Diurnal body temperature patterns in free-ranging populations of two

southern African arid-zone nightjars

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Abstract

Endotherms allocate large amounts of energy and water to the regulation of a precise body temperature (T_b), but can potentially reduce thermoregulatory costs by allowing T_b to deviate from normothermic levels. Many data on heterothermy at low air temperatures (T_a) exist for caprimulgids, whereas data on thermoregulation at high T_a are largely absent, despite members of this taxon frequently roosting and nesting in sites exposed to high operative temperatures. We investigated thermoregulation in free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*) and Freckled Nightjars (*Caprimulgus tristigma*) in the southern African arid zone. Individuals of both species showed labile T_b fluctuating around a single modal T_b (T_{b-mod}). Average T_{b-mod} was 39.7 °C for Rufous-cheeked Nightjars and 39.0 °C for Freckled Nightjars. In both species, diurnal T_b increased with increasing T_a. At $T_a \geq 38$ °C, Rufous-cheeked Nightjar mean T_b increased to 42 °C, equivalent to 2.3 °C above T_{b-mod}. Under similar conditions, Freckled Nightjar T_b was on average only 1.1 °C above T_{b-mod}, with a mean T_b of 40.0 °C. Freckled Nightjars are one of the most heterothermic caprimulgids investigated to date, but our data suggest that during hot conditions this species maintains T_b within a narrow range above T_{b-mod}, possibly reflecting an evolutionary tradeoff between decreased thermal sensitivity to lower T_b but increased sensitivity to high T_b. These findings reveal how general thermoregulatory patterns at similar T_a can vary even among closely related species.

Introduction

The scarce and unpredictable water resources, high air temperatures (T_a) and intense solar radiation typical of deserts make them among the most physiologically challenging environments occupied by any organisms (Bartholomew and Cade 1963). When operative temperature (T_e; Bakken 1976, Robinson et al. 1976) exceeds body temperature (T_b) animals rely on evaporative heat dissipation to defend a T_b set-point and avoid lethal heat stress (Dawson 1982). Consequently, at high T_e, animals encounter a trade-off between hyperthermia avoidance by means of evaporative cooling *versus* dehydration avoidance by conserving body water (Chew 1961, Cade and Dybas 1962, Willoughby and Cade 1967). Mismatches between water supply and demand are exacerbated in birds because of their small body size and high mass-specific rates of metabolism and evaporative water loss (EWL; Bartholomew and Dawson 1953, Bartholomew and Cade 1963, Wolf 2000, McKechnie and Wolf 2010).

The maintenance of water balance in hot environments may be particularly challenging for nocturnal birds, on account of the absence of diurnal water intake through drinking or the ingestion of food (Willoughby and Cade 1967, Fisher et al. 1972). Nightjars (Caprimulgidae) frequently roost and/or tend nests all day in open sites where solar radiation is intense and T_e regularly exceeds T_b (e.g., Cowles and Dawson 1951, Dexter 1956, Weller 1958, Howell 1959, Steyn 1971, Swisher 1978, Grant 1982, Ingels et al. 1984). Grant (1982), for instance, measured a black bulb temperature of approximately 58 °C at a Lesser Nighthawk (*Chordeiles acutipennis*) nest and observed the incubating adult gular fluttering continuously for nearly 8 hr. Nightjars, therefore, are

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a taxon that would seemingly experience strong selective pressure for physiological mechanisms that minimize EWL and avoid dehydration.

Once regarded as a non-adaptive constant (Scholander et al. 1950), endotherm T_b is now known to be highly variable (e.g., Tieleman and Williams 1999, McKechnie and Lovegrove 2002, Boyles et al. 2013, Ruf and Geiser 2015) and is increasingly being interpreted in an adaptive framework, whereby natural selection has influenced the mean and variance of the phenotype (Angilletta et al. 2010, Boyles et al. 2011a). At high T_a, birds can conserve water through facultative increases in T_b (i.e., hyperthermia; Weathers 1981, Dawson 1982, Tieleman and Williams 1999). However, the magnitude of hyperthermia should vary depending on the co-adaptation between thermoregulation and thermal sensitivity (Angilletta et al. 2006, Angilletta et al. 2010, Boyles et al. 2011a). Endotherms whose performance is thermally insensitive are predicted to thermoregulate imprecisely but still perform well over a wide range of T_b (i.e., thermal generalists). Conversely, endotherms that are thermal specialists should display less variation in T_b and perform optimally over a narrower range of T_b. These two categorizations are not dichotomous, but represent two ends of a thermal continuum (Angilletta et al. 2006). Thus, a species', or even an individual's, thermoregulatory strategy for coping with thermal heterogeneity will vary depending on its position along this thermal continuum.

To date, most research on adaptive thermoregulation in free-ranging nightjars has focused on facultative hypothermic responses to cool conditions, periods of low lunar illumination and/or food shortage (e.g., Brigham 1992, Fletcher et al. 2004, Lane et al. 2004a, McKechnie et al. 2007, Smit et al. 2011, Brigham et al. 2012). In contrast, our knowledge of thermoregulation in free-ranging caprimulgids at high T_a is essentially non-

existent, despite this taxon's frequent use of exposed nest and roost sites making it an ideal group for investigating adaptive thermoregulatory responses to hot conditions. Additionally, given their proclivity for expressing heterothermy, caprimulgids offer an intriguing opportunity to investigate whether T_b lability can also extend to high T_b. Here, we investigated patterns of core T_b in two free-ranging southern African nightjar species in hot, arid habitats. Our objectives were to address several questions regarding thermoregulation by free-ranging nightjars exposed to high T_a: 1) do nightjars express facultative hyperthermia, with increases in maximum and/or mean T_b during hot conditions?, 2) do free-ranging nightjars display a similar degree of heterothermy on days with higher maximum T_a compared to lower maximum T_a?, and 3) do nightjars display the bimodal circadian rhythm of T_b typical of most birds?

