F_{1,9} = 35.23$, $P < 0.001$), and there was no effect of humidity on TEWL for either species at this temperature (see above; fig. 3*C*). At 48°C, TEWL was reduced as humidity increased for both species, but TEWL was reduced more in the sociable weavers (species × humidity interaction: $F_{1,43} = 6.34$, $P = 0.016$; table 1; fig. 3*D*). At the lowest humidity, TEWL of sociable weavers (56.49 ± 8.39 mg g^{-1} h^{-1}) was 71.8% higher than that of Namaqua doves (32.89 ±

8.93 mg g^{-1} h^{-1}; $F_{1,21} = 45.00$, $P < 0.001$), whereas this difference at the highest humidity was 53.5% (weavers: 37.34 ± 3.16 mg g^{-1} h^{-1}; doves: 24.33 ± 3.60 mg g^{-1} h^{-1}; $F_{1,7} = 27.90$, $P = 0.001$).

The response of T_b to humidity differed between species and with temperature (temperature × humidity: $F_{1,84} = 18.02$, $P < 0.001$; humidity × species: $F_{1,84} = 9.50$, $P = 0.003$; fig. 3*E*, 3*F*); therefore, the differences between species were assessed within each temperature treatment. At 44°C (fig. 3*E*), the weavers increased T_b in response to humidity, whereas doves did not (species × humidity: $F_{1,40} = 32.22$, $P < 0.001$; table 1 and above). As such, at the lowest humidity, mean T_b was not different between the two species (weavers = 41.94° ± 1.45°C, doves = 41.46° ± 0.40°C; $F_{1,17} = 0.73$, $P = 0.405$), but there was a significant difference at the highest humidity (weavers = 43.26° ± 0.79°C, doves = 41.13° ± 0.77°C; $F_{1,18} = 17.37$, $P = 0.003$). At 48°C (fig. 3*F*), both species increased T_b with increasing humidity ($F_{1,44} = 55.40$, $P < 0.001$), but in all humidity treatments, weavers had higher T_b than doves ($F_{1,10} = 14.39$, $P = 0.003$; see above and table 1 for parameter estimates).

Discussion

Our data confirm that humidity has a strong effect on evaporative heat dissipation by birds experiencing air temperatures above T_b and that patterns of thermoregulation vary substantially depending on the water vapor gradient available for evaporative heat dissipation. Moreover, the effects of humidity on themoregulation vary with the primary avenue of evaporative heat loss, with birds that primarily use respiratory evaporation (e.g., panting) being less sensitive to elevated humidities. Birds living in many deserts are already subject to high air temperatures, large solar heat loads, and often-variable atmospheric humidity. During the coming century these regions will get hotter and the shade air temperatures that characterize the thermal refuges of birds will increasingly exceed avian T_b (Wolf et al. 1996; Meehl et al. 2009; Rahmstorf and Coumou 2011; Diffenbaugh and Field 2013; Joussaume et al. 2013).

Evaporative Heat Loss in Sociable Weavers

Although we investigated the effect of humidity on thermoregulation in just two species, our data suggest that the primary pathway of evaporative heat dissipation (i.e., respiratory or cutaneous) is an important determinant of sensitivity to elevated humidity. In the sociable weaver, a passerine that relies primarily on panting for evaporative cooling, we observed very high rates of evaporative water loss. These high rates of heat dissipation presumably counteracted the internal heat load generated by the high metabolic demand of panting and resulted in low EHD ratios (fig. 1*C*). Rapid panting could result in severe alkalosis (Calder and Schmidt-Nielsen 1966; Robertshaw 2006), exacerbating the physiological challenge of dissipating large heat loads actively. These birds were highly sensitive to humidity at higher temperatures (48° and 52°C), where the combined internal and external heat loads and the reduced evaporative gradient resulted in hyperthermic T_b and high rates of water loss. This suite of responses, although effective at maintaining stable T_b, albeit above the normothermic range, would result in rapid dehydration in the absence of access to free water. These observations suggest that species that rely heavily on panting and respiratory evaporation would have difficulty surviving during extended periods of hot, humid weather, such as during a heat wave that coincides with the summer rainy season, especially if access to free water is restricted. Our data suggest that, at a shade air temperature of 48°C, it would take approximately 2 h for sociable weavers to lose 10% of M_b as water (fig. 4). Under such conditions, birds will be forced to expend energy seeking water in the heat instead of remaining inactive in thermal refugia. Elevated humidity would also result in higher resting T_b, curtailing safety margins for activity-associated increases in T_b (Torre-Bueno 1976). It is thus unlikely that these birds could maintain high activity levels, especially if humidity is high, as the added internal heat load would easily force T_b to lethal limits.

