Seasonal Use of Torpor by Free-Ranging Australian Owlet-Nightjars (*Aegotheles cristatus*)

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ABSTRACT

With the exception of some data for common poorwills (*Phalaenoptilus nuttallii*) and anecdotal reports for a few other species, knowledge about the use of torpor by free-ranging birds is limited. Our study was designed to assess the use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). We selected this species for study because of their relatively small body size (50 g), arthropod diet, nocturnal sedentary nature, taxonomic affiliation with other birds for whom the use of torpor is well documented, use of cavity roosts, and because of the cold winter (mean July minimum ambient temperature [T_a] of approximately 0°C) in the study area. We tracked 12 owlet-nightjars carrying temperature-sensitive transmitters for a total of 906 bird-days (range of 15–115 d per individual). Five different individuals entered torpor on 96 d in total. Torpor bouts occurred only between May 8 and September 8, the coldest period of the year. The lowest skin temperature (T_{skin}) recorded for any bird was 19.6°C, and the lowest core temperature was 22.4°C. Surprisingly, torpor was rarely used at night because birds usually foraged then. Instead, torpor typically began near dawn, even on cold nights. Torpor bouts beginning at dawn lasted approximately 4 h. On 36% of days when torpor was used at dawn, birds reentered torpor later in the day. Torpor was not used during the breeding season, but this period also corresponds to the warm part of the year. There were no distinct daily minimum, maximum, or mean T_a thresholds that could be used to reliably distinguish days when dawn torpor was used from those when it was not, although torpor was commonly employed when daily minimum T_a fell below 3.9°C. Our results show that even though Australia is typically thought of as a warm continent, at least some of the avifauna use torpor as a regular means of saving energy. We hypothesise that the reasons for this species' use of torpor include its ability to remain active all night foraging, either for terrestrial arthropods while walking or for flying insects taken on the wing, and/or its habit of roosting in cavities, which allows them to remain hidden in the daytime.

Introduction

Heterothermy in birds and mammals is a precisely regulated physiological response to variable ambient temperatures (T_a) and food availability. It is characterised by shifts between low body temperatures (T_b) during daily torpor or hibernation and the normothermic state when T_b is high (Wang 1989; Geiser and Ruf 1995). Because climate and food availability can vary considerably, many endotherms use heterothermy on occasions of bad weather or low food availability to reduce energy use.

The most common pattern of heterothermy known to occur in diurnal birds is termed "nocturnal hypothermia," which consists of a lowering of body temperature by about 5°C and a reduction in metabolic rate of 30%–40% (Reinertsen 1983; Maddocks and Geiser 1997). Although daily torpor has been recorded from eight orders of birds, it appears to be most common in the hummingbirds (Trochilidae) and nightjar relatives (Caprimulgidae; Reinertsen 1983). During daily torpor bouts, which typically last several hours, T_b drops by 4°–35°C, and metabolic rate drops by more than 50%. Prolonged torpor bouts (hibernation) have only been recorded in a single avian species, the common poorwill, *Phalaenoptilus nuttallii* (Jaeger 1949; Brigham 1992; C. P. Woods, unpublished data). In hibernating poorwills, T_b falls to approximately 5°C, and metabolic rate falls by more than 90% (Withers 1977).

Torpor and hibernation are strategies commonly used by mammals but not birds (Reinertsen 1983; Heller 1989), likely due to birds' ability to migrate over long distances and thus to largely avoid adverse climatic conditions and prolonged food shortages. However, in contrast to the general pattern of migration for birds in the northern hemisphere, many Australian birds are sedentary or only migrate relatively short distances (Ford 1989), perhaps due to the continent's isolation, glacial history, and/or the typically less severe seasonal changes in cli-

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mate. There is very little published research on heterothermy in birds in general, and studies on Australian birds with respect to torpor are especially limited (Dawson and Fisher 1969; Chan 1994; Körtner et al. 2000). Körtner et al. (2000) found that a large (~500 g) Australian caprimulgiform, the tawny frogmouth (*Podargus strigoides*), regularly entered shallow torpor that occurred in bouts of about 7 h duration after a short bout of activity at dusk. Frogmouths either resumed foraging activity or moved roosts at dawn and thereafter only occasionally reentered torpor.

