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ORIGINAL PAPER

Avian thermoregulation in the heat: efficient evaporative cooling in two southern African nightjars

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Abstract Nightjars represent a model taxon for investigating physiological limits of heat tolerance because of their habit of roosting and nesting in sunlit sites during the heat of the day. We investigated the physiological responses of Rufous-cheeked nightjars (*Caprimulgus rufigena*) and Freckled nightjars (*Caprimulgus tristigma*) to high air temperatures (T_a) by measuring body temperature (T_b), resting metabolic rate (RMR) and total evaporative water loss (TEWL) at T_a ranging from 10 to 56 °C. Both species became hyperthermic at $T_a > T_b$. Lower critical limits of thermoneutrality occurred at T_a between 35 and 37 °C, whereas we detected no clear upper critical limits of thermoneutrality. Between $T_a \approx 37.0$ and 39.9 °C, rates of TEWL increased rapidly with T_a. At $T_a \geq 40$ °C, fractional increases in mass-specific TEWL rates were 78–106% of allometric predictions. Increasing evaporative heat dissipation incurred only small metabolic costs, with the RMR of neither species ever increasing by more than 20% above thermoneutral values. Consequently, both species displayed extremely efficient evaporative cooling; maximum evaporative heat dissipation was equivalent to 515% of metabolic heat production (MHP) at $T_a \approx 56$ °C in *C. rufigena* and 452% of MHP at $T_a \approx 52$ °C in *C. tristigma*. Our data reiterate that caprimulgids have evolved an efficient mechanism of evaporative cooling via gular fluttering, which minimizes metabolic heat production at high T_a and reduces total heat loads. This likely aids in reducing TEWL rates and helps nightjars cope with some of the most thermally challenging conditions experienced by any bird.

Keywords *Caprimulgus rufigena* · *Caprimulgus tristigma* · Respirometry · Evaporative water loss · Thermoregulation · Resting metabolic rate

Abbreviations

EHL	Evaporative heat loss
M_b	Body mass
MHP	Metabolic heat production
RMR	Resting metabolic rate
T_a	Air temperature
T_b	Body temperature
T_e	Operative temperature
TEWL	Total evaporative water loss
T_{lc}	Lower critical limit of thermoneutrality
T_{uc}	Upper critical limit of thermoneutrality

Introduction

Environmental temperature greatly influences the energy and water demands of an organism and, thereby, affects several components of fitness (McKechnie and Wolf 2010; du Plessis et al. 2012; Cunningham et al. 2013). When exposed to fluctuating air temperatures (T_a), endotherms must physiologically and/or behaviorally adjust heat fluxes to maintain a body temperature (T_b) setpoint (Porter and Gates 1969; Tattersall et al. 2012). Because they are primarily diurnal and non-fossorial, birds living in hot, arid

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environments routinely experience high T_a and intense solar radiation, resulting in operative temperatures (T_e) well above T_b (Bartholomew and Dawson 1979; Walsberg and Voss-Roberts 1983). Under such conditions, evaporative cooling is the only mechanism whereby birds can dissipate heat and avoid lethal hyperthermia (Bartholomew and Cade 1963). As T_a increases above T_b, birds maintain sublethal T_b through concomitant increases in total evaporative water loss (TEWL; Calder and Schmidt-Nielsen 1966; Dawson 1982). However, at very high T_a, TEWL can become substantial (McKechnie and Wolf 2010) and lead to rapid depletion of body water. For example, Wolf and Walsberg (1996) showed that TEWL in Verdins (*Auriparus flaviceps*) increased nearly 14-fold as T_a increased from 30 to 50 °C, and represented ~7% of body mass (M_b) per hour at the latter T_a. In hot, arid environments where drinking water is often scarce, birds thus face a fundamental tradeoff between balancing the need to evaporate large quantities of water to maintain sublethal T_b while at the same time maintaining adequate hydration.

Whereas diurnal birds residing in hot environments can potentially replenish body water throughout the day by drinking and/or feeding on water-rich food, nocturnal species rest during the day and, consequently, can experience sustained periods of elevated TEWL that may lead to significant water deficits (Grant 1982). Many nocturnal taxa, such as owls (Strigidae), minimize their water requirements by occupying relatively cool, shaded sites in trees or cavities, thereby minimizing their need for evaporative cooling (Ligon 1968, 1969; Ganey 2004). Nightjars (Caprimulgidae), in contrast, often roost and nest on the ground in open, exposed sites where they are subjected to intense solar radiation and high T_e that requires long periods with substantial evaporative cooling (e.g., Cowles and Dawson 1951; Dexter 1956; Weller 1958; Bartholomew et al. 1962; Steyn 1971; Grant 1982; Ingels et al. 1984). Grant (1982), for example, observed a female Lesser Nighthawk (*Chordeiles acutipennis*) spend almost 8 h incubating eggs in full sunlight where the black bulb temperature was ~58 °C. Moreover, T_e is typically highest during summer months when day length is longest and periods without access to water may exceed 14 h.

Early studies found that some caprimulgids possess highly efficient evaporative cooling by dissipating large heat loads evaporatively while exhibiting only small increases in resting metabolic rate (RMR; Bartholomew et al. 1962; Dawson and Fisher 1969; Lasiewski and Seymour 1972). However, to the best of our knowledge, no studies evaluating phenotypic variation in RMR and TEWL between seasons (e.g., summer versus winter) or between climatically different sites (e.g., arid versus mesic) have been conducted among caprimulgids. Most comparative research on the thermal physiology of caprimulgids has focused on hypometabolism and the use of torpor as a mechanism for energy savings (Brigham et al. 2012). Given the proclivity of caprimulgids for roosting and nesting in exposed sites that can produce significant heat stress, they present an opportunity to examine the physiological mechanisms that animals use to cope with heat stress in the most energy and water-efficient manner. In addition, individuals of the same species can occur in a range of habitats and thus experience varying environmental temperatures (Cleere and Nurney 1998). Furthermore, some species are non-migratory and are subjected to seasonal fluctuations in T_a. Consequently, they represent a good model taxon for investigating phenotypic flexibility and intraspecific variation in physiological variables related to heat tolerance, an area where avian data are limited (e.g., Noakes et al. 2016).

Here, we investigate the thermal physiology of caprimulgids exposed to high T_a and ask: (1) is there a strong hyperthermic response within species and among populations when exposed to high T_a? (2) Are there pronounced changes in RMR with increasing heat stress and do these values vary among populations within a species? (3) How do rates of TEWL vary with T_a and under conditions of extreme heat within species and among populations? and (4) does the thermoregulatory performance of nightjars vary intraspecifically in a manner correlated with habitat characteristics, with birds from a hot, arid site exhibiting greater heat tolerance via reduced total heat loads (e.g., low RMR), and high ratios of evaporative heat lost (EHL) to metabolic heat production (MHP) at any given T_a compared to conspecifics from a cooler, more mesic site? We also provide preliminary data on seasonal changes in thermoregulatory responses to heat within a species.

We studied two southern African nightjars that roost and nest in sites with high diurnal heat loads (R. S. O'Connor and A. E. McKechnie unpublished data). Rufous-cheeked nightjars (*Caprimulgus rufigena*) are common throughout the arid Nama Karoo and arid savanna regions of southern Africa, where they prefer open woodlands with clearings (Spottiswoode and Jackson 2005a). Rufous-cheeked nightjars nest in natural depressions in coarse soil where shade is minimal or absent (Cleere and Nurney 1998; Spottiswoode and Jackson 2005a). Freckled nightjars (*Caprimulgus tristigma*) are rupiculous breeders, laying their eggs in natural depressions on rocky outcroppings where incubating adults can experience daytime T_e approaching 60 °C (Steyn 1971; Spottiswoode and Jackson 2005b). We investigated the thermoregulatory responses of two populations of Freckled nightjars, one from a hot, arid site that experiences predominantly winter rainfall and another from a more mesic site characterized by summer rainfall.

Materials and methods

Study species and sites

Rufous-cheeked nightjars were captured on the properties Dronfield (28°39′S, 24°48′E, ~1218 m ASL) and Benfontein (28°48′S, 24°48′E, ~1170 m ASL) near Kimberley, South Africa during three separate periods (October 2013, October 2014 and March 2015). These field sites are ~26 km apart, and Rufous-cheeked nightjars were found in similar habitat and vegetation on both reserves, consisting of arid savannah grassland interspersed with *Vachellia erioloba* woodlands. During October and March, average rainfall in Kimberley is approximately 40 mm and average daily maximum T_a is 29.7 °C (South African Weather Service data from 2000 to present).