Interestingly, at the lower air temperatures examined (40° and 44°C), evaporative water loss of weavers was not affected by increasing humidity, suggesting a potential trade-off among evaporative cooling pathways. Panting at these temperatures, although less effective than cutaneous evaporation, appears to be unaffected by humidity. Recent developments in computational simulations of heat transfer during REWL in chickens (*Gallus gallus domesticus*) may allow for theoretical investigations into the mechanisms responsible for humidity insensitivity of REWL in passerines, as well as further development of hypotheses regarding the costs or benefits of hyperthermia in regard to evaporative heat dissipation

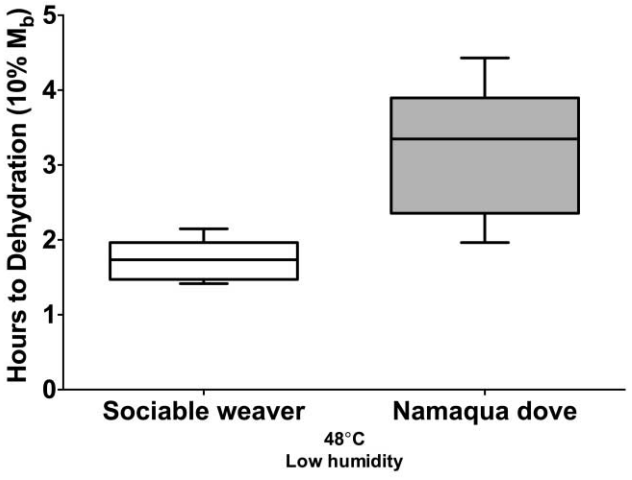

Figure 4. Time to mild dehydration, defined as 10% loss of mass as water, during heat exposure at 48°C and low humidity for sociable weavers and Namaqua doves.

(Sverdlova et al. 2013). Tieleman et al. (1999) have shown significant water savings due to condensation of exhaled water vapor as it passes over evaporatively cooled surfaces of the nasopharynx at relatively cool temperatures (15°, 25°C) but not at higher temperatures. Thus, at high temperatures, such as those investigated in this study, purported water conservation adaptations become secondary to the immediate demands of evaporative thermoregulation.

From an ecological standpoint, within the range of air temperatures and humidities most commonly experienced at the study site, evaporation by panting in conjunction with hyperthermia can compensate for the reduced WVD deficit during periods of high humidity. Recent work on another ploceid, the white-browed sparrow weaver (*Plocepasser mahali*), has revealed population-level adjustment of T_b, where individuals from arid desert populations maintain higher and more variable T_b than conspecifics from semiarid populations (Smit et al. 2013). Therefore, it seems that the use of hyperthermia is a common thermoregulatory strategy that likely results in water savings due to stored heat and a reduced temperature gradient (Tieleman and Williams 1999). Among desert birds the potential link between the effectiveness of evaporation (due to the use of active or passive evaporative pathways) and the degree of hyperthermia utilized in response to high temperatures has not been investigated.