Materials and methods

Study species and sites

We investigated thermoregulation in Rufous-cheeked Nightjars at Dronfield Nature Reserve (28°39' S, 24°48' E) near Kimberley, South Africa from 16 January to 1 March 2014. Dronfield consists of arid savannah and camelthorn (*Vachellia erioloba*) woodland. Rainfall occurs mainly in summer, with 117 mm falling during our study period. Thermoregulation by Freckled Nightjars (*Caprimulgus tristigma lentiginosus*) was investigated between 5 December 2014 and 6 February 2015 on a privately owned farm in the Namaqualand region of the Northern Cape province, South Africa (30°02' S, 17°57' E). This study site is situated in the northern Kamiesberg Mountains and has previously been described by Boyles et al. (2012) and Smit et al. (2011). Rainfall in this

region occurs predominantly in winter and only 2.6 mm fell during the study period. Weather data for each field site were recorded using a portable weather station (Vantage Pro2, Davis Instruments, Hayward, CA, USA), placed ~ 1.5 – 2 m above the ground. Air temperature was recorded every 5 min at Dronfield and every 15 min in Namaqualand.

Nightjars were captured at night either on roads with a handheld net and spotlight or by luring birds into mist-nets with conspecific call playback. After capture, nightjars were kept in a cage (~ 60 x 71 cm) constructed from PVC piping and shade cloth for 1-3 days. During this time, nightjars were also used for respiratory gas exchange measurements for the estimation of metabolic and EWL rates (O'Connor et al. 2017). While in captivity nightjars were hand-fed a diet of moist dog food, mealworms and water. On average, individuals lost ~3% of their body mass (M_b) following capture.

Body temperature measurements
Core T_b was measured using two types of temperature-sensitive data loggers, namely Thermochron iButtons (model DS1922L, Maxim Integrated, San Jose, CA, USA; resolution = 0.0625 °C) for Freckled Nightjars and WeeDots (Alpha Mach Inc., Ste-Julie, Qc, Canada; resolution = 0.025 °C) for Rufous-cheeked Nightjars. Data loggers were calibrated in a water bath against a mercury thermometer with an accuracy traceable to the US National Bureau of Standards at temperatures between 5 – 50 °C in 5 °C increments (mean ± SD iButton difference from thermometer = 0.4 ± 0.4 ℃, WeeDot difference = -0.2 ± 0.3 ℃). We programmed WeeDots to record T_b every 5 min and iButtons every 15 min. WeeDots come covered in a polyurethane coating to allow for submersion in wet environments. However, three metal contacts remain exposed for

uploading data to a personal computer, and prior to implanting, these contacts were coated with a multi-purpose marine sealant (Sikaflex-291, Sika, Madison Heights, MI, USA) to prevent possible corrosion. iButtons were coated in a biologically inert surgical wax before implantation. Average WeeDot and iButton masses were 1.3 ± 0.1 g and 3.3 ± 0.2 g, respectively.

Nightjars were transported to a veterinary clinic where a registered veterinarian surgically implanted the temperature-sensitive data loggers intraperitoneally. Seven Rufous-cheeked Nightjars received WeeDots and 14 Freckled Nightjars were implanted with iButtons. On the morning of implantation, mean M_b of Rufous-cheeked Nightjars was 53.8 ± 4.2 g and 65.3 ± 4.8 g for Freckled Nightjars. Both species were anesthetized with halothane (Safeline Pharmaceuticals [Pty] Ltd, Weltevredenpark, South Africa) via inhalation anesthesia. Nightjars were held in captivity for $3 - 12$ hr after surgery to ensure complete recovery. Often, individuals of both species were fully alert (e.g., standing on their own, "hissing/growling" and attempting to escape when held in the hand) within one hour following surgery. Nightjars were released at the site of capture at dusk on the same day of surgery. We attempted to recapture birds once we knew the data loggers had run out of memory. Recaptured nightjars were again transported to the veterinary clinic where the data loggers were extracted following the same procedure as for implantation. Nightjars were then released at the site of capture on the same day of data logger removal.

We also measured the core T_b of a single incubating female Rufous-cheeked Nightjar from 26 October to 11 November 2015 at Dronfield. Incubating T_b was measured using a passive-integrated transponder (PIT) tag (Biomark, Boise ID, USA)

injected into the peritoneal cavity (Whitfield et al. 2015). Before the study, a subset of 70 PIT tags was calibrated in a circulating water bath against a thermocouple (type T, Physitemp, Clifton, NJ, USA) at water temperatures from 39 to 46 °C (Whitfield et al. 2015). On average, PIT tags were within 0.02 ± 0.09 °C of thermocouple values (Whitfield et al. 2015). The incubating adult was tracked to her nest based on a signal from a radio transmitter (BD-2T, Holohil Systems, Carp, Ontario, Canada) attached dorsally between the scapulars with a backpack-style harness constructed from Teflon ribbon (Telonics, Mesa, AZ, USA). Upon discovery of eggs on the ground, we buried a Biomark racket antenna under the eggs, allowing us to record T_b only when the female was incubating. The racket antenna was connected to a 4-m long cable that was in turn connected to a portable transceiver system (model 2001F-ISO, Biomark, Boise, ID, USA). We powered the transceiver system using a 12 V, 7.5 A battery. The transceiver was programmed to record T_b every minute and we visited the site once each day to download the data to a personal computer and replace the battery. During these visits, the incubating bird rarely flushed and remained tight on the eggs.

Data analyses

All statistical analyses were conducted in R 3.2.4 (R Core Team 2016) with all values reported as mean ± standard deviation (SD). Species mean values were calculated by taking an average across individual bird averages. When reporting individual bird means, we provide the number of observations used in the calculation (designated with a lowercase n). Data were separated into four distinct periods, namely daily (midnight to midnight), diurnal (sunrise to sunset), twilight (civil and nautical twilight combined) and

nocturnal (end of dusk nautical twilight to start of dawn nautical twilight). The end of civil and nautical twilight are defined as when the sun is 6° and 12° below the horizon, respectively (Mills 2008). We used the end of nautical twilight as the start of the night because nightjars have been shown to reduce their activity at this point in the absence of lunar illumination (Mills 1986, Jetz et al. 2003). Sunrise and sunset times for each study site were determined using the function 'sunriset' in the R package *maptools* (Bivand and Lewin-Koh 2016). The end and start of nautical twilight for each study site was determined using SunCalc (http://www.suncalc.net/).