Freckled nightjars were captured at two sites over two summers and one additional winter period. The first site, which represents an arid climate and where individuals belong to the subspecies *C. t. lentiginosus*, was on a privately owned farm in the northern Kamiesberg Mountains in the Namaqualand region of the Northern Cape province, South Africa (30°02′S, 17°57′E, ~789 m ASL; same study site as described by Smit et al. 2011) during December 2013 and from December 2014 to March 2015. This site lies within the arid succulent Karoo ecoregion of western South Africa and is characterized by winter rainfall (Smit et al. 2011). Average rainfall in Namaqualand from December to March equals 8.5 mm and average daily maximum T_a is 29.2 °C (South African Weather Service data from 2000 to present). The second summer site (subspecies *C. t. granosus*), which represents a mesic climate, was Ezemvelo Nature Reserve (25°42′S, 28°59′E, ~1415 m ASL), near Bronkhorstspruit, Gauteng province, South Africa, with birds captured during November 2014. We captured additional individuals at Ezemvelo during the austral winter between 10 May and 11 June 2014. Ezemvelo is situated between the grassland and savannah biomes and consists of open grassland interspersed with rocky sandstone outcroppings and isolated woodland (Boyles et al. 2012). Average rainfall in Bronkhorstspruit during November equals 94.9 mm and average daily maximum T_a is 28.3 °C. During May and June, average rainfall in Bronkhorstspruit equals 12.3 mm and average daily maximum T_a is 22.5 °C (South African Weather Service data from 2009 to present).

Rufous-cheeked nightjars and Freckled nightjars were captured at night by luring birds into mist nets using playback of conspecific calls or using a handheld net to catch birds resting on roads. Following capture, nightjars were held for 1–2 nights in an enclosure (60 × 71 cm) constructed of PVC piping and shade cloth. Individuals held for multiple nights were hand-fed a diet of wet dog food, mealworms and water, as nightjars do not readily feed in captivity (Dawson and Fisher 1969; Withers 1977). To minimize the time birds spent in captivity, all physiological measurements were conducted in the field using portable equipment.

Measurements of body temperature, resting metabolic rate, and evaporative water loss

Body temperature was measured using temperature-sensitive passive integrated transponder (PIT) tags (Biomark, Boise ID, USA) injected into the peritoneal cavity. Prior to the study, a subset of 70 PIT tags was compared to thermocouple values (type T, Physitemp, Clifton, NJ, USA) in a circulating water bath at temperatures ranging from 39 to 46 °C (Whitfield et al. 2015). PIT tags deviated from thermocouple readings by 0.02 ± 0.09 °C (mean ± SD; Whitfield et al. 2015). We recorded T_b using a portable transceiver system (model 2001F-ISO, Biomark, Boise, ID, USA) connected to an external racket antenna placed within 10 cm of the metabolic chamber housing the study animal. PIT tag readings were logged every 15 s on a personal computer during respirometry trials.

We used open flow-through respirometry to measure the rates of carbon dioxide production ($\dot{V}_{CO_2}$) and TEWL of nightjars over a range of T_a spanning 10–56 °C. Individuals were placed in metabolic chambers with volumes of 9 l (*C. tristigma* and *C. rufigena*) or 4.6 l (*C. rufigena*) constructed from plastic containers. A 1-cm layer of mineral oil at the bottom of each metabolic chamber prevented evaporation from urine and feces affecting evaporative water loss estimates. A mesh platform with spaces large enough for feces to fall through was positioned above the mineral oil. Metabolic chambers were placed inside a modified ice chest (~75 l) fitted with a Peltier device (model AC-162, TE Technology Inc., Traverse City, MI, USA) and a custom-built controller (TC-36-25-RS486 and MP-2986) to regulate T_a (typically ±0.1 °C) inside the animal chamber. Air temperature inside each metabolic chamber was measured using a thermistor probe (model TC-100, Sable Systems, Las Vegas, NV, USA) inserted through a small hole in the lid and secured in place with a rubber grommet.

Atmospheric air was supplied to metabolic chambers by an air pump (model DOA-P13- BN, Gast Air Pumps, Benton Harbor, MI, USA) with a maximum output of ~30 L min^{-1}. Both before entering and after exiting the pump, atmospheric air was scrubbed of water vapor by passing the air stream through columns of silica gel and drierite connected in series. Once scrubbed of water vapor, the airstream was split into two channels with one used as a baseline gas and the other directed to the animal chamber. Baseline flow rates were controlled using a needle valve (model RFU 482-1/8, Camozzi, Brescia, Italy), whereas chamber flow rates were controlled with an Alicat mass-flow controller (model MCP-50SLpm-D/5M, Alicat Scientific Inc., Tucson, AZ, USA). To enhance the mixing of air within each chamber, a 90° fitting was attached at the air inlet and directed air towards the corner of the chamber. This directed the incurrent air stream away from the air outlet port, as well as preventing incurrent air from blowing directly onto the bird. Flow rates varied between approximately 1 and 30 l min^{-1}, depending on the experimental T_a. At lower T_a values when birds were not heat stressed, we used Eq. 4 of McNab (2006) to determine the "critical" flow rate, the minimum flow rate required for the complete mixing of gases in a given chamber volume. Flow accuracy ranged from ±11% at 1 l min^{-1} to ≤±3% at flow rates above 5 l min^{-1}. At higher T_a approaching and exceeding T_b, flow rates were regulated to keep chamber humidity below a dew point of −5 °C (relative humidity of ≈10% at 30 °C). Higher flow rates (and hence lower chamber humidity) aided in keeping birds calm when exposed to high T_a (Whitfield et al. 2015). Using Lasiewski's et al. (1966) equation for estimating chamber equilibrium times indicated that at the flow rates used at $T_a \geq 30$ °C mean chamber equilibrium times averaged 4.0 ± 2.0 min for the 4.6 l chamber and 7.0 ± 3.9 min for the 9 l chamber.

Excurrent air from the metabolic chamber and a baseline channel of incurrent air were sequentially subsampled using a MUX Flow-Multiplexer (Sable Systems, Las Vegas, NV, USA) in manual mode. At the start of each set of gas exchange measurements, baseline air was first subsampled for 5 min, followed by excurrent air from the metabolic chamber for 10–15 min. Birds experienced a ramped profile of increasing T_a (see below), and we subsampled baseline air for 3 min during each period when T_a was increasing, resulting in approximately four baselines per run. The subsampled air was pulled through a CO_2/H_2O gas analyzer (model LI-840A, LI-COR, Lincoln, NE, USA) and an O_2 analyzer that also measured barometric pressure (FC—10 Oxygen Analyzer, Sable Systems, Las Vegas, NV, USA). Gas analysers were calibrated using the same techniques as Whitfield et al. (2015). All tubing used in the system was Bev-A-Line tubing (Thermoplastic Processes Inc., Warren, NJ, USA). Voltage outputs from analyzers were digitized using a Universal Interface (model UI-2, Sable Systems, Las Vegas, NV, USA) and recorded at a sampling interval of 5 s using a personal computer with Expedata software (Sable Systems, Las Vegas, NV, USA).

Experimental protocol

All respirometry measurements took place during the day, the rest phase of nightjars and the time during which they naturally experience high T_a. Prior to being placed inside the metabolic chamber, birds were given water (~3.0–4.0 ml) with a syringe to ensure that they were well hydrated. After being placed in the chamber, birds initially spent 30 min at $T_a \approx$ 25–28 °C to habituate. Respirometry runs were separated into low (T_a = 10, 15, 20 and 25 °C) and high ($T_a \geq 30$ °C) T_a groups, with the experimental protocol varying depending on the T_a group. At low T_a, nightjars were held at a T_a set point for ~3 h before T_a was changed. In addition, birds were only measured at two different T_a values during the low T_a runs (e.g., at 10 and 15 °C or at 20 and 25 °C). Thus, for low T_a runs, birds were typically in the metabolic chamber for ~6 h. Air temperature changes during low T_a trials occurred in 5 °C increments with the first T_a set point and direction of T_a change (i.e., increase or decrease) randomized (e.g., 10–15 °C or 15–10 °C). For measurements at high T_a, we used a ramped T_a profile starting at 30 °C with subsequent T_a increases to 35, 38 and 40 °C. Above 40 °C, T_a was increased in 2 °C increments. When chamber T_a reached a stable value, birds were held at each T_a set point for 10–15 min. Runs were terminated based on the same criteria used by Whitfield et al. (2015), and thus, the duration an individual was kept in the chamber (average ≈159 min) depended on their heat stress responses. Among species, nightjars lost on average 4.5 ± 2.3 g (6.6 ± 3.1% of M_b) during high T_a trials. The behavior of birds during each trial was continuously monitored using an infrared camera and light, allowing us to determine whether birds were calm or exhibiting signs of distress and attempts to escape (Whitfield et al. 2015). Upon removal from the chamber, birds were immediately weighed and then given water and held in front of a fan if necessary. Once T_b decreased to normothermic levels (38–40 °C) birds were returned to the enclosure and then released at their site of capture that night.