Evaporative Heat Loss in Namaqua Doves

The Namaqua dove, like other Columbiformes (Marder and Ben-Asher 1983; Marder and Arieli 1988; McKechnie and Wolf 2004), relies primarily on CEWL at high temperatures. Although we did not measure REWL and CEWL separately in this study, the general absence of panting and low MRs at high temperatures in Namaqua doves exposed to high air temperatures confirms that this species is qualitatively similar to other columbids in this regard. Cutaneous evaporation minimizes metabolic heat production and may also reduce heat gains through the respiratory tract while ameliorating the risk of alkalosis by minimizing breathing frequency (Marder and Arieli 1988). We found that this species is highly effective at dissipating heat above that generated from metabolism. Evaporation is only marginally inhibited by increasing humidity at all air temperatures except for the highest temperature tested (56°C). In fact, doves actually reduced MR as humidity increased at the lower air temperatures (44° and 48°C). At air temperatures of 52° and 56°C, gular fluttering was employed to varying degrees by birds, mostly at higher humidities. The use of gular flutter at high humidity and air temperatures is reflected by the slight increase in metabolism but did not entail the severe metabolic cost associated with panting because gular flutter only circulates air to the gular pouch located in the throat and may also be insensitive to humidity mainly because of the movement of larger volumes of air, allowing evaporation despite a reduced evaporative gradient (Calder and Schmidt-Nielsen 1966; Bartholomew et al. 1968; Weathers and Schoenbaechler 1976; Robertshaw 2006; Sverdlova et al. 2013).

The effectiveness of cutaneous evaporation apparently precluded the need for hyperthermia as a thermoregulatory response to high temperature. Doves had lower overall rates of evaporative water loss, but because of their exceptionally low metabolic heat loads, this low rate of evaporation was adequate to dissipate heat even at the highest air temperatures tested. Thus, at an air temperature of 48°C, it would take Namaqua doves approximately 4 h to lose 10% of M_b as evaporated water (fig. 4), twice as long as the weavers. Additionally, doves were able to thermoregulate at higher air temperatures and maintained lower T_b at any given air temperature compared to weavers, providing them with a substantial safety margin. The maintenance of lower T_b during extremely hot weather could be a key factor in accommodating the internal heat loads associated with flight and could hence have far-reaching consequences for the temperature dependence of activity patterns. For instance, it was notable during our study that Namaqua doves sometimes fly to distant water sources even on days when T_a exceeded 40°C.

Comparative Performance of Weavers, Doves, and Other Birds

It is difficult to place the response of these two African species in a comparative context because of the lack of overlap in experimental temperature exposure between this study and others and because such comparisons cannot be used to infer adaptation due to the small number of species that have been tested (Garland and Adolph 1994; Garland et al. 2005). However, it is apparent that the evaporative water loss of weavers is less sensitive to humidity at 40° and 44°C when compared to that of hummingbirds, one of the only other taxa that have been investigated. Using the slopes of the regression relating evaporative water loss (mg g^{-1} h^{-1}) to ambient humidity (table 1), evaporative water loss in Anna's hummingbirds appears to be inhibited by the presence of humidity across the range of temperatures from 20° to 37°C (−0.31 to −0.61 mg m^3 g^{-2} h^{-1}; Powers 1992). When compared to ~30-g sociable weavers, which our data suggest are largely humidity insensitive up to 48°C, this represents a dramatic difference among species. Too few data exist currently to examine the relative roles of body mass, phylogeny, or adaptive variation in determining inter- and intraspecific variation in the effects of humidity on thermoregulation at high T_a, but the large differences between our two study species, and between the weavers and hummingbirds, suggest that future studies investigating sensitivity to humidity among species varying in body mass, phylogeny, and habitat may be informative.

The Namaqua doves exposed to $T_a < 50$°C in this study appear very similar to other doves, quail, and domestic fowl in terms of their responses to humidity. There was a very slight reduction in TEWL with increasing humidity at 44° and 48°C (−0.156 to −0.388 mg m^3 g^{-2} h^{-1}), which is similar to pub-

lished values for similar species (approximately -0.10 mg m^3 g^{-2} h^{-1} for *Columbia livia*; Webster and King 1987). Interestingly, in our study at 52°C, the slope increases, and no relationship exists between TEWL and humidity at 56°C. This corresponds to an increase in MR, which is likely a result of the increased use of gular flutter (A. R. Gerson, personal observation). Similar to what was seen at the lower temperatures in the weavers, respiratory evaporation seems to be more metabolically costly, but respiratory evaporation is not inhibited by a reduced vapor pressure gradient.

