# Torpor in an African caprimulgid, the freckled nightjar *Caprimulgus tristigma*

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Recent data suggest that facultative hypothermic responses such as torpor are more important in the energy balance of birds from tropical and sub-tropical regions than previously thought. We used telemetric measurements of skin temperature ($T_{skin}$) for five individuals on 151 bird-nights to investigate the occurrence of torpor during winter in an 81 g African caprimulgid, the freckled nightjar *Caprimulgus tristigma*. We found that freckled nightjars have the capacity to enter torpor, with a minimum observed $T_{skin}$ of 12.8°C. During the torpor bouts we observed, complete rewarming typically occurred after sunrise, and coincided with the availability of solar radiation. There was considerable inter-individual variability in the frequency and depth of torpor bouts, with one female nightjar exhibiting particularly frequent and deep torpor. Our results confirm the ability to use torpor by a nocturnal aerial insectivore from the Afrotropics, and reiterate the variability in patterns of torpor that can exist within a population.

The evolution of endothermy increased the likelihood that energy requirements would sometimes exceed availability, particularly in small species with high mass-specific rates of heat loss (Dawson and Whittow 2000). Approximately 100 bird species are known to reduce rest-phase energy requirements by means of facultative hypothermic responses, traditionally categorized as hibernation, torpor or shallow hypothermia (Prinzinger et al. 1991, Reinertsen 1996, McKechnie and Lovegrove 2002). One avian taxon containing species that commonly employ torpor (pronounced decreases in body temperature ($T_b$) for <24 h) is the suborder Caprimulgi (*sensu* Sibley and Ahlquist 1990). Species in this group are predominantly nocturnal aerial insectivores, and as a result, face significant decreases in prey availability at low air temperatures ($T_a$; Holyoak 2001, Brigham et al. 2006). Further energetic constraints are imposed on moonless and/or cloudy nights when ambient light levels are too low to permit prey acquisition (Jetz et al. 2003). In the last decade, telemetric studies of thermoregulation in free-ranging

caprimulgids have demonstrated that many species regularly reduce their $T_b$ below normothermic levels, but have also revealed considerable variation in patterns of torpor among species (Brigham 1992, Kissner and Brigham 1993, Brigham et al. 2000, Körtner et al. 2001, Fletcher et al. 2004, Lane et al. 2004). One North American species, the common poorwill *Phalaenoptilus nuttallii*, is the only bird known to hibernate (Jaeger 1948, Woods 2002, Woods and Brigham 2004).

Because patterns of torpor have been documented in species that differ widely in habitat and/or foraging behaviour, the Caprimulgi is a useful model taxon for elucidating the ecological determinants of torpor. In this study, we investigated patterns of winter thermoregulation in free-ranging freckled nightjars *Caprimulgus tristigma*. Like the common poorwill of North America, freckled nightjars winter in relatively arid habitats, are sedentary, and hawk flying insects from the ground (Holyoak 2001, Hockey et al. 2005). Moreover, freckled nightjars experience substantial seasonal

fluctuations in food availability, and activity levels are markedly reduced during winter (R. A. M. Ashdown and A. E. McKechnie unpubl. data). In view of their ecological similarities to common poorwills, we predicted that freckled nightjars would regularly exhibit pronounced torpor and potentially hibernate.

## Materials and methods

### Study site

Our study was conducted in Kgaswane Mountain Reserve ($25°43'$S, $27°11'$E), Northwest Province, South Africa, during the austral winter of 2006. The reserve is situated near the western end of the Magaliesberg mountain range at ca. 1,400 m a.s.l. The area experiences predominantly summer rainfall, with a mean annual precipitation of $612 \pm 181$ mm (1970–2005, South African Weather Service) in the nearby town of Rustenburg (ca. 5 km from the study site). Our study was conducted around the periphery of the wetland and savanna in the centre of the reserve, with nightjars typically roosting on surrounding rocky outcrops and boulder-strewn slopes. Vegetation in typical roosting habitat consisted of a mix of sparse, short grasses interspersed with dense shrubs, together with small trees among weathered rocks.