Although our measurements of EWL, RMR and T_b over short periods at each T_a set point could be criticized as not representing steady-state physiological data, the ramped temperature protocol we used here is in many ways analogous to the sliding cold exposure method used in summit metabolism studies (Swanson et al. 1996); as is the case when exposing birds to very low temperatures for the purposes of measuring the upper limits of cold tolerance, it is simply not practical to expose birds to T_a far above T_b for extended periods. Moreover, our methods follow those of several recent studies (e.g., Smith et al. 2015; Whitfield et al. 2015; McKechnie et al. 2016a, b), and therefore, the data we present here are directly comparable to those presented by these authors.

Data analyses

Carbon dioxide and H_2O traces were corrected for drift using the appropriate algorithms in Expedata. Resting values of $\dot{V}_{CO_2}$, TEWL, and T_b were taken as the average of the lowest, most stable 5-min period from CO_2 traces at each T_a set point. Data from birds that did not remain calm for 5 min at a T_a set point were excluded from analyses. Excurrent flow rates from metabolic chambers were calculated using Eq. 9.3 of Lighton (2008). Rates of $\dot{V}_{CO_2}$ and TEWL were calculated using Eqs. 9.5 and 9.6, respectively, of Lighton (2008). To convert ml H_2O into mg H_2O, we assumed 0.803 mg H_2O ml^{-1} water vapor (Lighton 2008). We calculated RMR [Watts (W)] assuming 27.8 kJ l CO_2^{-1} and a respiratory exchange ratio (RER) of 0.71 (i.e., lipid metabolism; Withers 1992). Evaporative heat loss (*W*) was calculated assuming 2.40 J mg H_2O^{-1} (Withers 1992).

All statistical analyses were conducted in R 3.2.1 (R Core Team 2015) with all values reported as mean ± standard deviation (SD). We fit broken-stick regression models using the ‘piecewise.linear’ function in the package *SiZer* (Sonderegger 2012) to identify inflection points in our T_b, RMR, TEWL, and EHL/MHP response variables. Data were subsequently split based on inflection points, and we fitted linear mixed-effects models to the data using the packages *lme4* (Bates et al. 2015) and *nlme* (Pinheiro et al. 2015) with T_b, RMR, TEWL and EHL/MHP included as response variables and T_a, sex, and M_b as predictor variables. In addition, because we had data from two different field sites over both summer and winter, we included site and season as predictor variables in our analysis of the data for Freckled nightjars. One Freckled nightjar (hereafter: bird 5599) had abnormally high RMR values between $T_a \approx 30–35$ °C and 38–52 °C and the mixed-effects models at these T_a ranges had Cook’s distances of 2.3 and 4.3, respectively, indicating that the data for this individual were highly influential on model parameter estimates (Quinn and Keough 2002). Thus, bird 5599 was ultimately excluded from the final analyses. In all models, individual identity was included as a random factor due to having repeated measurements on the same individual. Furthermore, because we collected data in three different periods spanning two summers for Rufous-cheeked nightjars and in two different periods over two summers for Freckled nightjars, we included capture period as a random factor in our models to account for any variation between periods. All models were initially run as maximal models with all predictors and their interactions included. The best models were selected based on Akaike Information Criterion adjusted for small sample sizes (AIC_c) using the ‘dredge’ function in the package *MuMIn* (Bartoń 2015). Models with AIC_c values differing by less than 2 (i.e., $\Delta AIC_c < 2$) were treated as fitting the data equally well, and consequently, the most parsimonious model was selected as the minimal adequate model (Quinn and Keough 2002; Crawley 2007). Residuals of our minimal adequate models were graphically inspected to ensure they met assumptions of normality and homogeneity of variance. Occasionally, our data violated these assumptions due to outliers and we avoided transformations to conserve patterns in relationships and decided to use robust regression analyses for linear mixed models using the package *robustlmm* (Koller 2015). Because *lme4* (Bates et al. 2015) does not inherently provide *P* values in its output (Bates 2006), we computed 95% confidence intervals (95% CI) for all fixed effects in our minimal adequate models using the function ‘confint.merMod’ in *lme4* (Bates et al. 2015). We assumed a significance of less than 5% ($P < 0.05$) if the 95% CI did not include the value of zero (Faraway 2006; du Prel et al. 2009). For each fixed effect in the minimal adequate model, we report the estimate and accompanying standard error (SE) and 95% CI.

Results

Body mass

A total of 25 Rufous-cheeked nightjars were captured over the three study periods. The average M_b of males and females the morning before measurements was 52.2 ± 4.5 and 53.9 ± 4.1 g, respectively. Prior to measurements, average M_b for summer Namaqualand Freckled nightjars was 64.7 ± 6.3 g ($n = 24$) and average M_b for summer Ezemvelo Freckled nightjars was 79.7 ± 4.4 g ($n = 5$), representing a significant between-population difference [95% CI = (−17.1, −5.1)]. Freckled nightjars at Ezemvelo were significantly ($F_{1,15} = 22.64$, $P < 0.001$) heavier in winter (88.1 ± 2.8 g, $n = 12$) compared to summer.

Body temperature

At $T_a \leq 15$ °C, Rufous-cheeked nightjar T_b averaged 37.9 ± 0.7 °C ($n = 5$). At $20 \leq T_a \leq 50$ °C, the minimal adequate model only included T_a [0.120 ± 0.008 °C °C^{-1}, (0.104, 0.136); Fig. 1a]. Body temperature increased from 38.2 ± 1.0 °C ($n = 9$) at $T_a \approx 20$ °C to 41.7 ± 0.6 °C at $T_a \approx 50$ °C ($n = 6$). At $T_a \geq 50$ °C, T_b stabilized at 41.6 ± 0.6 °C ($n = 16$, Fig. 1a).

At $10 \leq T_a \leq 30$ °C, T_b of Freckled nightjars from Namaqualand averaged 38.7 ± 0.8 °C ($n = 20$, Fig. 1b). Body temperature in Namaqualand Freckled nightjars had a significant inflection point at $T_a = 32.4$ °C (0.107, 0.263), above which T_b increased with T_a (Fig. 1b). Between $T_a \approx 35$ and 52 °C, there was no difference in T_b between Namaqualand and summer Ezemvelo nightjars [0.659 ± 0.427 °C, (−0.279, 1.534)], with T_b increasing at 0.140 ± 0.008 °C °C^{-1} [(0.124, 0.155), Fig. 1b]. For Namaqualand nightjars, T_b increased from 38.8 °C ($n = 10$) at $T_a \approx 35$ °C to 40.7 °C at $T_a \approx 52$ °C ($n = 2$). Similarly, between $T_a \approx 35$ and 52 °C, summer Ezemvelo nightjar T_b increased from 38.7 °C ($n = 4$) to 40.5 °C ($n = 2$).

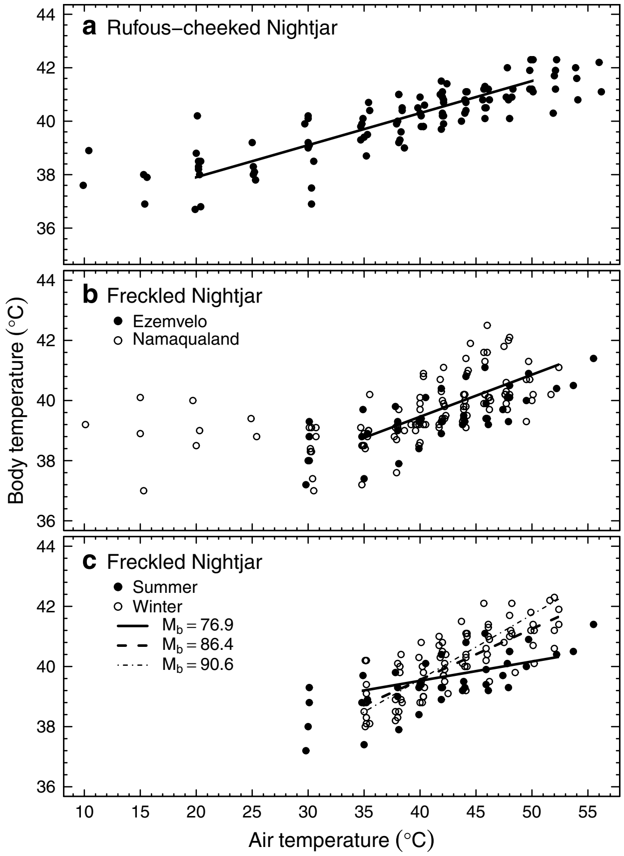

Fig. 1 Body temperature (T_b) as a function of air temperature (T_a) in **a** Rufous-cheeked nightjars (*Caprimulgus rufigena*), **b** Freckled nightjars (*Caprimulgus tristigma*) from a mesic (Ezemvelo) and arid (Namaqualand) site and **c** Freckled nightjars from Ezemvelo during summer and winter. The regression line in **a** is a linear model fitted to T_b versus T_a. In **b**, the regression line represents the slope from a linear model fitted to T_b versus T_a. In **c**, regression lines represent the slopes from a linear model fitted to T_b versus the interaction between T_a and body mass (M_b). The M_b values used represent cross sections at the 10th, 50th, and 90th percentiles of the M_b variable