Conclusions

Although this study was conducted on desert birds, such investigations should also be performed on tropical birds, where humidity may have severe impacts on heat dissipation ability. Although the high temperatures encountered in subtropical deserts do not occur in tropical environments, the combination of high humidity and moderately high temperature does result in wet bulb temperatures that can inhibit heat loss (Sherwood and Huber 2010). Because the metabolic response to humidity at temperatures equal to and above T_b has been investigated in only a few species, it is difficult to put these findings in an evolutionary or adaptive context; thus, it will be important to expand the investigation of the response to temperature and humidity across taxa living in many environments. Only then can the adaptive and evolutionary significance of the reliance on specific evaporative pathways (i.e., cutaneous vs. respiratory) be examined. Rising temperatures associated with global warming in tropical areas may pose a substantial threat to avian diversity in these areas (Quintero and Wiens 2013). However, further investigation into the humidity sensitivity of species in tropical areas may provide new insights into the physiological adaptations of birds to coping with reduced water vapor deficits. Tropical birds may rely more heavily on nonevaporative means of heat dissipation, as evidenced by the evolution of large bills that aid in the radiative dissipation of heat (Tattersall et al. 2009; Greenberg et al. 2012), or tropical birds may simply rely on higher rates of water loss as compensation. Our data expand our understanding of the role of humidity at high environmental temperatures in an ecological context and provide novel methodology for accurately determining rates of TEWL and upper thermal maximum temperatures in response to humidity and temperature using respirometry techniques.

Our data add to a growing body of literature that suggests that, in general, cutaneous evaporation is a more energetically and hygrically efficient way to dissipate large heat loads compared to respiratory mechanisms such as panting. However, a comparison of Namaqua doves and sociable weavers also raises the possibility that cutaneous evaporation may be more sensitive to humidity at higher temperatures compared to respiratory heat dissipation. For birds that rely primarily on cutaneous evaporation, high humidity forces the use of respiratory evaporation to compensate for reductions in evaporative water loss due to a reduced vapor pressure gradient and a reduction in the capacity for evaporation. Birds that rely primarily on respiratory panting, such as the sociable weaver, seem to be less sensitive to humidity over the range of temperatures investigated here but use hyperthermia more extensively than taxa that rely primarily on cutaneous evaporation as temperatures increase.

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Literature Cited

Arad Z., I. Gavrieli-Levin, U. Eylath, and J. Marder. 1987. Effect of dehydration on cutaneous water evaporation in heat-exposed pigeons (*Columba livia*). Physiol Zool 60:623–630.

Bakken G.S. 1976. A heat transfer analysis of animals: unifying concepts and the application of metabolism chamber data to field ecology. J Theor Biol 60:337–384.

Bartholomew G.A. and T.J. Cade. 1963. The water economy of land birds. Auk 80:504–539.

Bartholomew G.A., R.C. Lasiewski, and E.C. Crawford. 1968. Patterns of panting and gular flutter in cormorants, pelicans, owls, and doves. Condor 70:31–34.

Bernstein M.H. 1971. Cutaneous and respiratory evaporation in the painted quail, *Excalfactoria chinensis*, during ontogeny of thermoregulation. Comp Biochem Physiol A 38:611–617.

Calder W.A. and J.R. King. 1974. Thermal and caloric relations of birds. Pp. 259–413 in D.S. Farner and J.R. King, eds. Avian biology. Vol. 4. Academic Press, New York.

Calder W.A. and K. Schmidt-Nielsen. 1966. Evaporative cooling and respiratory alkalosis in the pigeon. Proc Natl Acad Sci USA 55:750–756.

Champagne A.M., A. Muñoz-Garcia, T. Shtayyeh, B.I. Tieleman, A. Hegemann, M.E. Clement, and J. Williams. 2012. Lipid composition of the stratum corneum and cutaneous water loss in birds along an aridity gradient. J Exp Biol 215: 4299–4307.

Chappell M.A., D.L. Goldstein, and D.W. Winkler. 1984. Oxygen consumption, evaporative water loss, and temperature regulation of California gull chicks (*Larus californicus*) in a desert rookery. Physiol Zool 57:204–214.

Crawley M.J. 2005. Statistics: an introduction using R. Wiley, Chichester.