We used the *nlme* (Pinheiro et al. 2016) and *lme4* (Bates et al. 2015) packages to fit linear mixed-effects models and perform three separate analyses on free-ranging diurnal T_b data. First, we modelled variation in diurnal T_b with T_a as a predictor variable. Second, we modelled variation in maximum diurnal T_b (T_{b-max}) as a function of maximum diurnal T_a (T_{a-max}). Lastly, we modelled diurnal heterothermy with T_{a-max} as a predictor variable using a comparative metric known as the heterothermy index (HI; Boyles et al. 2011b):

$$HI = \sqrt{\frac{\Sigma(T_{b-mod} - T_{b-i})^2}{n-1}},$$

where T_{b-mod} is the modal T_b, T_{b-i} is the measured T_b at time *i* and *n* is the number of times T_b is sampled. We follow Boyles et al. (2011b) and assume that T_b is adaptive and the most frequently occurring T_b should equal the optimal T_b. Thus, we use T_{b-mod} as a proxy of optimal T_b. We calculated a T_{b-mod} for each bird by pooling all T_b values collected for each recording period. A species average T_{b-mod} represents the average of individual bird T_{b-mod}.

For all linear mixed-effects models we included bird identity as a random effect due to repeated measurements on the same individual. We assessed the goodness-of-fit of each model by graphically inspecting residuals for homogeneity and normality. Frequently our models violated assumptions of homogeneity due to skewed distributions in our response variable and we subsequently either included a variance structure in our models (Zuur et al. 2009) or implemented a robust linear mixed-effects model using the R package *robustlmm* (Koller 2016). For each analysis, we report the effect size of the predictor variable on the response, represented as the parameter estimate (β), and the accompanying standard error (SE) and 95% confidence interval (95% CI). To further assess the magnitude of hyperthermia throughout the diurnal period, we calculated mean deviations in T_b from $T_{b\text{-mod}}$ (i.e., mean $\Delta T_b - T_{b\text{-mod}}$) across diurnal T_a.

Results

Rufous-cheeked Nightjar

Due to low recapture rates, we recovered WeeDots from only two male Rufous-cheeked Nightjars (hereafter: free-ranging T_b), resulting in a total of 21,210 T_b readings over 30 and 45 days. We also collected 8,869 measurements of T_b over 13 days from the incubating female. Individual mean T_b for the two free-ranging birds was 39.9 ± 0.9 °C (range = 36.2 – 43.6 °C, n = 8,394) and 39.7 ± 1.1 °C (range = 34.4 – 43.6 °C, n = 12,816). Both free-ranging T_b and incubating T_b were distributed unimodally (Figure 1A). Mean T_b, $T_{b\text{-mod}}$ and daily HI were all higher in free-ranging birds compared to the incubating bird (Table 1). Daily patterns of free-ranging T_b were characterized by transient increases in T_b before sunrise and after sunset, corresponding to periods of high

activity during twilight hours (Figure 2A). Consequently, free-ranging T_b was highest during twilight periods (Table 1). Average daily amplitude in T_b (daily $T_{b\text{-}max}$ − daily $T_{b\text{-}min}$) for the two free-ranging male Rufous-cheeked Nightjars was 5.0 ± 0.3 °C (range = $2.9 - 8.9$ °C).
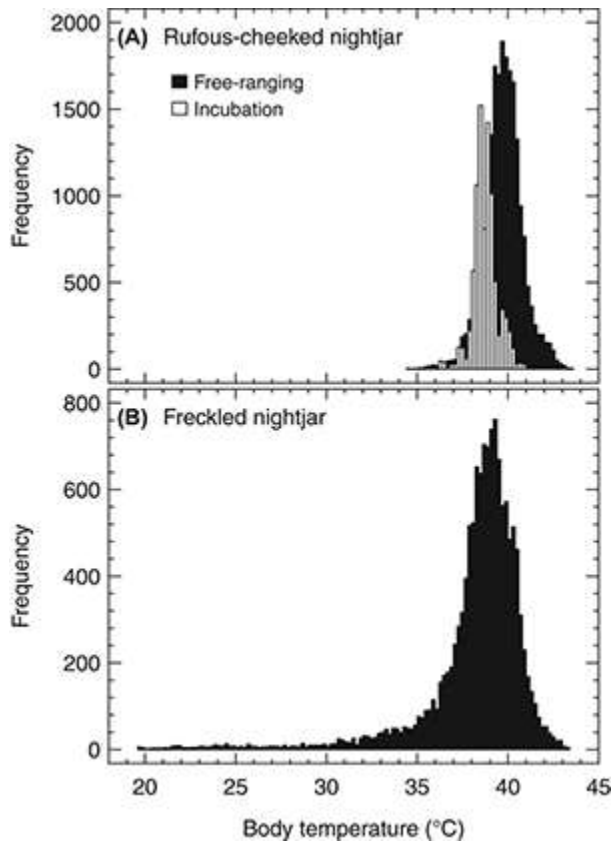

Figure 1.

Frequency distributions of summer core body temperatures (T_b) in (A) free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*; N = 2) from 16 January to 1 March 2014 and a single incubating Rufous-cheeked Nightjar from 26 October to 11 November 2015 at Dronfield Nature Reserve, Kimberly, South Africa and, (B) free-ranging Freckled Nightjars (*Caprimulgus tristigma*; N = 4) from 5 December 2014 to 6 February 2015 in the Namaqualand region of South Africa.