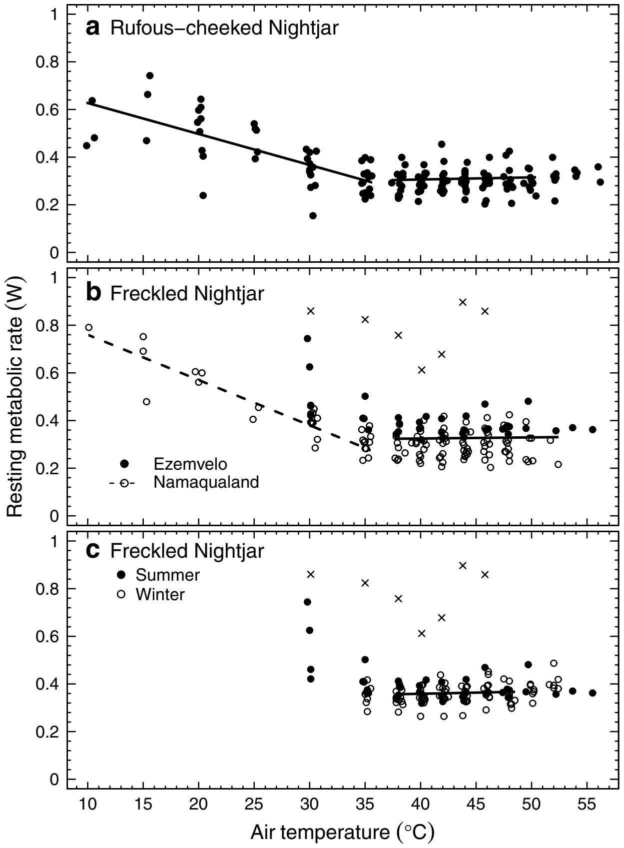

Fig. 2 Resting metabolic rate (RMR) as a function of air temperature (T_a) in **a** Rufous-cheeked nightjars (*Caprimulgus rufigena*), **b** Freckled nightjars (*Caprimulgus tristigma*) from a mesic (Ezemvelo) and arid (Namaqualand) site and **c** Freckled nightjars from Ezemvelo during summer and winter. In **a**, the regression lines between $T_a \approx$ 10–35 °C and 38–50 °C are from two linear models fitted to RMR versus T_a. In **b**, the regression line between $T_a \approx$ 10–35 °C is from a linear model fitted to RMR versus T_a in Namaqualand birds and the horizontal regression line is from a linear model fitted to RMR versus T_a. In **c**, the regression line is from a linear model fitted to RMR versus T_a. The outlier bird 5599 is marked with an *X* in **b**, **c**

Between $T_a \approx 35$ and 52 °C, the minimal adequate model explaining T_b among Ezemvelo Freckled nightjars included T_a ($F_{1,95} = 388.21$, $P < 0.0001$), M_b ($F_{1,15} = 0.56$, $P = 0.464$) and the interaction between T_a and M_b ($F_{1,95} = 34.74$, $P < 0.0001$; Fig. 1c). At $35 \leq T_a \leq 52$ °C, T_b of Ezemvelo Freckled nightjars did not differ between summer and winter ($F_{1,15} = 2.31$, $P = 0.150$; Fig. 1c), with mean winter $T_b = 40.1 \pm 1.1$ °C ($n = 83$) and summer $T_b = 39.5 \pm 0.8$ °C ($n = 31$).

Resting metabolic rate

At $10 \leq T_a \leq 35$ °C, the minimal adequate model for RMR in Rufous-cheeked nightjars only included T_a [-0.013 ± 0.002 W °C^{-1}, (-0.016, -0.010); Fig. 2a]. Resting metabolic rate decreased from 0.52 ± 0.1 W at $T_a \approx 10$ °C ($n = 3$) to 0.30 ± 0.06 W at $T_a \approx 35$ °C ($n = 15$). A significant inflection point in RMR occurred at $T_a = 35.8$ °C (0.010, 0.020), which we interpret as the lower critical limit of thermoneutrality (T_{lc}). At $38 \leq T_a \leq 50$ °C, the minimal adequate model only included sex (-0.133, -0.056), with females having a higher RMR (0.375 ± 0.051 W, $n = 12$) than males (0.284 ± 0.034 W, $n = 70$). At T_a between 38 and 50 °C, RMR did not vary with T_a [0.0009 ± 0.0006 W °C^{-1}, (-0.0003, 0.002); Fig. 2a].

For Namaqualand Freckled nightjars, the minimal adequate model for RMR at $10 \leq T_a \leq 35$ °C included T_a [-0.020 ± 0.001 W °C^{-1}, (-0.022, -0.018)] and M_b [0.009 ± 0.002 W g^{-1}, (0.005, 0.012)]. At $T_a \approx 10$ °C, RMR in Namaqualand Freckled nightjars was 0.79 W and decreased to 0.31 ± 0.04 W ($n = 11$) at $T_a \approx 35$ °C. An inflection point in RMR for Namaqualand Freckled nightjars occurred at $T_a = 35.1$ °C (0.013, 0.025) and for summer Ezemvelo Freckled nightjars at $T_a = 36.6$ °C [(0.009, 1.104); Fig. 2b], which we interpret as the T_{lc}.

At $38 \leq T_a \leq 52$ °C, the minimal adequate model explaining variation in RMR between Ezemvelo and Namaqualand Freckled nightjars only included M_b [0.005 ± 0.001 W g^{-1}, (0.003, 0.008)]. Over the same T_a range, RMR remained stable with increasing T_a [0.0005 ± 0.0008 W $°C^{-1}$, (−0.001, 0.002); Fig. 2b], averaging 0.37 ± 0.04 W ($n = 27$) in Ezemvelo Freckled nightjars and 0.30 ± 0.06 W ($n = 81$) in Namaqualand nightjars. When the data were analyzed using mass-specific values between $T_a \approx 38$ and 52 °C, T_a [0.008 ± 0.011 mW g^{-1} $°C^{-1}$, (−0.014, 0.030)] and site [0.095 ± 0.326 mW g^{-1}, (−0.791, 0.676)] remained non-significant. Mass-specific RMR between $T_a \approx 38$ and 52 °C for Namaqualand nightjars was 4.48 ± 0.70 mW g^{-1} and for summer Ezemvelo nightjars 4.70 ± 0.42 mW g^{-1}.

At $38 \leq T_a \leq 48$ °C, the null model emerged as the top model for RMR in summer and winter Ezemvelo Freckled nightjars. Over this T_a range, RMR did not vary with T_a [0.0009 ± 0.0007 W $°C^{-1}$, (−0.0004, 0.002); Fig. 2c], nor did it differ between seasons [(−0.055, 0.022); Fig. 2c], with mean winter RMR = 0.35 ± 0.04 W ($n = 61$) and mean summer RMR = 0.37 ± 0.03 W ($n = 24$). Winter Ezemvelo birds displayed a shallow inflection point in RMR at $T_a = 49.5$ °C (−0.004, 0.061), with RMR increasing to 0.41 ± 0.04 W ($n = 6$) at $T_a \approx 52$ °C (Fig. 2c). Mass-specific RMR between $T_a \approx 38$ and 48 °C was significantly higher in summer than winter among Ezemvelo birds ($F_{1,15} = 12.463$, $P = 0.003$), with mass-specific RMR values of 4.68 ± 0.36 and 4.0 ± 0.44 mW g^{-1}, respectively.