### Air temperature measurements

We measured $T_a$ in the central area of the reserve using a miniature data logger (iButton Thermochron, Dallas Semiconductor, Dallas, USA, resolution $= 0.5°C$) housed in a ventilated polystyrene cup suspended in the shade approximately 3 m above the ground. After the study, the iButton was calibrated in a water bath over the $T_a$ range encountered during data collection, using a mercury thermometer (resolution $= 0.2°C$) with an accuracy traceable to the US National Bureau of Standards. Air temperature was also recorded with a monolytic temperature transducer (LM 335, calibrated as described above) connected to the data logger we used to record detailed $T_{skin}$ traces from focal individuals (see below).

### Skin temperature measurements

During March 2006, we caught six freckled nightjars (3 males, 3 females) at night using a handheld spotlight and net, or by playing back vocalisations to lure birds into mist nets. Immediately following capture, a temperature-sensitive FM transmitter (3.0 g) emitting a frequency between 150.380 and 150.787 MHz (model PD-2T, Holohil Systems, Carp, Ontario,

Canada) was attached dorsally between the scapulars of each bird, using a harness constructed from Teflon ribbon (6.5 mm width, Telonics, Mesa AZ, USA.). The harness design was modified from that shown in Fig. 18.2 of Kenward (2000). Each transmitter had previously been calibrated in a water bath at temperatures between $5°C$ and $45°C$, using a mercury thermometer (resolution $= 0.2°C$) with an accuracy traceable to the US National Bureau of Standards. The $r^2$-values for the transmitter calibration curves ranged from 0.988 to 0.999. The skin temperature ($T_{skin}$) of tagged individuals was monitored during the winter of 2006 using two methods. First, we used a custom-built data logger (McKechnie et al. 2004) during the period 28 May–28 July to record data from a single transmitter at a time, with the pulse interval recorded every ten minutes when the focal bird was within range of the receiver. Second, we collected data manually every 0.5–3 h during the period 6–28 July, using a broad-band communications receiver (IC-R10, Icom, Bellevue, WA) and timing a minimum of 20 pulse intervals using a stopwatch. $T_{skin}$ was estimated from pulse intervals using the calibration curve previously determined for each transmitter. The modulation of pulses also allowed us to assess whether an individual was active or roosting at any particular time. One tagged bird (male) was eaten by a black-backed jackal *Canis mesomelas* between April 22 and May 14 and around the same time, another tagged bird (female) moved to a relatively inaccessible roost site beyond the boundary of the reserve. The data presented here were collected from the remaining four birds (two males, two females) tagged in March, and an additional female bird that we captured on 15 July. We held the latter individual in a field laboratory for 16 h, to compare $T_{skin}$ and $T_b$ (see below), before releasing it on the evening of 15 July with a transmitter attached.

### Skin vs body temperature

To assess the relationship between our measures of $T_{skin}$ and core $T_b$, we simultaneously measured both variables at $T_a$s between $9.9°C$ and $27.7°C$ for the single female nightjar caught on 15 July which we held captive for 16 h. We measured $T_b$ using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-18, Physitemp, Clifton NJ) inserted ca. 2 cm into the cloaca, a depth at which a slight withdrawal did not result in a decrease in the temperature reading. A second thermocouple was used to simultaneously measure $T_a$. The bird was normothermic throughout its time in captivity.

## Data analysis

Values are presented as means $\pm$ SD. The regression model that provided the best fit to the $T_b$, $T_{skin}$ and $T_a$ data for the one bird in which we measured these variables simultaneously was determined following Song et al. (1997) To objectively distinguish between normothermy and torpor, we calculated the lower limit of normothermic $T_{skin}$ for each tagged individual, below which we assumed it to be in torpor. We assumed that normothermic $T_{skin}$ is normally distributed and centred on the modal $T_{skin}$ value. We then fitted a normal distribution shaped by $T_{skin} \geq$ modal value to the data for each individual, and calculated the lower 99% confidence limit. To account for variability associated with $T_b - T_{skin}$ gradients, we conservatively took the lower limit of normothermic $T_{skin}$ as the lower 99% $T_{skin}$ value $-3^{\circ}$C. Our estimates of the lower limit of normothermic $T_{skin}$ averaged $30.4 \pm 0.3^{\circ}$C for three female birds, and $35.4^{\circ}$C for two males.