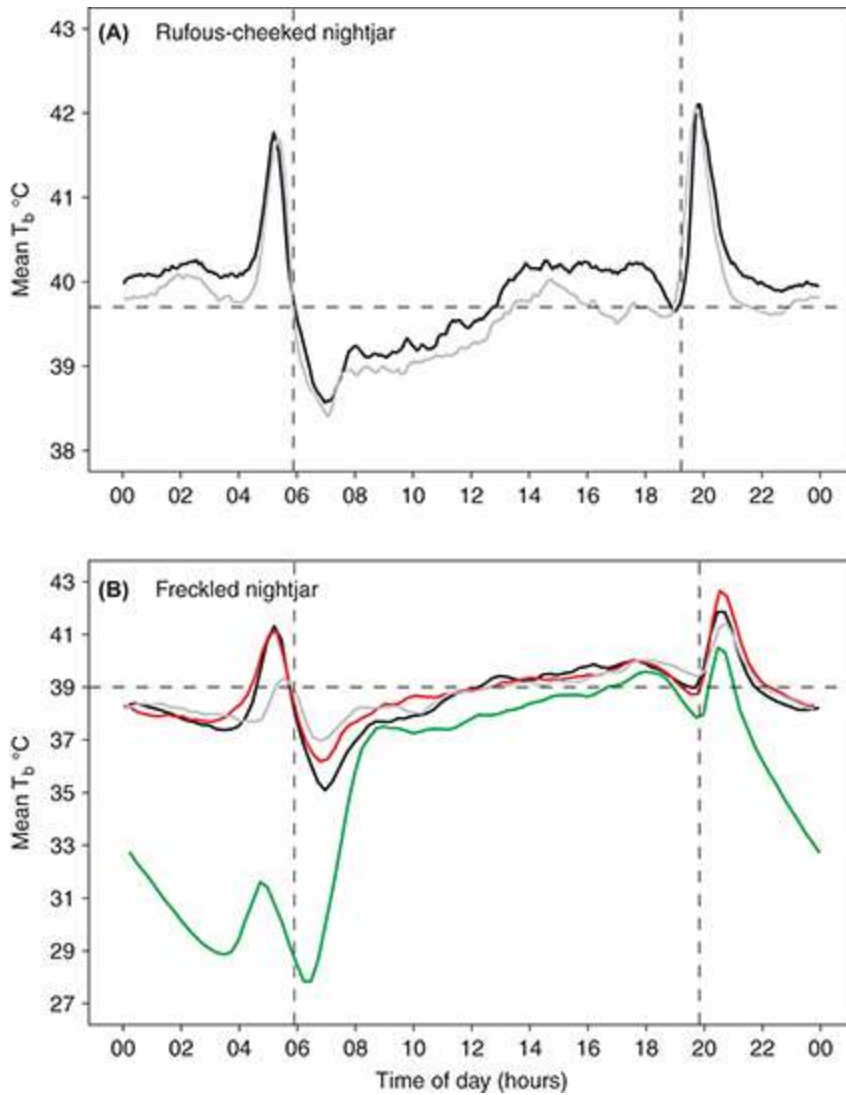**Figure 2.**
Mean daily body temperature (T_b) traces for (A) free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*; N = 2) from 16 January to 1 March 2014 at Dronfield Nature Reserve, Kimberley, South Africa and, (B) free-ranging Freckled Nightjars (*Caprimulgus tristigma*; N = 4) from 5 December 2014 to 6 February 2015 in the Namaqualand region of South Africa. Each coloured line represents an individual bird. The green line is the very heterothermic Freckled Nightjar. Vertical dashed lines represent mean sunrise and sunset times for each study period. Horizontal dashed lines represent mean modal T_b. Note the transient increases in mean T_b just before sunrise and right after sunset, representing periods of high activity during twilight hours. Time is shown as a 24-h day (0 = 00:00 hours; 22 = 22:00 hours)

Table 1. Mean ± standard deviation values for body temperature (T_b), modal T_b (T_{b-mod}), heterothermy index (HI), maximum T_b (T_{b-max}) and T_b amplitude (T_{b-amp}) from free-ranging and incubating Rufous-cheeked Nightjars (*Caprimulgus rufigena*) and free-ranging Freckled Nightjars (*Caprimulgus tristigma*). Data for Rufous-cheeked Nightjar T_b were recorded at 5-min intervals spanning 30 and 45 days, whereas incubating T_b was measured at 1-min intervals over 13 days. Freckled Nightjar T_b was measured at 15-min intervals over 21, 36, 42 and 42 days. Variable means represent averaged values across individual bird averages. Variable ranges of the raw data are given in brackets below means.

| Variable | Rufous-cheeked Nightjar | | Freckled Nightjar (N = 4) |
	Free-ranging (N = 2)	Incubating (N = 1)	
T_b	39.8 ± 0.2 °C	38.8 ± 0.7 °C	37.9 ± 1.7 °C
	[34.4 – 43.6 °C]	[36.2 – 41.9 °C]	[19.6 – 43.4 °C]
T_{b-mod}	39.7 ± 0.0 °C	38.8 °C	39.0 ± 0.3 °C
	[39.7 – 39.7 °C]	[NA]	[38.7 – 39.4 °C]
Daily[a] HI	1.0 ± 0.1 °C	0.7 ± 0.2 °C	2.7 ± 1.9 °C
	[0.6 – 1.7 °C]	[0.4 – 1.1 °C]	[0.7 – 10.4 °C]
Diurnal[b] T_b	39.5 ± 0.2 °C	38.8 ± 0.7 °C	38.3 ± 0.8 °C
	[34.4 – 43.2 °C]	[36.2 – 41.9 °C]	[19.6 – 42.7 °C]
Nocturnal[c] T_b	40.0 ± 0.2 °C	38.9 ± 0.3 °C	36.9 ± 3.0 °C
	[35.8 – 42.9 °C]	[38.3 – 41.9 °C]	[20.7 – 42.6 °C]
Twilight[d] T_b	41.3 ± 0.1 °C	39.7 ± 0.5 °C	39.2 ± 2.8 °C
	[38.8 – 43.6 °C]	[38.8 – 40.9 °C]	[20.1 – 43.4 °C]
Diurnal T_{b-max}	41.2 ± 0.1 °C	40.4 ± 0.7 °C	40.7 ± 0.3 °C
	[39.6 – 43.2 °C]	[39.3 – 41.9 °C]	[38.4 – 42.7 °C]
Diurnal T_{b-amp}[e]	3.5 ± 0.2 °C	2.7 ± 0.9 °C	7.3 ± 3.8 °C
	[1.1 – 7.8 °C]	[1.6 – 4.6 °C]	[1.8 – 20.2 °C]
Diurnal HI	0.9 ± 0.1 °C	0.7 ± 0.2 °C	2.1 ± 1.2 °C
	[0.3 – 2.0 °C]	[0.4 – 1.1 °C]	[0.4 – 7.7 °C]