Evaporative water loss

Between $T_a \approx 10$ and 38 °C, the minimal adequate model for TEWL in Rufous-cheeked nightjars only included T_a [0.007 ± 0.001 g H_2O h^{-1} $°C^{-1}$, (0.005, 0.009); Fig. 3a]. At $T_a \approx 10$ °C, TEWL averaged 0.10 ± 0.04 g H_2O h^{-1} ($n = 3$) and increased to 0.28 ± 0.05 g H_2O h^{-1} at $T_a \approx 38$ °C ($n = 13$). A significant inflection point in TEWL occurred at $T_a = 39.5$ °C (0.088, 0.119), above which TEWL increased rapidly (Fig. 3a). Between $T_a \approx 40$ and 56 °C, the minimal adequate model for TEWL only included T_a [0.099 g H_2O h^{-1} $°C^{-1}$, (0.093, 0.105); Fig. 3a], with TEWL reaching 2.49 ± 0.24 g H_2O h^{-1} ($n = 2$) at $T_a \approx 56$ °C.

Total evaporative water loss for Freckled nightjars from Namaqualand remained low and stable at $10 \leq T_a \leq 25$ °C, averaging 0.14 ± 0.03 g H_2O h^{-1} ($n = 9$). Significant inflection points in TEWL occurred at $T_a = 38.3$ °C (0.074, 0.110) for Namaqualand nightjars and at $T_a = 37.0$ °C (0.091, 0.183) for summer Ezemvelo nightjars, above which TEWL increased rapidly (Fig. 3b).

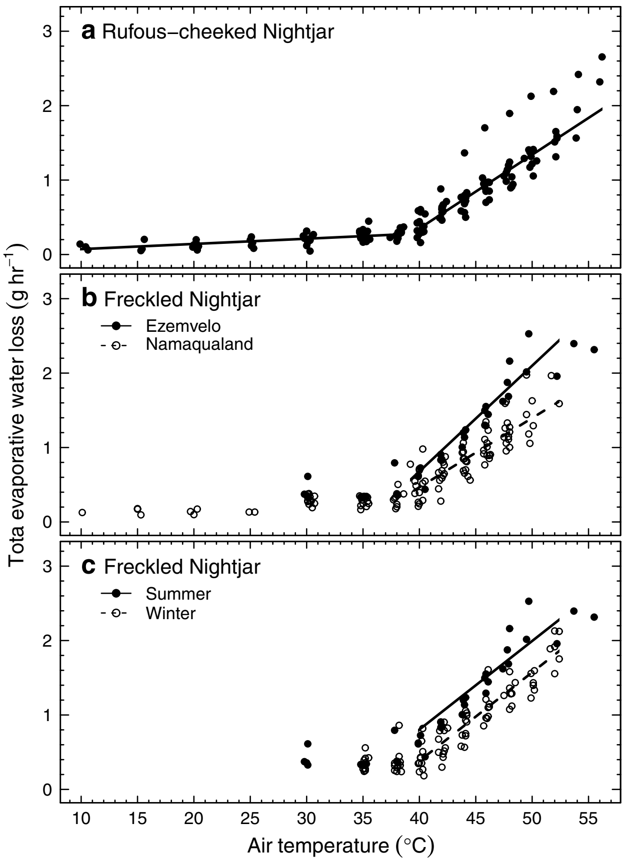

Fig. 3 Total evaporative water loss (TEWL) as a function of air temperature (T_a) in **a** Rufous-cheeked nightjars (*Caprimulgus rufigena*), **b** Freckled nightjars (*Caprimulgus tristigma*) from a mesic (Ezemvelo) and arid (Namaqualand) site and **c** Freckled nightjars from Ezemvelo during summer and winter. In **a**, the regression lines between $T_a \approx 10$–38 °C and 40–56 °C are from two linear models fitted to TEWL versus T_a. In **b**, regression lines are from a linear model fitted to TEWL versus the interaction between site and T_a. In **c**, regression lines represent the common regression slope from a linear model fitted to TEWL versus season with T_a as a covariate

The minimal adequate model explaining summer TEWL at $40 \leq T_a \leq 52$ °C in Ezemvelo and Namaqualand Freckled nightjars included T_a [0.142 ± 0.010 g H_2O h^{-1} $°C^{-1}$, (0.123, 0.163)], site [1.747 ± 0.523 g H_2O h^{-1}, (0.742, 2.802)] and the interaction between T_a and site [−0.049 ± 0.011 g H_2O h^{-1} $°C^{-1}$, (−0.072, −0.026); Fig. 3b]. The slope of the interaction between T_a and site for Namaqualand birds was 0.093 g H_2O h^{-1} $°C^{-1}$ and for Ezemvelo birds was 0.142 g H_2O h^{-1} $°C^{-1}$. At $T_a = 40$–52 °C, average summer TEWL was lower in Namaqualand nightjars (0.91 ± 0.38 g H_2O h^{-1}, $n = 73$) compared to Ezemvelo nightjars (1.31 ± 0.55 g H_2O h^{-1}, $n = 23$). For Namaqualand Freckled nightjars, TEWL = 0.13 g H_2O h^{-1} at 10 °C, increasing to

1.78 ± 0.27 g H_2O h^{-1} ($n = 2$) at 52 °C. For summer Ezemvelo Freckled nightjars, TEWL = 0.42 ± 0.13 g H_2O h^{-1} ($n = 4$) at $T_a \approx 30$ °C, increasing to 2.32 g H_2O h^{-1} at 56 °C. Between $40 \leq T_a \leq 52$ °C, the minimal adequate model for mass-specific TEWL included T_a (1.488 ± 0.072 mg H_2O g^{-1} h^{-1} °C^{-1}, (1.349, 1.636)] and site (−5.164, −1.096), with mass-specific TEWL averaging 13.51 ± 5.44 mg H_2O g^{-1} h^{-1} in Namaqualand birds and 16.41 ± 6.85 mg H_2O g^{-1} h^{-1} in summer Ezemvelo birds.

Among Ezemvelo Freckled nightjars, TEWL at $T_a < 40$ °C remained low and stable in both winter and summer (Fig. 3c). There was a significant inflection point in winter TEWL at $T_a = 39.9$ °C (0.078, 0.151), above which TEWL increased rapidly (Fig. 3c). The minimal adequate model for TEWL among Ezemvelo Freckled nightjars at $T_a \approx 40$–52 °C included T_a (0.119 ± 0.004 g H_2O h^{-1} °C^{-1}, $F_{1,67} = 781.515$, $P < 0.0001$) and season ($F_{1,15} = 24.665$, $P < 0.001$). Mean TEWL was higher in summer (1.31 ± 0.55 g H_2O h^{-1}, $n = 23$) than winter (0.98 ± 0.48 g H_2O h^{-1}, $n = 62$, Fig. 3c). Winter TEWL = 0.35 ± 0.10 g H_2O h^{-1} at $T_a \approx 35$ °C ($n = 10$) and increased to 1.90 ± 0.22 g H_2O h^{-1} at 52 °C ($n = 6$). The minimal adequate model for mass-specific TEWL between $T_a \approx 40$ and 52 °C included T_a ($F_{1,66} = 811.814$, $P < 0.0001$), season ($F_{1,15} = 42.272$, $P < 0.0001$) and the interaction between T_a and season ($F_{1,66} = 14.552$, $P < 0.001$). Mass-specific TEWL averaged 11.21 ± 5.60 mg H_2O g^{-1} h^{-1} for winter birds and 16.41 ± 6.85 mg H_2O g^{-1} h^{-1} in summer birds between $T_a \approx 40$–52 °C.

Ratio of evaporative heat loss to metabolic heat production

In Rufous-cheeked nightjars, at T_a below thermoneutrality EHL/MHP increased significantly and linearly with T_a [0.020 ± 0.002 °C^{-1}, (0.016, 0.023); Fig. 4a] from 0.13 ± 0.07 at 10 °C ($n = 3$) to 0.63 ± 0.10 at 38 °C ($n = 13$). The slope of EHL/MHP versus T_a changed significantly at $T_a = 39.2$ °C (0.176, 0.234), corresponding to rapid increases in TEWL. Between $T_a \approx 40$ and 56 °C, the minimal adequate model for EHL/MHP only included T_a [0.214 ± 0.009 °C^{-1}, (0.196, 0.233); Fig. 4a]. At $T_a \geq 44$ °C, all birds were dissipating more than 100% of MHP through evaporation. At $T_a \approx 56$ °C, mean EHL/MHP = 5.15 ± 1.2 ($n = 2$; Fig. 4a).

In Freckled nightjars at our Namaqualand study site, EHL/MHP remained low between $T_a \approx 10$ and 25 °C, with EHL/MHP = 0.11 at $T_a \approx 10$ °C and 0.21 ± 0.02 at $T_a \approx 25$ °C ($n = 2$). Rapid increases in EHL/MHP occurred above $T_a = 38.5$ °C (0.165, 0.269) and above $T_a = 36.8$ °C (0.138, 0.286) in Namaqualand and summer Ezemzelo Freckled nightjars, respectively. At $40 \leq T_a \leq 52$ °C, the minimal adequate model for EHL/MHP included T_a [0.230 ± 0.008 °C^{-1}, (0.213, 0.246)] and site [−0.535 ± 0.190, (−0.907, −0.163)], with Ezemvelo nightjars having higher EHL/MHP values (Fig. 4b). In Namaqualand Freckled nightjars, maximum EHL/MHP was 4.5 ± 0.5 at $T_a \approx 52$ °C ($n = 2$).