## Results

The body mass of the five tagged nightjars and two additional individuals caught at the study site in 2005 was $81.1 \pm 14.2$ g. During the period when we collected data manually (July 6–28), birds were typically active for approximately one hour following dusk, with sporadic activity bouts until ca. midnight.

In the female nightjar that we used for simultaneous measurements of $T_b$ and $T_{skin}$, $T_{skin}$ was predictably related to $T_b$, with $T_b - T_{skin}$ decreasing non-linearly with $T_b - T_a$. The relationship was best described by a polynomial regression model, where $T_b - T_{skin} = -5.8302 + 0.5415(T_b - T_a) - 0.0074(T_b - T_a)^2$ ($r^2 = 0.890$). Even when $T_b$ was ca. $30^{\circ}$C higher than $T_a$, $T_{skin}$ typically remained within $4^{\circ}$C of $T_b$. Moreover, the $T_b - T_{skin}$ gradient we measured is likely to be an overestimate, since measurements were made directly after the transmitter was attached, and backpack-mounted $T_{skin}$ tags tend to settle in closer contact with the skin following the release of tagged individuals (R. M. Brigham pers. obs.).

We obtained manual $T_{skin}$ measurements for a total of 116 bird-nights, and detailed $T_{skin}$ traces using the data logger for a further 35 bird-nights. Four out of the five tagged individuals entered torpor during the course of the study period, with only the female tagged in July never becoming torpid. In most cases, $T_{skin} > 37^{\circ}$C was maintained until ca. 23:00 (ca. 5 hr after sunset; Fig. 1). Thereafter, $T_{skin}$ typically declined to below $33^{\circ}$C until approximately sunrise (Fig. 1). The minimum $T_{skin}$ was $25.3 \pm 7.6^{\circ}$C (mean of single lowest $T_{skin}$ value for each individual). However, minimum
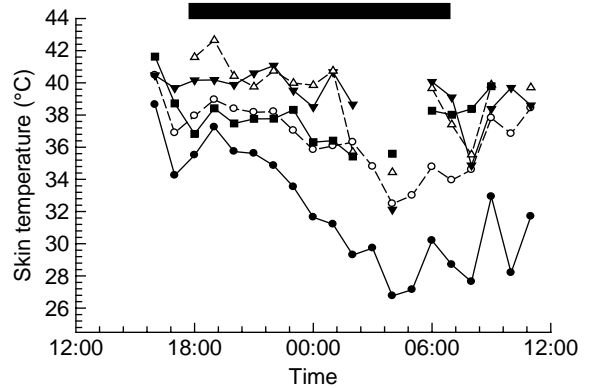


Fig. 1. Hourly mean skin temperature ($T_{skin}$) in five freckled nightjars *Caprimulgus tristigma* on 116 bird-nights during July 2006. Data were pooled to the nearest hour (e.g., a datum for 06:00 is the mean of all measurements between 05:30 and 06:30). Individuals are indicated using different symbols. Gaps for some individuals indicate periods when data were collected >1 h apart. For the sake of clarity, error bars are not plotted. The dark bar at the top indicates the period between sunset and sunrise.

$T_{skin}$ differed greatly among individuals, varying from $12.8^{\circ}$C to $32.8^{\circ}$C (Fig. 2).