Australian owlet-nightjars, *Aegotheles cristatus* (Aegothelidae), are poorly studied and rarely seen members of the order Caprimulgiformes, yet they are one of the most widespread nocturnal birds in woodland habitats throughout Australia (Schodde and Mason 1980). None of the hundred or so other species of Caprimulgidae, to which the owlet-nightjars are probably most closely related, nest and roost in cavities like *Aegotheles* (Cleere 1998). Most true nightjars (Caprimulgidae) roost and nest on the ground and rely on cryptic plumage to avoid detection. Most information about the ecology of owlet-nightjars is anecdotal (summarised in Schodde and Mason 1980; Hollands 1991; Debus 1994). We selected this species for study because of its relatively small body size (~50 g), largely arthropod diet, nocturnal sedentary nature, taxonomic affiliation with other birds for which the use of torpor is well documented, and because of the relatively cold winters (minimum mean T_a of ~0° during July) in the study area. We predicted that if the physiological response of owlet-nightjars to food shortages and adverse environmental conditions were similar to poorwills (Brigham 1992), then they would use short bouts of torpor lasting for several hours, principally on cold nights after a short bout of early evening foraging, but only outside of the breeding season (October–January; Brigham and Geiser 1997). We expected that owlet-nightjars would be one of the most likely candidates to use torpor given that, like many mammals who use daily torpor, they roost in cavities that may offer some level of protection from potential predators and not on the ground like most other species in the order (Brigham et al. 1998).

Material and Methods

Study Area

This study was principally conducted between August 15, 1996, and August 5, 1997, in Eastwood State Forest (30°35′S, 151°44′E) about 10 km southeast of Armidale, New South Wales. An additional individual carrying an implanted temperature-sensitive transmitter for measurement of core T_b was tracked at the study site from June 13 to August 16, 1999. One individual with both implanted and external temperature-sensitive tags was held captive during the winter (May–September) of 1999 to directly assess the relationship between T_{skin} and T_b.

The tree community of the 215-ha state forest is dominated by broad-leaved stringybark (*Eucalyptus caliginosa*), with Blakely's red gum (*Eucalyptus blakelyi*), ribbon or manna gum (*Eucalyptus viminalis*), yellow box (*Eucalyptus melliodora*), and fern-leaf wattle (*Acacia filicifolia*) also commonly occurring. The understory is open, and the ground cover consists chiefly of grasses (Ford et al. 1986). The area surrounding the forest has been extensively cleared, with the exception of a few patches of woodland on adjacent private properties.

Telemetry

We used external temperature-sensitive radio transmitters (model PD-2T, Holohil Systems, Carp, Ontario) both to assess temporal patterns of activity and to determine whether free-ranging owlet-nightjars used torpor. In 1999, we also used implanted single-stage transmitters (Sirtrack, Havelock North, New Zealand) to measure core T_b. In total, we monitored 12 free-ranging individuals (11 adults and one fledgling) over the course of the study. Owlet-nightjars were most often captured by luring them into mist nets by using call playbacks. After we captured the birds, we measured body mass and outfitted birds with 1.8-g transmitters, which were attached by using a backpack-style harness made of elastic thread modified after the method of Kenward et al. (1982, Fig. 2), a practice approved by the University of New England Animal Ethics Committee. Adult body mass at capture ranged from 42.0 g to 53.3 g ($\overline{X} = 48.2$). All birds except one were released within 1 h of capture. The individual we followed in 1999 had a 3.0-g transmitter implanted (see below) and was released 20 h after being captured. We presume that birds of both sexes were captured, but there are no external characteristics that reliably discriminate sex. However, our capture technique would presumably be biased toward males because they are more likely to respond to call playbacks.

The effective range of the external transmitters varied from 200 m to 1,000 m, depending on terrain. Each transmitter emitted a steady signal unless the orientation of the antenna changed when birds flew; stationary and moving birds could be distinguished by variability in transmitter pulse intensity. The transmitters were affixed so that the harness kept the temperature sensor in contact with the bird's skin in the interscapular region; thus, we recorded T_{skin} in a manner analogous to that used by a number of studies on small endotherms (e.g., Barclay et al. 1996). Transmitters were calibrated by the manufacturer to measure temperature from 0° to 40°C (± 0.5°C) based on fluctuations in pulse rate. T_{skin} was assessed 24 h a day for individuals within range of the receiver station. T_{skin} data were collected for 11 of the birds by using a five-element Yagi antenna attached to an automated Lotek SRX_400 (Lotek Engineering, Aurora, Ontario) receiver running version 3.61 W21 software. The receiver was programmed to register an event when it detected five consecutive (noise-free) transmitter pulses (pulse rate about 1/s at high temperatures). The receiver scanned all active (up to seven at any one time) transmitter frequencies once every 5 min and stored a data record if five consecutive pulses met the criteria. In addition to providing a means of measuring T_{skin} every 5 min, the fluctuations in signal intensity allowed us to assess whether birds were active (see Brigham et al. 1999 for description) whenever they remained in range of the receiver. Data were downloaded to a laptop computer at 2–7-d intervals.