For winter Ezemvelo Freckled nightjars, EHL/MHP increased rapidly above $T_a = 39.8$ °C [(0.118, 0.248); Fig. 4c]. The minimal adequate model for EHL/MHP between $T_a \approx 40$ and 52 °C included season ($F_{1,15} = 24.568$, $P < 0.001$), T_a ($F_{1,66} = 922.255$, $P < 0.0001$) and the interaction between season and T_a ($F_{1,66} = 12.597$, $P < 0.001$; Fig. 4c). The slope of the

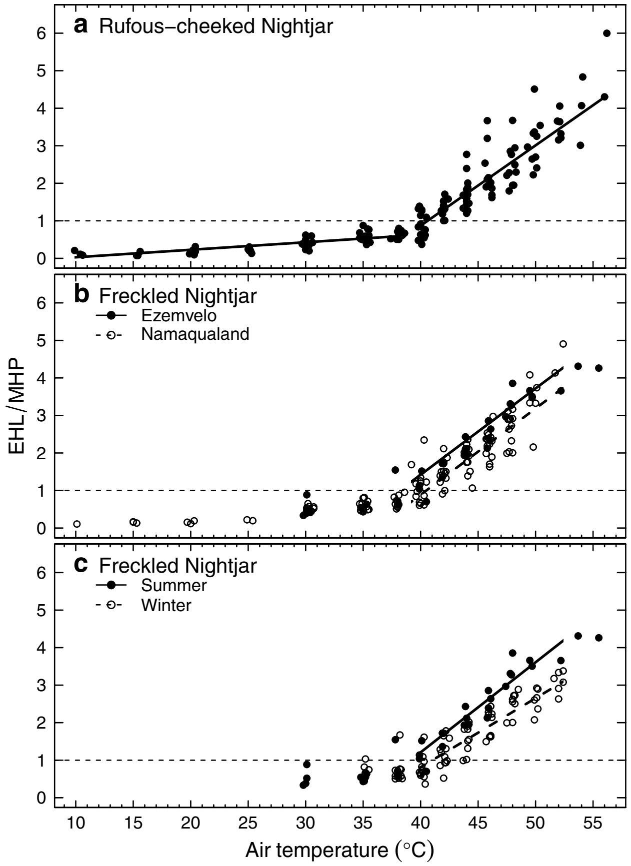

Fig. 4 The ratio of evaporative heat loss to metabolic heat production (EHL/MHP) as a function of air temperature (T_a) in **a** Rufous-cheeked nightjars (*Caprimulgus rufigena*), **b** Freckled nightjars (*Caprimulgus tristigma*) from a mesic (Ezemvelo) and arid (Namaqualand) site and **c** Freckled nightjars from Ezemvelo during summer and winter. In **a**, the regression lines are from two linear models fitted to EHL/MHP versus T_a between $T_a \approx 10$–38 °C and 40–56 °C. In **b**, regression lines represent the common slope from a linear model fitted to EHL/MHP versus site with T_a as a covariate. In **c**, regression lines are from a linear model fitted to EHL/MHP versus the interaction between season and T_a

interaction between T_a and season for winter Ezemvelo birds was 0.184 °C^{-1} and for summer Ezemvelo birds was 0.240 °C^{-1}.

Discussion

Rufous-cheeked nightjars and Freckled nightjars exhibited a pronounced capacity to tolerate high heat loads and were able to maintain T_b far below T_a. Moreover, even at the highest T_a to which they were exposed, all individuals of both species maintained T_b below ~42.5 °C. At T_a values above 37.0–39.9 °C, TEWL increased rapidly with increasing T_a, whereas RMR remained stable, resulting in efficient evaporative cooling (i.e., large increases in EHL with small increases in MHP at a given T_a). The maximum evaporative cooling capacity of both species exceeds that of most birds investigated to date. In the following discussion, we compare the thermoregulatory patterns and evaporative cooling efficiency at high T_a in the two nightjar species we studied with data from other caprimulgids. We subsequently place our results in a broader context and compare the physiological responses of our study species at high T_a to those of other avian taxa studied under similar conditions.

Body temperature

Both nightjar species displayed relatively labile T_b that was positively related to T_a. Qualitatively similar patterns of $\mathrm{T_b}$ lability have been documented in Common Nighthawks (*Chordeiles minor*; Lasiewski and Dawson 1964), Spotted nightjars (Dawson and Fisher 1969) and Poorwills (*Phalaenoptilus nuttallii*; Lasiewski and Seymour 1972). Increases in $\mathrm{T_b}$ at moderate to high T_a appears common among birds and has been observed in phylogenetically diverse taxa (Weathers and Schoenbaechler 1976; Weathers 1981; Tieleman and Williams 1999). Increases in T_b at high T_a should enhance a bird's water economy in hot environments through a more favorable $T_b - T_a$ gradient, thereby increasing the potential for dry heat loss when $T_a < T_b$ and decreasing the potential for dry heat gain when $T_a > T_b$ (Tieleman and Williams 1999). In addition, heat stored internally during the day can be dissipated later through non-evaporative pathways when T_a is conducive (Weathers and Schoenbaechler 1976; Weathers 1981; Tieleman and Williams 1999). For example, through heat stored in body tissue, Rufous-cheeked nightjars could have saved a maximum of 128 mg H_2O at $T_a \approx 50$ °C by allowing T_b to increase 1.7 °C relative to T_b at $T_a \approx 38$ °C. Similarly, Namaqualand Freckled nightjars could have saved 139 mg H_2O at $T_a \approx 50$ °C by allowing T_b to increase 1.5 °C relative to T_b at $T_a \approx 38$ °C. Thus, for nocturnal species like nightjars, where during the day prolonged periods of high rates of evaporative water loss are common, a labile T_b would presumably contribute to the conservation of body water and avoidance of dehydration.

Both Rufous-cheeked nightjars and Freckled nightjars increased T_b as T_a increased within the TNZ without concomitant increases in metabolic heat production, a phenomenon previously reported for a number of avian species (Weathers and Schoenbaechler 1976; Weathers 1981; Tieleman and Williams 1999). However, given the thermal sensitivity of biochemical reaction rates, one might expect an increase in metabolic rate with T_b due to a Q_{10} effect. For example, assuming a Q_{10} of 2.5, we would have expected mean RMR in Rufous-cheeked nightjars to increase from 0.299 W at $T_a = 38$ °C to 0.350 W at $T_a = 50$ °C when mean T_b increased from 40 to 41.7 °C. Yet, at $T_a = 50$ °C, mean RMR = 0.296 W. Traditionally, Q_{10} has been used to describe relationships between metabolic rate and temperature in ectotherms and some authors have argued whether Q_{10} effects should be applied to endotherms (Snyder and Nestler 1990; Heldmaier and Ruf 1992), or even whole-animal energy metabolism in general (Chaui-Berlinck et al. 2002, 2004). Perhaps, avian species are actively suppressing metabolism as T_b increases within the TNZ (e.g., hyperthermia-induced hypometabolism; Lovegrove et al. 2014), explaining the apparent lack of a Q_{10} effect. To the best of our knowledge, however, no exact physiological mechanisms have been presented to explain this phenomenon.

Although both species increased T_b with T_a, absolute limits of T_b remained low compared to that of other avian taxa under similar conditions of heat stress. For example, at $T_a \approx 48$ °C, average T_b in both nightjars was 39.9–41.0 °C (Table 1), compared to 43.0–44.7 °C in three southern African ploceid passerines (Whitfield et al. 2015). In Spinifex Pigeons (*Geophaps plumifera*), T_b increased to 43.4 °C at $T_a \approx 47$–51 °C (Withers and Williams 1990), whereas over the same T_a range, the mean T_b of Ezemvelo Freckled nightjars was only 40.8 °C. Relatively small increases in T_b are apparently common among caprimulgids when exposed to extreme T_a, highlighting their capacity to defend large $T_a - T_b$ gradients (Dawson and Fisher 1969; Lasiewski and Seymour 1972). The ability of caprimulgids to maintain these large thermal gradients is likely primarily attributable to the energetically efficient mechanism of gular flutter (Bartholomew et al. 1962). Presumably, this allows nightjars to nest on the bare ground where T_e is high, but predation risk to incubating adults is reduced (Amat and Masero 2004).