[a] Defined as the period from midnight to midnight

[b] Defined as the period between sunrise and sunset

[c] Defined as the period between the end of nautical dusk twilight and start of nautical dawn twilight

[d] The combined periods of civil and nautical dusk and civil and nautical dawn twilight

[e] Calculated as $T_{b-max} - T_{b-min}$ during the diurnal period

During the diurnal period, free-ranging Rufous-cheeked Nightjars had a higher mean T_b, greater amplitude in T_b and higher HI than the incubating bird (Table 1). The two free-ranging birds regularly decreased their T_b after sunrise and subsequently increased T_b with increasing T_a throughout the day (Figure 2A and Table 2). At $T_a \leq 30$ °C, free-ranging Rufous-cheeked Nightjars typically maintained a mean T_b below T_{b-mod} (Figure 3A). At $T_a > 33$ °C, diurnal T_b increased sharply with T_a and mean T_b was consistently above T_{b-mod} (Figure 3A). During periods when $T_a \geq 38$ °C, mean diurnal T_b in free-ranging Rufous-cheeked Nightjars was 42.0 ± 0.4 °C (range $= 40.6 - 42.8$ °C) and mean $\Delta T_b - T_{b-mod}$ was 2.3 ± 0.4 °C (range $= 0.9 - 3.1$ °C). In contrast, T_b in the incubating bird was relatively stable at high T_a and did not deviate far from T_{b-mod} (Figure 3A). For example, at $T_a > 33$ °C, mean diurnal T_b in the incubating bird was 39.0 ± 0.7 °C (range $= 38.1 - 41.9$ °C), only 0.2 °C above T_{b-mod}. Consequently, diurnal T_{b-max} was higher in free-ranging birds than the incubating bird (Table 1). For free-ranging birds, diurnal T_{b-max} was positively and linearly related to T_{a-max} (Figure 4A and Table 2). However, T_{a-max} did not influence diurnal HI in the two free-ranging birds (Figure 5A and Table 2).
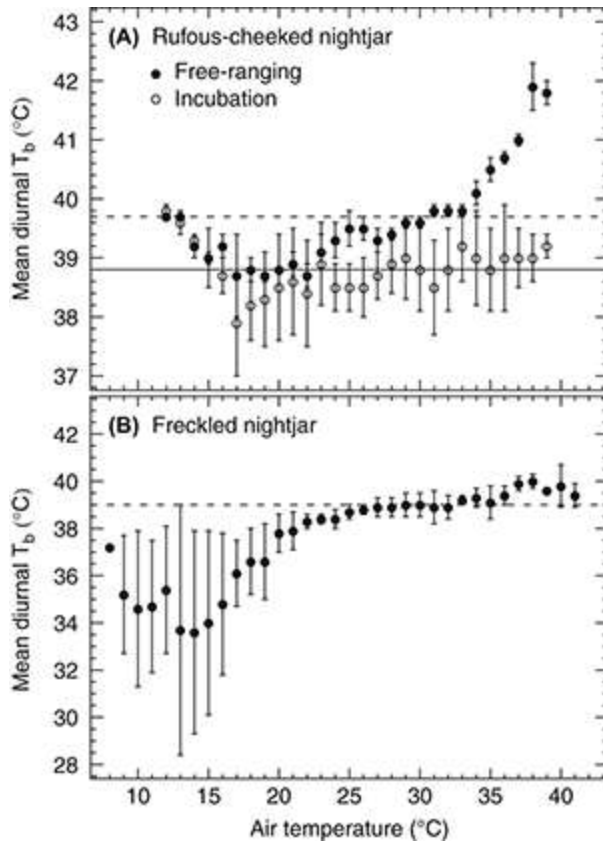
Figure 3.