For logistic reasons, the data for two birds (one individual was monitored with both systems) were recorded by using custom-made data loggers (Körtner and Geiser 1998) connected to a three-element Yagi antenna placed within 100 m of each bird's roosting location. The recording system consisted of a modified scanner receiver (i.e., using the signal detection output of a radio chip; Uniden Bearcat UBC60XLT) and a data logger based on a microprocessor (BASIC Stamp I, Parallax) powered by a 4- or 7-AmpH gel battery (battery life of 3 or 5 wk). The data logger measured the interval between two transmitter pulses and stored the data on an 8-kilobyte EEPROM (electrically erasable, programmable, read-only memory). Temperatures were recorded every 10 min, and data were downloaded to a laptop computer at 1–2-wk intervals. Given the precise nature of how both systems measured interpulse intervals, the data recorded by them are equivalent in terms of accuracy. The location of roosting birds was determined on most mornings, and sometimes during the night, to ensure that birds with transmitters roosted within range of data loggers. Occasionally, the antenna orientation or the location of the data logger had to be adjusted.

Due to the transient fluctuations in avian T_{b} (Reinertsen and Haftorn 1983) and to the fact that T_{b} of active birds can vary between 35° and 44°C under laboratory conditions (Bartholomew et al. 1962), we followed Brigham (1992) and operationally defined owlet-nightjars as having entered torpor when T_{skin} fell below 30°C. We never recorded or directly observed owlet-nightjars to be active (walking or flying) when T_{skin} was below 30°C.

We measured T_{a} ($\pm 0.5°\mathrm{C}$) from August 15, 1996, to June 15, 1997, by using a temperature-sensitive transmitter mounted 1 m above the ground on the trunk of a tree within 100 m of a known owlet-nightjar cavity roost. The Lotek receiver recorded signals from this transmitter in the same manner as for transmitters on birds. For the remainder of the study, T_{a} was measured at hourly intervals at two distant locations in the forest by using custom-made data loggers. The loggers were based on a microprocessor (Basic Stamp II, Parallax) and were equipped with eight temperature transducers (AD592; accuracy $\pm 0.35°\mathrm{C}$) each. Data were stored on an EEPROM, and the temperature records were downloaded every 3 wk. For analysis purposes, we used the mean from these two locations as our measure of T_{a} because neither was within 100 m of where owlet-nightjars roosted.

The captive bird (caught in Eastwood State Forest on November 13, 1998) was housed in a 3.6 × 1.8 × 2.0-m outdoor aviary, where it was exposed to natural photoperiod and temperature fluctuations. Water and food (primarily *Tenebrio* larvae but also beetles, moths, and grasshoppers) were provided ad lib. T_{skin} was measured as for free-ranging birds. T_{b} was measured in the captive and free-ranging birds by using implanted temperature-sensitive transmitters (Sirtrack) that were calibrated to the nearest 0.1°C against a precision mercury thermometer in a water bath. The wax-coated transmitters were implanted intraperitoneally while the birds were under isoflurane anaesthesia. Signals for both the internal and external transmitters of the captive bird were recorded directly to a microcomputer (Körtner and Geiser 1998).

Linear regressions were fitted by using the method of least squares (Zar 1984). Differences among physiological variables were tested by using one-way ANOVA or Student's *t*-test, as appropriate (Zar 1984). Differences in counts were tested by using a χ^2 test (Zar 1984). For all statistical analyses, we used a significance level of 0.05. Means are presented ± 1 SD. In reporting the results, N represents the number of torpor bouts, whereas n is the number of individual birds (unless otherwise noted).

Results

We found a highly significant correlation between T_{b} and T_{skin} for the captive bird ($r^2 = 0.85$, $P < 0.01$, $n = 11{,}014$ measurements; Fig. 1), which indicates that T_{skin} is a reliable indicator of core T_{b}. Further evidence that T_{skin} can be used to predict T_{b} comes from the fact that minimum measured T_{b} can be predicted from $T_{\mathrm{b}} - T_{\mathrm{skin}}$. On average, T_{skin} underestimated T_{b} by 3.0° ± 0.8°C. The underestimate ranged from a minimum of 1.0°C to a maximum of 5.9°C over a range of T_{a} from $-1.4°$ to 20.9°C. Values of T_{b} ranged from 26.4° to 42°C.