Resting metabolic rate

A distinct TNZ was not evident for either species. Lower critical limits of thermoneutrality occurred at $T_a \approx 35$–37 °C. There was some indication for upper

Table 1 Physiological variables (mean ± SD) from Rufous-cheeked nightjars (*Caprimulgus rufigena*) and Freckled nightjars (*Caprimulgus tristigma*) at air temperatures (T_a) of ≈48 and ≈52 °C

	Rufous-cheeked nightjar	Freckled nightjar		
		Namaqualand	Ezemvelo summer	Ezemvelo winter
$T_a \approx 48$ °C				
N^a	11	12	4	8
T_b (°C)^b	41.0 ± 0.6 (6)^f	40.6 ± 0.9	39.9 ± 0.5	41.0 ± 0.7
RMR (W)^c	0.31 ± 0.6	0.32 ± 0.06	0.36 ± 0.02	0.35 ± 0.05
TEWL (g h^{-1})^d	1.13 ± 0.28	1.22 ± 0.21	1.84 ± 0.24	1.30 ± 0.16
EHL/MHP^e	2.47 ± 0.55	2.63 ± 0.44	3.35 ± 0.37	2.50 ± 0.33
$T_a \approx 52$ °C				
N	6	2	1	6
T_b (°C)	41.5 ± 0.8 (5)	40.1 ± 0.6	40.4	41.6 ± 0.7
RMR (W)	0.31 ± 0.06	0.27 ± 0.07	0.36	0.41 ± 0.04
TEWL (g h^{-1})	1.63 ± 0.30	1.78 ± 0.27	1.96	1.89 ± 0.22
EHL/MHP	3.51 ± 0.34	4.52 ± 0.55	3.66	3.09 ± 0.28

Data at $T_a \approx 48$ °C are presented for species comparisons with data from Whitfield et al. (2015) and Smith et al. (2015). Data at $T_a \approx 52$ °C represent the highest shared T_a among nightjars. Data for Freckled nightjars were collected during the austral summer from a mesic (Ezemvelo) and arid (Namaqualand) site and an additional winter period at Ezemvelo

[a] Sample size

[b] Body temperature

[c] Resting metabolic rate

[d] Total evaporative water loss

[e] Ratio of evaporative heat loss to metabolic heat production

[f] Occasionally, birds moved out of range from the antenna receiving T_b signals and consequently a T_b was not always recorded. Thus, the number in brackets after the T_b mean represents the recorded T_b sample size

critical limits of thermoneutrality (T_{uc}) at $T_a \approx 50$ °C, although the inflection points were not significant. Similar T_{lc} values have been reported for Poorwills ($T_{lc} \approx 35$ °C; Bartholomew et al. 1962), Common Nighthawks ($T_{lc} \approx 35$ °C; Lasiewski and Dawson 1964) and Spotted nightjars ($T_{lc} \approx 32$ °C; Dawson and Fisher 1969). Dawson and Fisher (1969) attributed a high T_{lc} in Spotted nightjars to a low basal metabolic rate, a phenotype common among caprimulgids (Lane et al. 2004). Several species of columbid birds (Marder and Arieli 1988; Withers and Williams 1990; McKechnie et al. 2016b) and houbara bustards (Tieleman et al. 2002b) have shown similar patterns of either a very high T_{uc} or no discernible T_{uc}, a pattern that contrasts with the large increases in RMR at $T_a > T_b$ observed in many other avian taxa (Trost 1972; Weathers 1997; Williams 1999; Tieleman et al. 2002a; Whitfield et al. 2015; McKechnie et al. 2016a). Both caprimulgids and columbids implement gular fluttering as a mechanism for evaporative heat dissipation, whereas many avian taxa (particularly passerines), only use panting to unload heat (Lasiewski and Bartholomew 1966; Bartholomew et al. 1968; Dawson 1982). The movement of the thorax associated with panting produces a larger muscular cost than that of gular fluttering, resulting in elevated metabolic rates and increased endogenous heat production (Whittow 1976). Lasiewski et al. (1966), for example, observed Zebra Finches (*Taeniopygia castonatis*) at $T_a \approx 43.5$ °C incapable of dissipating all of their metabolic heat resulting in an EHL/MHP of 0.96. Consequently, gular fluttering aids in limiting endogenous heat production thus allowing for more efficient evaporative cooling.

In addition to gular fluttering, cutaneous evaporative water loss (CEWL) appears to be an efficient mechanism for dissipating heat at high T_a and low humidities, allowing for large increases in evaporative water loss with small or nonexistent increases in RMR (Marder and Arieli 1988; McKechnie and Wolf 2004; McKechnie et al. 2016b). Marder and Arieli (1988), for example, observed heat-acclimated Rock Pigeons (*Columba livia*) defending normothermic T_b at $T_a \approx 60$ °C without any discernible increases in RMR and suggested that this species' TNZ may extend up to $T_a \approx 65$ °C. In addition, McKechnie et al. (2016b) found that four species of austral columbids exposed to T_a above the TNZ showed only small increases in RMR, with one species, the Namaqua Dove (*Oena capensis*), initiating panting/gular fluttering only at $T_a \approx 55$ °C. The contribution of CEWL to TEWL is variable among avian taxa (Dawson 1982) and apparently influenced by habitat (Marder et al. 2003). To the best of our knowledge, only one study has measured CEWL in a caprimulgid (Lasiewski et al. 1971).

These authors found that at $T_a \approx 35$ °C CEWL represented 51% of TEWL in a single Poorwill, suggesting that the contribution of CEWL to evaporative cooling in caprimulgids is substantial and comparable to other birds (Wolf and Walsberg 1996), at least at moderate T_a. If CEWL remains substantial at $T_a > T_b$, this will contribute, in concert with gular fluttering, to the low RMR values observed in nightjars during periods of high evaporative water loss.

Among Freckled nightjars at Ezemvelo, mass-specific RMR between $T_a \approx 38$ and 48 °C was significantly greater (by 16%) during summer compared to winter. The seasonal metabolic acclimatization we documented in Freckled nightjars, whereby RMR at thermoneutrality is lower in winter than in summer, is similar to the pattern reported for some other southern Hemisphere birds (Smit and McKechnie 2010), although a more recent analysis found that the direction of seasonal metabolic adjustments is more variable in subtropical species (McKechnie et al. 2015). Smit and McKechnie (2010) argued that the downregulation of metabolism during winter in some southern hemisphere birds is primarily influenced by demands for energy and/or water conservation, and not cold tolerance as the case for temperate-zone species, although the functional significance of these seasonal adjustments remains unclear (McKechnie et al. 2015). Doucette and Geiser (2008) documented a lack of seasonal variation in metabolic rate of Australian Owlet-nightjars (*Aegotheles cristatus*; Aegothelidae). To the best of our knowledge, however, our study is the first to quantify seasonal adjustments in the metabolic rate of a member of the Caprimulgidae.

Evaporative water loss

In both Rufous-cheeked nightjars and Freckled nightjars, TEWL increased sharply above $T_a = 37–40$ °C. The magnitude of fractional increases in TEWL in our two study species was similar to that observed in other caprimulgids. Lasiewski and Dawson (1964) observed a fivefold increase in TEWL between $T_a \approx 35$ and 44 °C in Common Nighthawks, whereas Dawson and Fisher (1969) reported a 20-fold increase in TEWL of Spotted nightjars at $T_a \approx 56.5$ °C relative to values at $T_a \approx 23–25$ °C.

At $T_a \approx 25$ °C, TEWL of Rufous-cheeked nightjars was equivalent to 3.8 g H_2O day^{-1} and in Namaqualand Freckled nightjars 3.2 g H_2O day^{-1}, 258 and 208%, respectively, of the values predicted by Williams (1996) for arid-zone species. Similarly, TEWL of Common Nighthawks at $T_a \approx 25$ °C exceeded allometric predictions by 25% (Lasiewski and Dawson 1964). These comparatively high rates of TEWL may be due to the fact that 25 °C is below the T_{lc} in these species, and RMR is hence greater than thermoneutral values (Lasiewski and Dawson 1964). At $T_a \geq 40$ °C, the rates of increase in TEWL (i.e., the slopes of mass-specific TEWL versus T_a) were 92, 78, 106, and 84% of those predicted allometrically by McKechnie and Wolf (2010) in Rufous-cheeked nightjars, Namaqualand Freckled nightjars, summer Ezemvelo and winter Ezemvelo Freckled nightjars, respectively. Lasiewski and Dawson (1964) observed a rate of increase in TEWL of 1.4 mg H_2O g^{-1} h^{-1} °C^{-1} between $T_a \approx 35$ and 44 °C in Common Nighthawks (M_b ~ 72.5 g), 82% of that predicted allometrically by McKechnie and Wolf (2010). With the exception of Ezevmelo Freckled nightjars in summer, a general pattern of low fractional increases in TEWL (i.e., shallower slopes of TEWL versus T_a) seems to emerge among the caprimulgids investigated to date, suggesting that at high T_a, nightjars may have lower TEWL rates than expected based on body size, consistent with the notion of highly efficient evaporative cooling in this taxon.