Mean diurnal (i.e., sunrise to sunset) body temperature (T_b) as a function of air temperature (T_a) in (A) free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*; N = 2) from 16 January to 1 March 2014 and a single incubating Rufous-cheeked Nightjar from 26 October to 11 November 2015 at Dronfield Nature Reserve, Kimberley, South Africa and, (B) free-ranging Freckled Nightjars (*Caprimulgus tristigma*; N = 4) from 5 December 2014 to 6 February 2015 in the Namaqualand region of South Africa. Each data point represents mean diurnal T_b averaged across individuals to the nearest whole T_a (e.g., mean diurnal T_b at T_a = 20 °C represents the combined average T_b of each individual birds average T_b recorded at $19.5 \leq T_a < 20.5$). Horizontal dashed lines represent the mean modal T_b for free-ranging individuals whereas the solid horizontal line represents the modal T_b for the incubating Rufous-cheeked Nightjar. Error bars represent standard deviation.
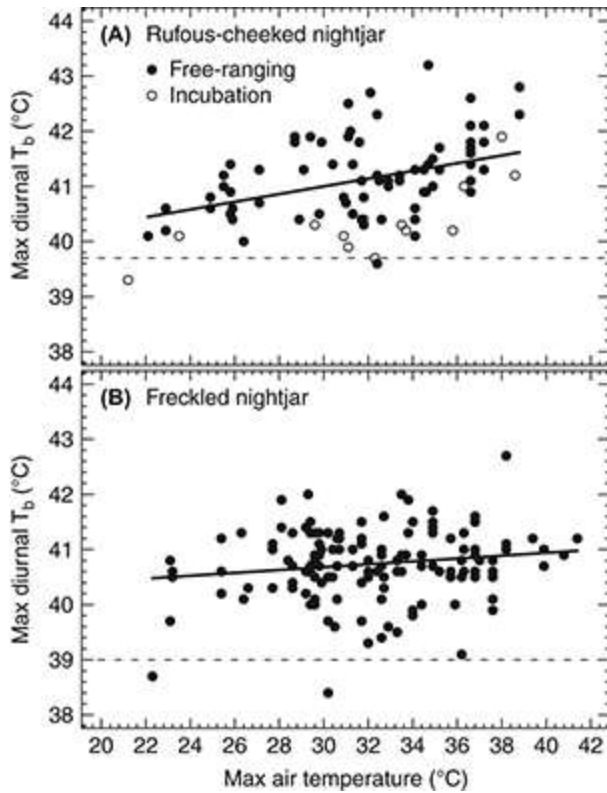
Figure 4.

Maximum diurnal (i.e., sunrise to sunset) body temperature (T_b) as a function of maximum air temperature in (A) free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena;* N = 2) from 16 January to 1 March 2014 and a single incubating Rufous-cheeked Nightjar from 26 October to 11 November 2015 at Dronfield Nature Reserve, Kimberley, South Africa and, (B) free-ranging Freckled Nightjars (*Caprimulgus tristigma*; N = 4) from 5 December 2014 to 6 February 2015 in the Namaqualand region of South Africa. Horizontal dashed lines represent the mean modal T_b for free-ranging birds. Regression lines in both panels represent the parameter estimates from linear mixed-effects models fit to only free-ranging T_b data. In all models bird identity was included as a random variable to account for repeated measures within individuals.
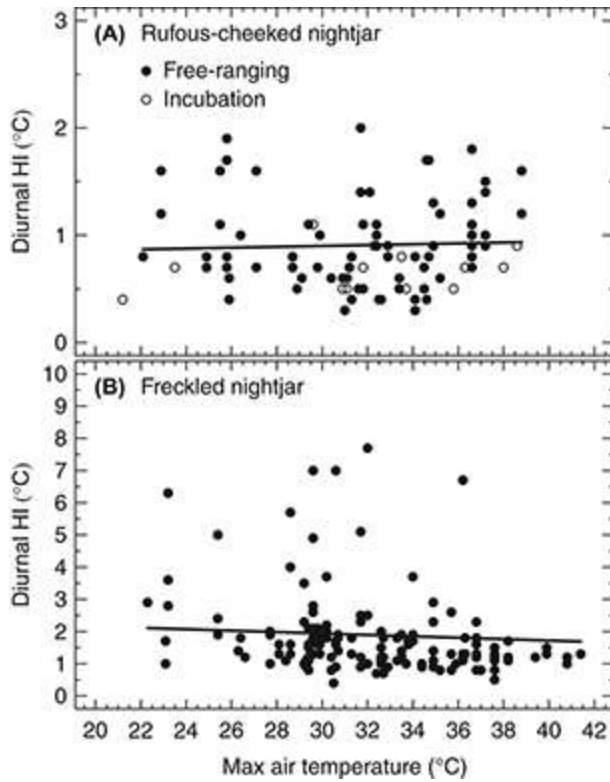
Figure 5.

Diurnal (i.e., sunrise to sunset) heterothermy index (HI) as a function of maximum air temperature in (A) free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*; N = 2) from 16 January to 1 March 2014 and a single incubating Rufous-cheeked Nightjar from 26 October to 11 November 2015 at Dronfield Nature Reserve, Kimberley, South Africa and, (B) free-ranging Freckled Nightjars (*Caprimulgus tristigma*; N = 4) from 5 December 2014 to 6 February 2015 in the Namaqualand region of South Africa. Regression lines in both panels represent the parameter estimates from linear mixed-effects models fit to only free-ranging T_b data. In all models bird identity was included as a random variable to account for repeated measures within individuals.

Table 2. Parameter estimates ± standard error ($\beta \pm$ SE) from linear mixed-effects models for free-ranging Rufous-cheeked Nightjars (*Caprimulgus rufigena*) and Freckled Nightjars (*Caprimulgus tristigma*). Models include body temperature as a function of air temperature ($T_b \sim T_a$), maximum body temperature as a function of maximum air temperature ($T_{b\text{-}max} \sim T_{a\text{-}max}$) and heterothermy index as a function of $T_{a\text{-}max}$ (HI $\sim T_{a\text{-}max}$). All models represent data collected during the diurnal period, defined as the period between sunrise and sunset. Lower CI = lower 95% confidence interval. Upper CI = upper 95% confidence interval. Values in parentheses below parameter estimates represent the number of observations included in the model (e.g., for the model $T_b \sim T_a$, n = 11,703 diurnal T_b observations from N = 2 Rufous-cheeked Nightjars). In all models bird identity was included as a random factor to account for repeated measures within individuals.