We monitored the 12 free-ranging birds carrying transmitters for a total of 906 bird-days. Individuals were followed from 15 to 115 d, with 10 individuals carrying active transmitters for more than 40 d each. Four truncated records were the result of depredation events that occurred while birds were active. To the best of our knowledge, birds always roosted alone in tree cavities, even newly fledged young (Brigham and Geiser 1997; Brigham et al. 1998); therefore, our temperature measurements were not confounded by any sort of huddling behaviour.

As predicted, we found strong evidence for the use of torpor by owlet-nightjars but only between August 19 and September 8, 1996; May 8 and August 5, 1997; and June 13 and July 21, 1999, periods that correspond to the cold season in the study area (Fig. 2). There was no evidence for birds using torpor during the breeding season (October–January; Brigham et al. 1997). The fledgling we tracked survived for 15 d after leaving

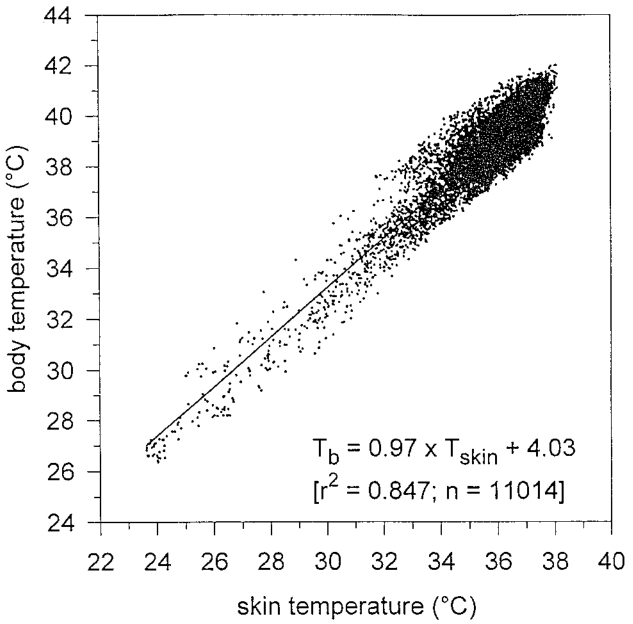

Figure 1. Plot of simultaneously collected T_{skin} and T_{b} values measured using an external and implanted temperature-sensitive radio transmitter. Data come from a captive owlet-nightjar over a range of ambient temperatures.

the nest, and it never entered torpor. All five birds we monitored during the torpor season (which we define as May 8–September 8) entered torpor. These individuals entered torpor on a total of 96 bird-days, although our records for 2 bird-days are incomplete and were not used further in the analysis. The lowest T_{skin} recorded was 19.6°C (Fig. 3), which occurred at 0936 hours on June 29, 1997. Minimum T_{skin} during torpor bouts was 25.1° ± 2.5°C (Fig. 4). The lowest core T_{b} measured for the free-ranging bird carrying an implanted transmitter was 22.4°C. The duration of the longest bout of torpor was 540 min (9 h) on June 27, 1997 (Fig. 4).

Contrary to our expectations, birds rarely entered torpor at night. Only two individuals did so and then only on seven occasions. Typically, tagged birds foraged until dawn (which begins when the sun is less than 12° below the horizon and lasts until sunrise) and entered torpor within 30 min of returning to cavity roosts. Dawn torpor was the most commonly observed and occurred on 90 of 94 bird-days when torpor occurred. On 34 bird-days, owlet-nightjars (all five individuals that used torpor) reentered torpor after arousing from dawn bouts (daytime torpor bouts) for periods that lasted approximately 90 min (Fig. 4). Daytime bouts commenced at least 4 h after sunrise. On only one occasion did a bird enter torpor only at night. True night is defined as the period when the sun is >12° below the horizon. On three occasions, birds (two different individuals) entered torpor only during daytime bouts. Overall, there were significant differences in the duration of torpor bouts and minimum T_{skin} during night, dawn, and daytime torpor bouts (duration $F = 17.3$, df $= 2,120$, $P < 0.001$; T_{skin} $F = 9.1$, df $= 2,119$, $P < 0.001$; Fig. 4). The statistical difference in bout length and minimum T_{skin} can be attributed to shorter daytime bouts and shallower torpor events at night.