The four tagged individuals that entered torpor varied considerably in the frequency, depth and duration of bouts. One female bird entered torpor every night during the study period, and 38% of our $T_{skin}$ measurements for this individual were indicative of torpor (Fig. 2a). The latter individual typically defended a $T_b$ setpoint between $25–30^{\circ}$C for most of the night, partially rewarmed to above $30^{\circ}$C before sunrise, and then exhibited transient cooling before rewarming again after sunrise (Fig. 3a, d). Minimum $T_{skin}$ during this transient cooling period was sometimes lower than the torpor setpoint defended earlier (Fig. 3a). Similar patterns were exhibited by a second female, which also reduced $T_{skin}$ to below $30^{\circ}$C on several nights during the study (Fig. 2b). Both females typically rewarmed 1–2 h after sunrise. On the morning of 13 July, they delayed rewarming until ca. 3 hr after sunrise (Fig. 3c), the approximate time at which thick cloud cover cleared. In contrast, the two males entered torpor only rarely, with 17% and 18% of $T_{skin}$ values within their respective torpor ranges (Fig. 2c, d). Moreover, modal normothermic $T_{skin}$ was ca. $3^{\circ}$C higher, and the range of normothermic $T_{skin}$ narrower, in male nightjars compared with females (Fig. 2).

## Discussion

Our results reveal that freckled nightjars possess the physiological capacity to use torpor, confirming the
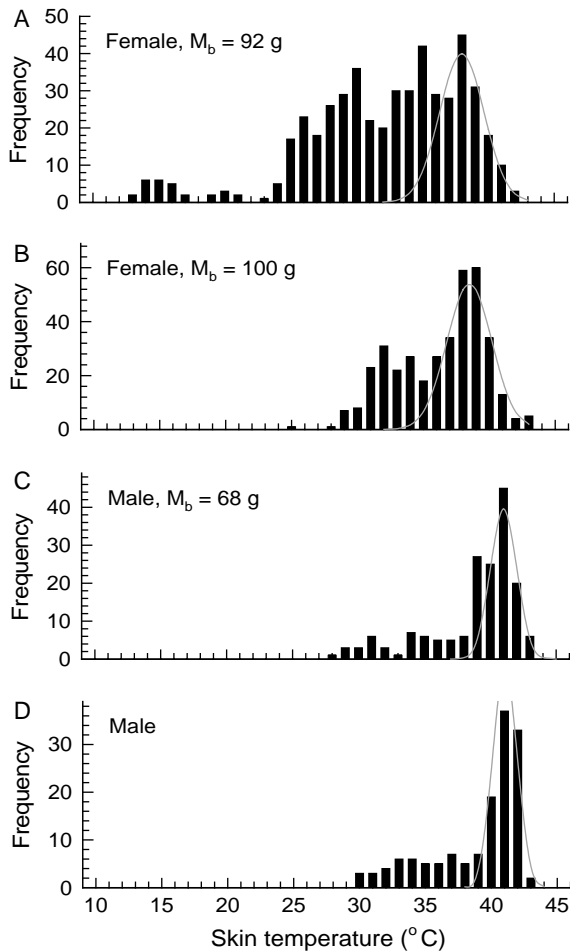
Fig. 2. Frequency distributions of skin temperature ($T_{skin}$) in four freckled nightjars *Caprimulgus tristigma* during July 2006. Each graph shows data for one individual. Sex and body mass ($M_b$) upon capture are provided for each individual, with the exception of the individual in graph D, which was not weighed. The grey line in each graph represents a normal distribution fitted to $T_{skin} \geq$ modal value.



Fig. 3. Skin temperature ($T_{skin}$, dots) recorded in a female freckled nightjar *Caprimulgus tristigma* during four non-consecutive 24 h periods during July 2006. Air temperature ($T_a$) is shown as a solid line. The dark bar at the top of each panel indicates the period between sunset and sunrise. The traces in panels A and D were typical for this individual, with panels B and C showing a 48 h period during which the bird reduced its $T_b$ to unusually low levels. The $T_{skin}$ of 12.8°C recorded at 07:20 on 13 July was the lowest value recorded during the study. In panels A and D, episodes of partial rewarming referred to in the text are indicated by arrows.