Dawson W.R. 1954. Temperature regulation and water requirements of the brown and Abert towhees, *Pipilo fuscus* and *Pipilo aberti*. Pp. 81–124 in W.H. Furgason, A.M. Bullock, and A.M. Schechtman, eds. University of California Publications in Zoology 59. University of California Press, Berkeley.

———. 1982. Evaporative losses of water by birds. Comp Biochem Physiol A 71:495–509.

Dawson W.R. and G.C. Wittow. 2000. Regulation of body temperature. In G.C. Wittow, ed. Sturkies avian physiology. Academic Press, Oxford.

Diffenbaugh N.S. and C.B. Field. 2013. Changes in ecologically critical terrestrial climate conditions. Science 341:486–492.

Garland T., Jr., and S.C. Adolph. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol Zool 67:797–828.

Garland T., Jr., A.F. Bennett, and E.L. Rezende. 2005. Phylogenetic approaches in comparative physiology. J Exp Biol 208:3015–3035.

Goldstein D.L. 1984. The thermal environment and its constraint on activity of desert quail in summer. Auk 101:542–550.

Greenberg R., V. Cadena, R.M. Danner, and G. Tattersall. 2012. Heat loss may explain bill size differences between birds occupying different habitats. PLoS ONE 7:e40933.

Haugen M., J.B. Williams, P. Wertz, and B.I. Tieleman. 2003. Lipids of the stratum corneum vary with cutaneous water loss among larks along a temperature-moisture gradient. Physiol Biochem Zool 76:907–917.

Hoffman T.C. and G.E. Walsberg. 1999. Inhibiting ventilatory evaporation produces an adaptive increase in cutaneous evaporation in mourning doves *Zenaida macroura*. J Exp Biol 202:3021–3028.

Joussaume S., J. Penner, and F. Tangang, eds. 2013. Climate change 2013: the physical science basis. Working group I contribution to the IPCC fifth assessment report. Final draft underlying scientific-technical assessment. IPCC, Stockholm.

Lasiewski R.C., A.L. Acosta, and M.H. Bernstein. 1966. Evaporative water loss in birds. I. Characteristics of the open flow method of determination, and their relation to estimates of thermoregulatory ability. Comp Biochem Physiol 19:445–457.

Lighton J.R.B. 2008. Measuring metabolic rates. Oxford University Press, New York.

Lovegrove B. 1999. The living deserts of Southern Africa. L. Martin, ed. Fernwood, Vlaeberg.

Marder J. and Y. Arieli. 1988. Heat balance of acclimated pigeons (*Columba livia*) exposed to temperatures up to 60°C T_a. Comp Biochem Physiol A 91:165–170.

Marder J. and J. Ben-Asher. 1983. Cutaneous water evaporation. I. Its significance in heat-stressed birds. Comp Biochem Physiol A 75:425–431.

Marder J. and I. Gavrieli-Levin. 1986. Body and egg temperature regulation in incubating pigeons exposed to heat stress: the role of skin evaporation. Physiol Zool 59:532–538.

———. 1987. The heat-acclimated pigeon: an ideal physiological model for a desert bird. J Appl Physiol 62:952–958.

McKechnie A.E. and B.O. Wolf. 2004. Partitioning of evaporative water loss in white-winged doves: plasticity in response to short-term thermal acclimation. J Exp Biol 207: 203–210.

Meehl G.A., C. Tebaldi, G. Walton, D. Easterling, and L. McDaniel. 2009. Relative increase of record high maximum temperatures compared to record low minimum temperatures in the U.S. Geophys Res Lett 36:L23701.

Muñoz-Garcia A. and J.B. Williams. 2011. Cutaneous water loss and the development of the stratum corneum of nestling house sparrows (*Passer domesticus*) from desert and mesic environments. Physiol Biochem Zool 84:277–286.

Nagy K.A. 1983. The doubly labeled water method: a guide to its use. University of California Press, Los Angeles.

Ophir E., Y. Arieli, J. Marder, and M. Horowitz. 2002. Cutaneous blood flow in the pigeon *Columba livia*: its possible relevance to cutaneous water evaporation. J Exp Biol 205:2627–2636.

Pinheiro J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2001. nlme: linear and nonlinear mixed effects models. R package version 3.1-101.