Minimum T_{skin} in dawn torpor bouts was a significant predictor of minimum T_{skin} in daytime bouts ($y = 0.50x + 13.6$; $r^2 = 0.30$, $P < 0.05$; $N = 32$). Likewise, the duration (min) of dawn torpor bouts significantly predicted the duration of daytime bouts ($y = 0.34x + 30.7$; $r^2 = 0.22$, $P < 0.05$; $N = 31$).

Birds likely use cues about their own physiological state (e.g., Skutelsky 1996) and current environmental conditions to decide whether or not to enter torpor. Given that birds in our study typically entered torpor at dawn after foraging, one potential environmental cue they might use is T_{a} at dawn, which typically corresponds to the daily minimum T_{a}. Not surprisingly, values for mean daily minimum, mean daily maximum, and mean T_{a} during the 1996–1997 part of the study when torpor was used (May–September) were significantly lower than

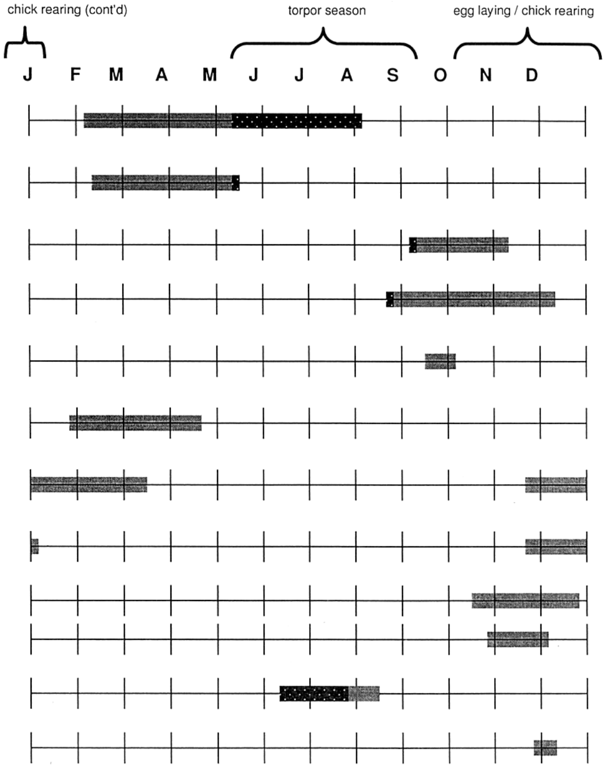

Figure 2. Summary of time periods over which 12 individual owlet-nightjars (11 adults, one fledgling) carried functioning radio transmitters. Stippled areas indicate the periods of time during which torpor bouts did (*dark-stipple bars*) and did not (*light bars*) occur. The period of the year when egg laying and chick rearing took place is indicated by the wavy line at the top.