Both whole-animal and mass-specific summer TEWL at $T_a \geq 40$ °C were lower in Namaqualand Freckled nightjars compared to Ezemvelo conspecifics, supporting our prediction that birds from a more arid site have lower TEWL once M_b is considered. Moreover, the mass-specific rate of increase in TEWL was shallower in Namaqualand compared to Ezemvelo nightjars, despite the former birds being smaller than the latter, and hence contrasting with expectations from allometric scaling (McKechnie and Wolf 2010). Several studies have indicated that birds inhabiting hot, arid environments have evolved reduced TEWL rates compared to mesic counterparts (Dawson 1982; Williams 1996; Williams and Tieleman 2005). Tieleman et al. (2002a) investigated four species of lark, two mesic and two arid, and found that TEWL was 27% lower in arid compared to mesic species. Furthermore, fractional increases in TEWL at $T_a \approx 40$ °C relative to $T_a \approx 25$ °C were smaller in the arid-zone species (Tieleman et al. 2002a). Our comparison of TEWL in two populations of Freckled nightjars is hence consistent with the notion of rates of TEWL in arid-zone birds generally being lower than those of their mesic counterparts.

Although M_b was significantly lower during summer, Ezemvelo nightjars had greater TEWL at any given T_a during summer compared to winter, contrary to our prediction of a lower TEWL in summer-acclimatized individuals. Weathers and Caccamise (1978) investigated seasonal changes in the thermal physiology of Monk Parakeets (*Myiopsitta monachus*) and found that TEWL at $T_a \approx 20–30$ °C was lower in winter, a result the authors related to reduced water availability in winter. Several workers have found that birds can significantly augment CEWL through changes in water vapor diffusion resistance via alterations in the composition of lipids in the stratum corneum (Haugen et al. 2003; Muñoz-Garcia et al. 2008; Williams et al. 2012). Arad et al. (1987), for example, observed an overall reduction in TEWL in dehydrated pigeons at $T_a \approx 45$ °C due to reductions in CEWL. Therefore, if CEWL represents a large percentage of TEWL in nightjars, as suggested by Lasiewski et al. (1971), phenotypic flexibility in resistance to water vapor diffusion during the dry season would likely have adaptive value.

Ratio of evaporative heat loss to metabolic heat production

Caprimulgids have long been recognized as having a pronounced capacity for evaporative cooling (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Dawson and Fisher 1969; Dawson 1982) and our data for two southern African species are consistent with this notion. The efficiency of evaporative cooling in nightjars becomes apparent when compared to that of other species for which data exist. For example, at $T_a \approx 48$ °C, Whitfield et al. (2015) recorded average EHL/MHP ratios of 1.41, 1.46 and 1.61 in Scaly-feathered Weavers (*Sporopipes squamifrons*), White-browed sparrow-Weavers (*Plocepasser mahali*), and Sociable Weavers (*Philetairus socius*), respectively. In comparison, the lowest average EHL/MHP value we recorded at $T_a \approx 48$ °C was 2.47 (Table 1). Bartholomew et al. (1962) found Poorwills had an EHL/MHP ratio that was 1.8 times greater than Dawson's (1958) measurements for cardinals at $T_a \approx 40$ °C. The low resting metabolic rates of nightjars (Lane et al. 2004), coupled with the energetically efficient mechanism of gular fluttering, appears to allow this group of birds to rapidly dissipate heat evaporatively with only small or no increases in metabolism. In male Rufous-cheeked nightjars, for instance, between $T_a \approx 38$ and 56 °C RMR increased by just 15%, whereas TEWL increased by 845%, allowing these birds to maintain a mean T_b equivalent to 14.4 °C below T_a. Lasiewski (1969) documented Poorwills increasing their oxygen consumption by 13% and TEWL by 750% at $T_a \approx 47$ °C relative to $T_a \approx 35$ °C. At $T_a \approx 56$ °C, Rufous-cheeked nightjars were dissipating approximately 515% of their metabolic heat production. This value exceeds those previously reported for species that have also exhibited efficient cooling capacities (Dawson and Fisher 1969; Marder and Arieli 1988). Smith et al. (2015), for example, measured an EHL/MHP of 3.08 at $T_a = 56$ °C and an EHL/MHP of 3.69 at $T_a = 58$ °C in Mourning doves (*Zenaida macroura*) and White-winged doves (*Zenaida asiatica*), respectively. McKechnie et al. (2016b) measured an EHL/MHP ratio of 4.70 at $T_a = 60$ °C in Namaqua doves (*Oena capensis*). Therefore, to the best of our knowledge, the EHL/MHP of 5.15 measured here for Rufous-cheeked nightjars is the highest avian value yet reported.

The maximum EHL/MHP ratios estimated here were calculated on an assumed RER = 0.71, corresponding to lipid metabolism. However, if RMR is recalculated assuming an RER = 1.0 (i.e., a thermal equivalence of 21.4 J ml^{-1} CO_2; Withers 1992), corresponding to carbohydrate metabolism, estimated RMR is 23% lower. Consequently, maximum EHL/MHP ratios increase by 30%, with maximum evaporative cooling capacities of 7.8, 6.4, 5.6, and 4.4 in Rufous-cheeked nightjars, Namaqualand Freckled nightjars, summer Ezemvelo Freckled nightjars and winter Ezemvelo Freckled nightjars, respectively. This uncertainty highlights an unfortunate and largely unavoidable limitation of our approach to measuring heat tolerance at high T_a. The high flow rates required to keep chamber humidity low prevent accurate recordings of oxygen consumption and consequently RER. However, given that nightjars feed on the wing and must be hand-fed in captivity, we feel confident that our birds were post-absorptive during measurements and likely metabolizing lipids.

At $40 \leq T_a \leq 52$ °C, summer Ezemvelo Freckled nightjars were more efficient at dissipating metabolic heat compared to Namaqualand conspecifics, contrary to our prediction that evaporative cooling should be more efficient in Namaqualand birds. This result is likely due to TEWL being lower in Namaqualand compared to summer Ezemvelo Freckled nightjars. Conversely, Freckled nightjars at Ezemvelo had a greater EHL/MHP ratio during summer compared to winter. Since RMR between $T_a \approx 40$–52 °C remained relatively stable across seasons, the variation in the efficiency of evaporative cooling likely reflects differences in TEWL rates rather than metabolic variation.

Conclusions

Caprimulgids' capacity for efficient evaporative cooling appears to arise from rates of evaporative water loss that are quantitatively similar to those of other birds, combined with metabolic rates that remain at minimal resting levels even when T_e is far above T_b. Low resting metabolic heat production, together with the lack of a discernible T_{uc}, limits nightjars' endogenous heat production, minimizing their total heat load and allowing them to rapidly dissipate heat gained from the environment. In addition, fractional rates of increase in TEWL for the two nightjar species studied here were generally lower than expected for their size. Nevertheless, at high T_a, nightjars are still forced to evaporate substantial amounts of water for extended periods, raising questions as to the hydration status of these birds at sunset and how this may affect drinking patterns and prey selection.

Nightjars inhabit some of the hottest environments on the planet. For instance, several species reside in extremely hot deserts and semi-desert habitats [e.g., Common Poorwill; Egyptian Nightjar (*Caprimulgus aegyptius*); Nubian Nightjar (*Caprimulgus nubicus*); Sykes's Nightjar (*Caprimulgus mahrattensis*); Cleere and Nurney 1998]. A nocturnal lifestyle coupled with roosting and nesting in sites exposed to full solar radiation exposes nightjars to some of the highest T_e experienced by any endotherm. Moreover, their nocturnal habits mean that they must often endure very high T_e for extended periods between sunrise and sunset, especially in summer with lengthy daylight periods. Yet, nightjars appear reluctant to use pronounced hyperthermia, especially when compared to other species exposed to high T_a (Lasiewski and Seymour 1972; Whitfield et al. 2015; Noakes et al. 2016). Incubating in such conditions places additional thermoregulatory pressures on these birds, because it forces incubating adults to maintain a T_b within a narrow range well below T_a. Such thermally challenging conditions have undoubtedly exerted strong selective pressures on nightjars to evolve physiological traits that provide the basis for pronounced heat tolerance.

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Compliance with ethical standards

Ethical approval All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. This study was approved by the University of Pretoria Animal Ethics Committee (Project EC068-13) and complies with current South African laws.

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