Powers D.R. 1992. Effect of temperature and humidity on evaporative water loss in Anna's hummingbird (*Calypte anna*). J Comp Physiol B 162:74–84.

Quintero I. and J.J. Wiens. 2013. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecol Lett 16:1095–1103.

Rahmstorf S. and D. Coumou. 2011. Increase of extreme events in a warming world. Proc Natl Acad Sci USA 108: 17905–17909.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ro J. and J.B. Williams. 2010. Respiratory and cutaneous water loss of temperate-zone passerine birds. Comp Biochem Physiol A 156:237–246.

Robertshaw D. 2006. Mechanisms for the control of respiratory evaporative heat loss in panting animals. J Appl Physiol 101: 664–668.

Schmidt-Nielsen K. 1997. Animal physiology. 5th ed. Cambridge University Press, New York.

Sherwood S.C. and M. Huber. 2010. An adaptability limit to climate change due to heat stress. Proc Natl Acad Sci USA 107:9552–9555.

Smit B., C.T. Harding, P.A.R. Hockey, and A.E. McKechnie. 2013. Adaptive thermoregulation during summer in two populations of an arid-zone passerine. Ecology 94:1142–1154.

Sverdlova N.S., F. Arkali, U. Witzel, and S.F. Perry. 2013. Computational fluid dynamics model of avian tracheal

temperature control as a model for extant and extinct animals. Respir Physiol Neurobiol 189:67–75.

Tattersall G.J., D.V. Andrade, and A.S. Abe. 2009. Heat exchange from the toucan bill reveals a controllable vascular thermal radiator. Science 325:468–470.

Tieleman B.I. and J.B. Williams. 1999. The role of hyperthermia in the water economy of desert birds. Physiol Biochem Zool 72:87–100.

———. 2002. Effects of food supplementation on behavioural decisions of hoopoe larks in the Arabian Desert: balancing water, energy and thermoregulation. Anim Behav 63:519–529.

Tieleman B.I., J.B. Williams, G. Michaeli, and B. Pinshow. 1999. The role of the nasal passages in the water economy of crested larks and desert larks. Physiol Biochem Zool 72:219–226.

Torre-Bueno J.R. 1976. Temperature regulation and heat dissipation during flight in birds. J Exp Biol 65:471–482.

Walsberg G.E. and K.A. Voss-Roberts. 1983. Incubation in desert-nesting doves: mechanisms for egg cooling. Physiol Zool 56:88–93.

Walsberg G.E. and B.O. Wolf. 1995. Variation in the respiratory quotient of birds and implications for indirect calorimetry using measurements of carbon dioxide production. J Exp Biol 198:213–219.

Weathers W.W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. Auk 114: 341–353.

Weathers W.W. and D.C. Schoenbaechler. 1976. Contribution of gular flutter to evaporative cooling in Japanese quail. J Appl Physiol 40:521–524.

Webster M.D. and M.H. Bernstein. 1987. Ventilated capsule measurements of cutaneous evaporation in mourning doves. Condor 89:863–868.

Webster M.D., G.S. Campbell, and J.R. King. 1985. Cutaneous resistance to water-vapor diffusion in pigeons and the role of the plumage. Physiol Zool 58:58–70.

Webster M.D. and J.R. King. 1987. Temperature and humidity dynamics of cutaneous and respiratory evaporation in pigeons, *Columba livia*. J Comp Physiol B 157:253–260.

Whitfield M.C. 2014. Evaporative cooling capacity and heat tolerance in Kalahari Desert birds: effects of body mass and phylogeny. MS diss. Department of Zoology and Entomology, University of Pretoria.

Williams J.B. 1996. A phylogenetic perspective of evaporative water loss in birds. Auk 113:457–472.

Williams J.B. and B.I. Tieleman. 2005. Physiological adaptation in desert birds. BioScience 55:416–425.

Wolf B.O. and G.E. Walsberg. 1996. Respiratory and cutaneous evaporative water loss at high environmental temperatures in a small bird. J Exp Biol 199:451–457.

Wolf B.O., K.M. Wooden, and G.E. Walsberg. 1996. The use of thermal refugia by two small desert birds. Condor 98:424–428.