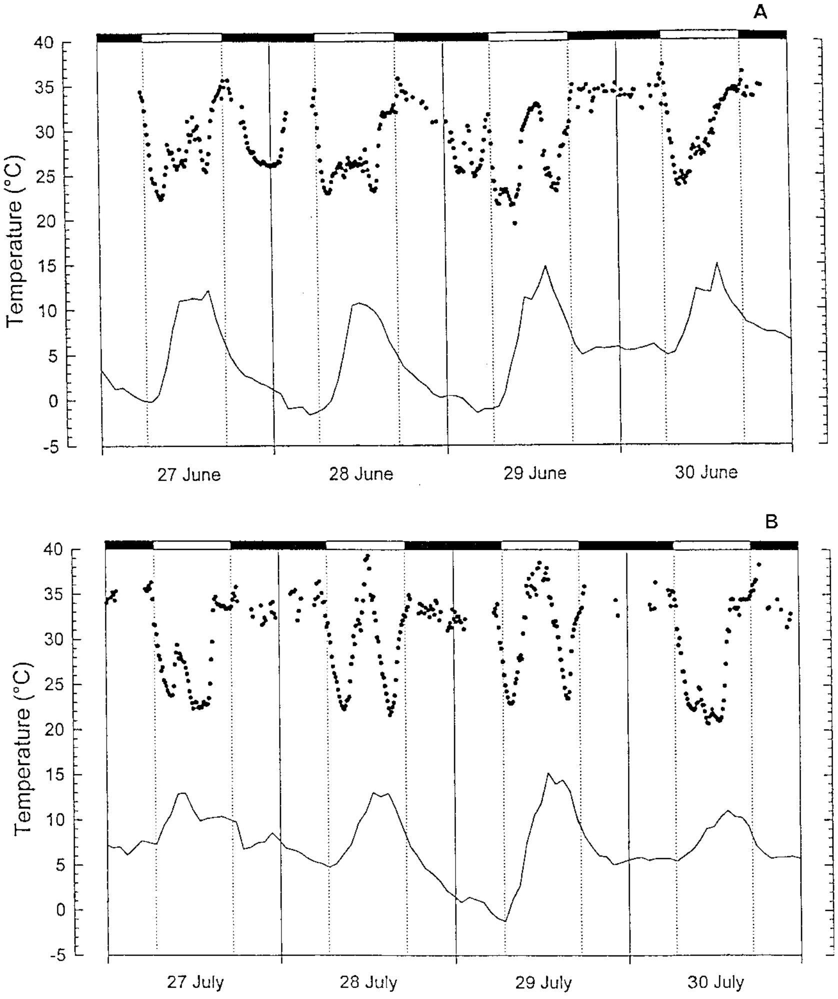

Figure 3. Plot of T_{skin} values (*dots*) for an individual owlet-nightjar (bird 777) and T_a (*solid line*) in relation to time for the period of (*A*) June 27–30, 1997, and (*B*) July 27–30, 1997, that illustrates in detail the pattern of use of torpor. The lowest T_{skin} recorded (19.6°C) occurred on June 29. Dark and light bars at the top of the figure correspond to the dark and light phases of the day. Note the use of both night and daytime torpor in June and the regular entry into biphasic daytime torpor but not night torpor in July.

those during the period when torpor was not used (October–April; mean minimum: 12.0° ± 4.0°C vs. 4.8° ± 5.0°C; mean maximum: 24.7° ± 4.2°C vs. 14.4° ± 3.4°C; and mean daily: 17.1° ± 3.3°C vs. 8.8° ± 3.9°C, respectively; *t*-tests, $P <$ 0.001 in all cases). There were, however, no significant differences in T_a between dates during the torpor season when any form of torpor was used ($N = 76$) versus dates when it was not ($N = 22$; mean minimum: 3.9° ± 4.3°C vs. 9.2° ± 6.1°C; mean maximum: 13.8° ± 3.0°C vs. 17.5° ± 3.6°C; and mean daily: 8.1° ± 3.3°C vs. 12.6° ± 4.5°C, respectively; *t*-tests, $P >$ 0.15 in all cases). The mean minimum T_a for all dates when dawn torpor was recorded ranged from −6.9° to 11.0°C. Minimum daily T_a never fell below 3.9°C (mean minimum T_a for days when dawn torpor was recorded) during the 1996–1997 breeding season.

Unfortunately, we never had more than two individuals carrying tags simultaneously during the torpor season. On 10 of the 11 nights when pairs of birds were monitored during this period, which albeit occurred at the beginning and end of the torpor season, birds used opposite strategies (one entered torpor and one did not).

Night torpor may be temperature dependent. Although our sample size is small (only two individuals on seven occasions in total), night torpor only occurred on nights when T_a fell below 4°C. This suggests that the cues for using dawn/day and night torpor may differ.

A plot of the differential between T_a and T_{skin} for one bird followed through the majority of the torpor season shows that T_{skin} differs between about 21° and 39°C over a T_a range of 0°–17°C. Because the minimum T_{skin} was not a function of T_a,

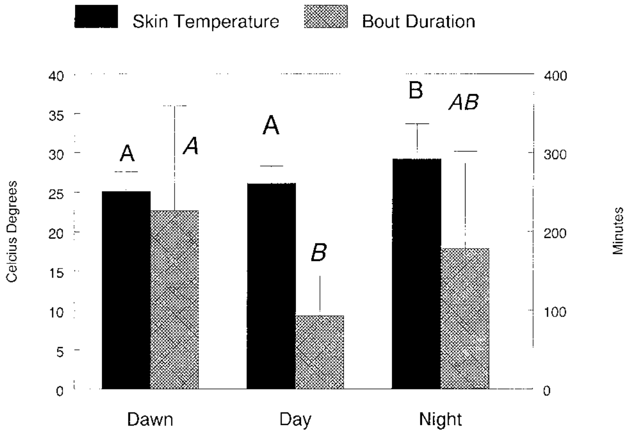

Figure 4. Histogram showing $\overline{X}$ and SE of minimum T_{skin} (*solid bars*) and torpor bout duration (*open bars*) for the three general periods of the 24-h cycle when owlet-nightjars entered torpor. Different letters above the bars indicate significant differences among the three periods. The sample sizes (N = bouts; n = birds) are as follows: *dawn* ($N = 61$, $n = 4$); *day* ($N = 34$, $n = 4$); *night* ($N = 7$, $n = 2$).

it appears that torpid owlet-nightjars regulated T_{skin} at or above 21°C. Thermoregulation during both normothermia and torpor is further emphasised by the relationship between the $T_{skin} - T_a$ differential and T_a. Both differentials increased with decreasing T_a and clearly show that owlet-nightjars are thermoregulating at low T_a in both physiological states (Fig. 5). However, the amplitude of the differential was largely independent of T_a.