Model	$\beta \pm$ SE	Lower CI	Upper CI
Rufous-cheeked Nightjar (N = 2)			
Diurnal $T_b \sim$ diurnal T_a	0.104 ± 0.001 (n = 11,703)	0.101	0.106
Diurnal $T_{b\text{-}max} \sim$ diurnal $T_{a\text{-}max}$	0.073 ± 0.015 (n = 74)	0.045	0.102
Diurnal HI $\sim$ diurnal $T_{a\text{-}max}$	0.004 ± 0.012 (n = 74)	-0.016	0.028
Freckled Nightjar (N = 4)			
Diurnal $T_b \sim$ diurnal T_a	0.095 ± 0.003 (n = 7,759)	0.089	0.101
Diurnal $T_{b\text{-}max} \sim$ diurnal $T_{a\text{-}max}$	0.026 ± 0.013 (n = 139)	0.0006	0.051
Diurnal HI $\sim$ diurnal $T_{a\text{-}max}$	-0.022 ± 0.010 (n = 139)	-0.042	-0.002

Freckled Nightjar

We recovered iButtons from four Freckled Nightjars (three male, one female), yielding 13,353 T_b readings spanning 21, 36, 42 and 42 days. Freckled Nightjar T_b was left-skewed with a unimodal distribution (Figure 1B). Body temperature was similar among three of the birds, with individual means of 38.7 ± 2.0 °C (range = 28.8 – 43.4 °C, n =

3,942), 38.9 ± 2.0 °C (range = $29.1 - 43.4$ °C, n = 3,939) and 38.8 ± 1.6 °C (range = 31.7

– 42.6 °C, n = 3,456). One male decreased its T_b below 30 °C on 15 of 21 nights,

resulting in a lower average T_b of 35.4 ± 5.1 °C (range = $19.6 - 41.9$ °C, n = 2,016). The

exclusion of data from this bird did not alter the main results, particularly pertaining to

the diurnal period (e.g., 95% confidence intervals from mixed-effects models

overlapped), and we thus opted to include this individual in our final analyses. Modal T_b

was similar among the four birds, only ranging by 0.7 °C (Table 1). Body temperature

showed conspicuous, transient increases before sunrise and after sunset (Figure 2B),

resulting in T_b being greatest during twilight hours followed by diurnal and nocturnal

periods (Table 1). Average daily amplitude of T_b was 9.0 ± 3.6 °C (range = $3.3 - 20.2$

°C).

Freckled Nightjars displayed a highly variable diurnal T_b with conspicuous

declines after sunrise and before sunset (Figure 2B and Table 1). However, although

diurnal T_b increased with T_a (Table 2), at high T_a Freckled Nightjars did not allow their

T_b to rise much above $T_{b\text{-mod}}$ (Figure 3B). For example, at $T_a \geq 38$ °C, mean diurnal T_b

was 40.0 ± 0.5 °C (range = $37.5 - 41.5$ °C) and mean $\Delta T_b - T_{b\text{-mod}}$ was 1.1 ± 0.4 °C (range

= $-1.2 - 2.6$ °C). Consequently, $T_{b\text{-max}}$ increased only marginally with $T_{a\text{-max}}$ (Figure 4B

and Table 2). On cooler days when $T_{a\text{-max}} \leq 26$ °C, mean diurnal $T_{b\text{-max}}$ was 40.3 ± 0.7 °C

(range = $38.7 - 41.2$ °C), whereas, on warmer days when $T_{a\text{-max}} \geq 36$ °C, mean diurnal $T_{b\text{-max}}$ was just 40.7 ± 0.4 °C (range = $39.1 - 42.7$ °C). Freckled Nightjars were slightly less

heterothermic on days with higher $T_{a\text{-max}}$ (Figure 5B and Table 2).

Discussion

To the best of our knowledge, this is the first study focusing on diurnal T_b patterns in free-ranging caprimulgids occupying hot, arid environments. Both species increased their mean and maximum diurnal T_b with increasing T_a, a physiological response common among birds (Weathers 1981, Tieleman and Williams 1999). Facultative hyperthermia can reduce EWL by storing heat in the body to be dissipated later through nonevaporative pathways, increasing non-evaporative heat loss when $T_a < T_b$ and decreasing heat gain when $T_a > T_b$ (Withers 1992, Tieleman and Williams 1999). The capacity to elevate T_b under laboratory conditions has been reported in several crepuscular and nocturnal avian species (e.g., Bartholomew et al. 1962, Lasiewski and Dawson 1964, Ligon 1968, Dawson and Fisher 1969, Ligon 1969, Weathers et al. 2001, O'Connor et al. 2017). Chaplin et al. (1984) observed an elevated diurnal T_b in fasted Great Horned Owls (*Bubo virginianus*) at high T_a and suggested that, because these owls obtain water from their diet (Duke et al. 1973), it may represent a physiological response to low preformed water intake. Thus, for nocturnal species where diurnal water intake is absent, an elevated diurnal T_b could help to reduce water losses and avoid dehydration.

The average increase in diurnal T_b above T_{b-mod} at $T_a \geq 38$ °C for the two free-ranging Rufous-cheeked Nightjars was similar in magnitude to that of several captive diurnal species at $T_a = 45$ °C (Tieleman and Williams 1999; 3.3 ± 1.28 °C). In the laboratory at $T_a = 38\text{-}40$ °C (O'Connor et al. 2017), this same population of Rufous-cheeked Nightjars maintained a mean T_b 1.9 °C lower than the free-ranging mean T_b of 42 °C at similar T_a. The dissimilarity in hyperthermia between free-ranging and captive Rufous-cheeked Nightjars at similar T_a likely reflects the complexity of natural thermal

environments compared to controlled laboratory conditions. Air temperature alone is rarely an accurate indicator of thermal stress, which instead incorporates solar radiation, wind and humidity (Porter and Gates 1969). The importance of multiple environmental variables presumably explains the overlapping hyperthermic responses of free-ranging Rufous-cheeked Nightjars with those reported by Tieleman and Williams (1999) at higher T_a.