occurrence of this phenomenon in an Afrotropical caprimulgid. One female in our study population exhibited much deeper and more frequent torpor than other tagged individuals, but we consider it highly unlikely that these low $T_{skin}$ measurements reflect an experimental artifact (e.g., a loose harness), for two reasons. First, the timing of changes in $T_{skin}$ in this individual (e.g., partial rewarming before sunrise discussed above) was predictable between days, and occurred independently of $T_a$. Second, had the tag on this bird not been in close contact with its skin, we would expect $T_{skin}$ measurements to fluctuate unpredictably during periods of activity, a pattern that did not occur. Although some studies have revealed only ir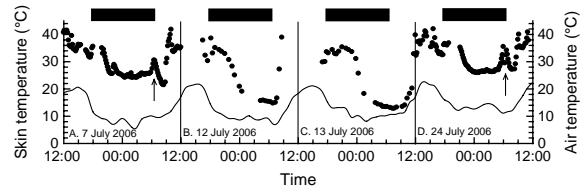regular bouts of torpor by a subset of individuals in a population (Fletcher et al. 2004, Lane et al. 2004), the use of torpor in our study differed among individuals in a much more consistent fashion, with more pronounced and frequent torpor in two out of three females compared to males (Fig. 2).

Our simultaneous measurements of $T_b$, $T_{skin}$ and $T_a$ for an individual *C. tristigma* are consistent with observations that $T_{skin}$ is a good predictor of $T_b$ in free-ranging caprimulgids (Brigham 1992, Brigham et al. 2000, Körtner et al. 2001). The lowest $T_{skin}$ we recorded in a freckled nightjar (12.8°C) occurred at $T_a =$ ca. 10°C (Fig. 2c), suggesting that the corresponding $T_b$ value was very close to $T_{skin}$, on account of the small $T_{skin} - T_a$ gradient. It is noteworthy that the individual for whom this $T_{skin}$ was recorded typically maintained $T_{skin} > 25$°C during torpor bouts, but on two nights reduced $T_b$ to considerably lower levels (Fig. 3).

Freckled nightjars were typically active shortly after sunset before reducing $T_b$ around midnight, with $T_b$ minima occurring shortly before sunrise (Fig. 1 and 3). A pattern of predominantly nocturnal torpor is the same as that exhibited by tawny frogmouths *Podargus strigoides* (Körtner et al. 2001), but contrasts with the pattern of mainly diurnal torpor exhibited regularly by Australian owlet-nightjars *Aegotheles cristatus* and occasionally by whip-poor-wills *Caprimulgus vociferus* (Brigham et al. 2000, Lane et al. 2004). Foraging by nightjars in the hours following sunset typically reflects the peak in food availability that occurs at this time (Jetz et al. 2003), and the activity pattern we observed in *C. tristigma* likely corresponds to temporal changes in aerial insect abundance during the course of a night. Our observation that complete rewarming occurred later during the cloudy morning of 13 July than on sunny mornings, provides circumstantial evidence for solar radiation-assisted rewarming. Solar radiation-assisted rewarming from torpor appears to be

important in several other species of caprimulgids (Körtner et al. 2001, Woods 2002, Woods and Brigham 2004), as well as in several mammalian species (Geiser et al. 2002, Mzilikazi et al. 2002)

We found no evidence of hibernation similar to that observed in common poorwills (Jaeger 1948, Woods 2002, Woods and Brigham 2004). The ecological similarities between freckled nightjars and common poorwills led us to hypothesize that freckled nightjars also use multi-day torpor bouts, but our data suggest that ecological factors alone may not determine the occurrence of avian hibernation. However, freckled nightjars also occur in very arid habitats in the western parts of southern Africa (Hockey et al. 2005), and we believe that investigations of these populations are required before firm conclusions can be drawn regarding the unique nature of common poorwill hibernation.

In summary, our data confirm that a non-migratory African caprimulgid uses torpor during the colder and drier part of the annual cycle, and add to the increasing body of literature pointing to the importance of facultative hypothermic responses in the energy balance of taxonomically diverse birds from tropical and subtropical regions (Prinzinger et al. 1981, Krüger et al. 1982, Brigham et al. 2000, Merola-Zwartjes and Ligon 2000, Schleucher 2001, McKechnie and Lovegrove 2002).

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