Discussion

Our temperature data for the captive owlet-nightjar carrying both internal and external transmitters validate the assumption that T_{skin} is a reliable indicator of core T_b over a wide range of ambient temperatures. These data corroborate the results from studies where similar transmitters were carried by poorwills, bats, and sugar gliders (*Petaurus breviceps*; Brigham 1992; Audet and Thomas 1996; Barclay et al. 1996; Körtner and Geiser 2000). We thus have considerable confidence that our T_{skin} data for free-ranging birds can be used to accurately assess the degree to which torpor is used. Further supporting this contention was the fact that the Lotek telemetry system allowed us to measure activity by individuals objectively (Brigham et al. 1999). We found no evidence whatsoever for activity by individuals we defined as torpid.

Assuming the data for the five birds we followed during the cold part of the year are representative, our results support the prediction that Australian owlet-nightjars regularly enter torpor during the cold part of the year. It is noteworthy that our analysis assumes that use of torpor by an individual on any date is an independent event. In all likelihood, this assumption is untrue because our data are pseudoreplicated to some degree. However, our small sample size and the unequal distribution of torpor bouts among individuals due to the period of time we tracked them precludes a repeated measures analysis. Our data also support the prediction that torpor would not be used during the breeding season. However, contrary to our expectations, there were several substantial differences in the nature of torpor bouts between poorwills and frogmouths, on the one hand, and owlet-nightjars, on the other. Unlike poorwills and frogmouths (Brigham 1992; Körtner et al. 2000), owlet-nightjars rarely entered torpor at night; instead, on the vast majority of dates (96%), torpor bouts began at dawn. Dawn torpor bouts (approximately 4 h) were shorter in duration than the bouts of poorwills, which typically last about 8 h (R. M. Brigham, unpublished data). Also, unlike poorwills, owlet-nightjars often (after 36% of dawn bouts) reentered torpor in the afternoon. Regardless of when they occurred, owlet-nightjar torpor bouts are considerably shallower than those of poorwills, even though the minimum daily temperatures during the winter in the Armidale area are lower than

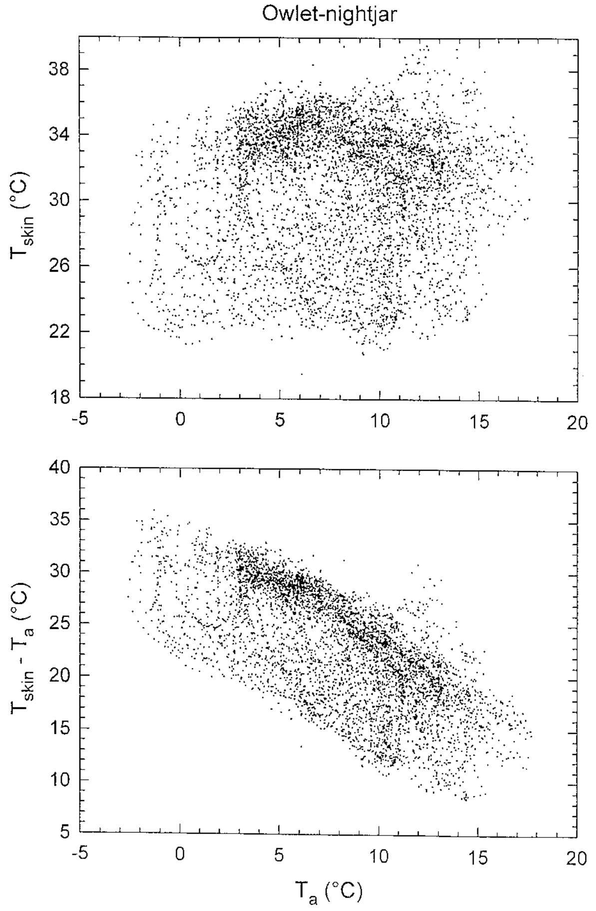

Figure 5. Plot of T_{skin} and $T_{skin} - T_a$ as a function of T_a for all values measured for an individual owlet-nightjar (bird 777) during day- and nighttime.

the temperatures regularly experienced by poorwills in the spring and fall when they enter torpor in Canada (Brigham 1992; Csada and Brigham 1994). The lowest minimum T_{skin} we recorded for an owlet-nightjar was >15°C higher than that recorded for poorwills. We found no evidence that owlet-nightjars used prolonged torpor (hibernated) in any fashion equivalent to poorwills (Jaeger 1949; C. P. Woods, unpublished data).