At $T_a \geq 38$ °C, Freckled Nightjars did not allow their T_b to deviate much above $T_{b\text{-}mod}$. Under laboratory conditions, the same population of Freckled Nightjars regulated T_b at a similar level (39.5 °C) when exposed to $T_a = 38\text{-}42$ °C, increasing their T_b to 40.7 °C only at $T_a = 52$ °C (O'Connor et al. 2017). These data suggest that Freckled Nightjars defend T_b within a narrow range at $T_a > T_b$. Yet, Freckled Nightjars represent one of the most heterothermic caprimulgids investigated to date, with accounts of free-ranging individuals reducing skin temperature to near 10 °C (McKechnie et al. 2007, Smit et al. 2011). If, for instance, Freckled Nightjars evolved thermoregulatory strategies favouring energy conservation over heat tolerance, a thermal sensitivity tradeoff could have arisen, leading to a generalist T_b phenotype where both their optimal T_b and upper thermal limit has shifted downwards (Angilletta et al. 2010, Boyles et al. 2011a). In general, enzymes that perform well at low temperatures appear to function poorly at high temperatures (Hochachka and Somero 2002, Angilletta et al. 2003). We argue that the evolution of a T_b distribution shifted downward may have selected for increased enzymatic performance at lower T_b, in turn decreasing enzymatic performance at higher T_b. It is noteworthy that the phenotypic traits of caprimulgids associated with energy conservation (e.g., low resting metabolic rate; Lane et al. 2004b) and energy acquisition (e.g., enlarged and highly

vascularized buccal area; Cowles 1967) are probably the same traits that allow them to tolerate extremely high T_a by reducing their total heat load and increasing the surface area for EWL.

We found that diurnal HI was independent of T_{a-max} in Rufous-cheeked Nightjars, reflecting quantitatively similar deviations in T_b both below and above T_{b-mod} across cooler and warmer days. In contrast, Freckled Nightjars expressed a higher diurnal HI on cooler days because of their proclivity for reducing T_b below T_{b-mod} at cooler T_a, as seen during morning hours. This thermoregulatory pattern of reducing T_b during the morning has been observed in several crepuscular and nocturnal species (Brigham et al. 2000, Geiser 2004, Lane et al. 2004a, Smit and McKechnie 2010). The advantages of facultative reductions in T_b during the morning hours are two-fold. First, a reduced T_b decreases the energetic cost of maintaining an elevated T_b at low T_a. Secondly, reducing T_b around sunrise, nightjars may be able to exploit solar radiation as an exogenous energy source and passively rewarm to normothermic T_b, thereby reducing metabolic cost of rewarming (McKechnie and Wolf 2004).

Diurnal T_b was more variable in the two free-ranging male Rufous-cheeked Nightjars compared to the one incubating female. Incubation likely places large thermoregulatory demands on adults because of the sensitivity of developing embryos to both low and high temperatures (Webb 1987, Conway and Martin 2000, DuRant et al. 2013). Consequently, incubating adults would be predicted to thermoregulate more precisely, a requirement that limits adaptive thermoregulatory strategies and increases energy and water demands (Grant 1982, Haftorn and Reinertsen 1985, Thomson et al. 1998, Lane et al. 2004a). Walsberg and Voss-Roberts (1983), for example, observed

body temperatures 0.3 - 1.9 °C lower in incubating Turtle doves (*Streptopelia risoria*) compared to non-incubating individuals. Although based on very small sample sizes, our data raise the possibility that, during the diurnal period when T_a approaches or exceeds T_b, incubating female Rufous-cheeked Nightjars thermoregulate more precisely compared to non-incubating individuals, likely placing greater strain on their water balance.

Both Rufous-cheeked Nightjars and Freckled Nightjars had relatively labile T_b distributed unimodally, a pattern that contrasts with the distinct circadian rhythm of T_b typical of most birds and mammals, which results in a bimodal T_b distribution (Aschoff 1982, Refinetti and Menaker 1992, Smit et al. 2013). Absolute differences between mean active-phase (twilight and nocturnal periods combined) and mean rest-phase T_b were only 0.7 and 0.9 °C for Rufous-cheeked Nightjars and Freckled Nightjars, respectively, values substantially smaller than the 2.3 °C expected from the scaling of this trait (Prinzinger et al. 1991). Small differences between rest-phase and active-phase T_b have been reported in several crepuscular and nocturnal species (Siegfried et al. 1975, Chaplin et al. 1984, Bech and Nicol 1999, Smit et al. 2008). Consequently, the shape of the circadian rhythm in T_b for crepuscular and nocturnal birds does not appear to conform to the exaggerated active/rest-phase T_b differences seen among diurnal species (e.g., Bartholomew and Dawson 1954, McKechnie and Smit 2010, Smit et al. 2013), at least not during the summer when diurnal T_a is higher. Our understanding of the circadian rhythm of T_b for crepuscular and nocturnal birds, especially that of highly heterothermic groups like caprimulgids, would benefit from free-ranging T_b studies on non-migratory species

during winter to see if diurnal T_b remains elevated at colder daytime T_a or exhibits a more reduced rest-phase T_b.

Summary

Free-ranging Rufous-cheeked Nightjars and Freckled Nightjars increased T_b with increasing T_a during the diurnal period, an adaptive thermoregulatory pattern reducing EWL. At $T_a \geq 38$ ºC, Rufous-cheeked Nightjars had a mean $\Delta T_b - T_{b\text{-mod}}$ of 2.3 ºC, whereas Freckled Nightjars had a mean $\Delta T_b - T_{b\text{-mod}}$ of 1.1 ºC. Given that Freckled Nightjars are one of the most heterothermic caprimulgids investigated to date, the reduced T_b lability above $T_{b\text{-mod}}$ raises questions regarding the co-adaptation between thermoregulation and thermosensitivity among highly heterothermic groups. Furthermore, the observed variation in hyperthermia magnitude at similar T_a underscores the importance of field-based studies for determining thermoregulatory costs at the species, and individual, level. We advocate more field-based studies measuring complex physiological responses like T_b are needed to provide a more accurate picture of the thermoregulatory strategies used by animals under natural conditions. Freckled Nightjars displayed a marginally higher HI at lower $T_{a\text{-max}}$, whereas Rufous-cheeked Nightjars expressed a similar HI across all $T_{a\text{-max}}$. Finally, both species displayed an atypical circadian rhythm of T_b, resulting in a unimodal T_b distribution that contrasts with the bimodal T_b distribution common among mammals and birds.

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