Interestingly, the timing of bouts differed markedly between owlet-nightjars and frogmouths even though both species were studied at the same site. One possible reason for the difference could be owlet-nightjars' ability to forage all night. These birds can forage while walking as well as from perches and while on the wing (Brigham et al. 1999). Foraging on the ground likely enables them to eat considerable numbers of ground-dwelling arthropods (Rose 1997), a strategy neither poorwills nor frogmouths can exploit. That owlet-nightjars almost always remained active all night (Brigham et al. 1999) implies that, regardless of temperature or other environmental conditions (e.g., moonlight), foraging opportunities exist on most nights, unlike for poorwills or frogmouths.

An alternative explanation for the concentration of torpor bouts during the daytime may reflect the unique (for Caprimulgiformes) habit owlet-nightjars have of roosting in cavities (Brigham et al. 1998). Cavity roosting allows birds to remain hidden in relative safety during the daytime, unlike poorwills and frogmouths, which both roost in exposed locations during the day. Known predation events on owlet-nightjars all occurred when birds were away from their roosts while foraging (Brigham et al. 1998). Further, it is likely that owlet-nightjars are exposed to lower T_a inside the roost than outside, at least during the morning (Kalcounis and Hecker 1996).

The tree cavities used as roosts by owlet-nightjars outside the torpor period were close to the ground and had no distinct aspect, which suggests that they are not chosen for exposure to high levels of solar radiation (Brigham et al. 1998). Low cavities in the large diameter part of a tree with substantial canopy closure should remain thermally stable (Kalcounis and Hecker 1996). Unfortunately, the low number of roost sites used by birds that entered torpor precluded a statistical analysis of cavity orientation, height, and so forth. Throughout the study period, radiotagged birds routinely changed roosts, using two to six different cavities. Because arousals from dawn torpor bouts often coincided with maximum T_a, we postulate that rewarming is partially due to the warming of tree roosts by the morning sun, although we could not directly evaluate this.

Similar to poorwills and insectivorous bats, owlet-nightjars showed no clear T_a threshold that allowed for the unambiguous separation of days on which owlet-nightjars did or did not enter daytime torpor (Audet and Fenton 1988; Brigham 1992). This conclusion is supported by the fact that on 10 of 11 nights when two birds carried transmitters, the two individuals used the opposite strategies (one entering torpor and one not). Further support comes from the fact that one bird entered torpor every morning for 64 consecutive days despite variable ambient conditions. We strongly suspect that temperature and arthropod availability are likely factors that in part determine whether birds will enter torpor, especially during the night. It is also likely there are factors specific to individuals that are also important. The fact that there was a significant predictive relationship between minimum T_{skin} and torpor bout duration during dawn bouts relative to daytime bouts supports the contention that the environmental conditions on any given day influence the characteristics of torpor. Although our data do not allow us to ascertain whether torpor during the day is used only in situations where individuals face energy emergencies (Carpenter and Hixon 1988; Bech et al. 1997), the similarity of bout duration and the common occurrence of torpor over a long period, which is more frequent than in any other species of which we are aware, argue against this hypothesis. It remains to be worked out how to evaluate body condition of free-ranging animals on a regular enough basis to answer this question definitively. In contrast to daytime torpor, night torpor occurred only on cold nights, which suggests that it is only used in situations where foraging is not successful.

In conclusion, our data suggest that torpor is a strategy regularly used by Australian owlet-nightjars at a temperate study site during the colder periods of the year. It remains to be seen, however, whether our observations on the thermoregulatory behaviour of owlet-nightjars are consistent across the species' entire geographical range. Given the ubiquitous distribution of these birds across the continent, an evaluation of variation in the thermoregulatory strategy by this species is warranted. What is clear from our data is that overall patterns of torpor use by these birds cannot be accurately predicted solely from knowledge about the ecology and torpor patterns of other Caprimulgiformes. Further data for this and other species are needed to elucidate more general patterns of avian torpor use in the field.

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