

Do Owls Use Torpor? Winter Thermoregulation in Free-Ranging Pearl-Spotted Owlets and African Scops-Owls

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ABSTRACT

Numerous avian taxa use torpor, which involves pronounced reductions in body temperature (T_b) to below normothermic levels. However, the occurrence of this phenomenon in owls (Strigidae) remains largely unknown. We investigated winter patterns of thermoregulation in the crepuscular 80-g pearl-spotted owlet *Glaucidium perlatum* and the strictly nocturnal 61-g African scops-owl *Otus senegalensis* by obtaining telemetric measurements of skin temperature (T_{skin}) from free-ranging individuals in the Kalahari Desert of southern Africa. Pearl-spotted owlets remained homeothermic throughout the study period, whereas African scops-owls routinely used shallow torpor, with T_{skin} reduced by 3.3°–8.6°C (pooled mean, 5.3° ± 1.1°C) below normothermic levels for 3–4 h after sunrise. The mean lowest T_{skin} recorded in three African scops-owl individuals was 29.0° ± 0.1°C. The thermoregulatory differences between these two species may be related to their diets and activity patterns. African scops-owls are almost exclusively insectivorous and experience a marked reduction in food availability on cold winter nights. In contrast, pearl-spotted owlets have more flexible activity patterns and include larger or diurnal vertebrate prey in their diet.

Introduction

Many birds are heterothermic endotherms and downregulate body temperature (T_b) to below normothermic levels during the rest phase. Heterothermic responses have been reported in 11 orders, in species ranging in body mass (M_b) from <3 to

6,500 g, and in a much wider variety of ecological contexts than previously thought (Körtner et al. 2000; McKechnie and Lovegrove 2002). Within the Coraciiformes, for instance, heterothermy occurs in both the smallest and largest representatives, namely, the 5-g Puerto Rican tody *Todus mexicanus* and the 360-g laughing kookaburra *Dacelo novaeguineae* (Merola-Zwartjes and Ligon 2000; Cooper et al. 2008).

Torpor, often defined as a reduction in rest-phase T_b below 30°C (Hudson 1978; Reinertsen 1996; Schleucher 2001; reviewed by Barclay et al. 2001), appears to be particularly important in offsetting the energetic costs of thermoregulation in birds whose food resources exhibit large spatial or temporal fluctuations in availability, for example, frugivores (Coliidae and Columbidae), nectarivores (Trochilidae and Nectariniidae), and insectivores (Todidae, Apodidae, Caprimulgidae, and Hirundinidae; McKechnie and Lovegrove 2002; Schleucher 2004). However, to better understand the adaptive value and evolution of avian torpor, a more thorough assessment of the phylogenetic distribution of this trait is needed (McKechnie and Lovegrove 2002; Schleucher 2004).

One of the most puzzling phylogenetic patterns in the occurrence of avian torpor concerns the order Strigiformes (sensu Sibley and Ahlquist [1990], but see Hackett et al. [2008]), which contains the suborders Caprimulgi (nightjars and allies) and Strigi (owls). Whereas the capacity for pronounced torpor is widespread in caprimulgids (Lane et al. 2004), it has not been reported in owls (Ligon 1969; Hohtola et al. 1994), an observation that is surprising in view of the close phylogenetic relationship of these two groups (Sibley and Ahlquist 1990). Only shallow reductions in T_b have been reported in two relatively large owl species, the snowy owl *Nyctea scandiaca* and the barn owl *Tyto alba* (Gessaman and Folk 1969; Thouzeau et al. 1999). In the latter study, barn owls that were starved in the cold for 8 d never reduced T_b by more than 5°C, despite M_b loss of >25% (Thouzeau et al. 1999). Several studies of smaller species, however, failed to document any evidence whatsoever for heterothermic responses, leading the authors to conclude that small owls can endure extended periods of energy stress without using torpor (Ligon 1969; Hohtola et al. 1994).

It is noteworthy, however, that all thermoregulatory studies on owls to date have been carried out under artificial conditions in laboratories, and we know very little about how wild owls thermoregulate in natural habitats. Data from free-living birds are particularly important in light of recent studies showing that many birds use torpor only under natural conditions (Brigham et al. 2000; Körtner et al. 2001; Fletcher et al. 2004; Lane et al. 2004; Cooper et al. 2008).

In arid environments with unpredictable rainfall and low productivity, torpor is thought to play an important role in

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balancing energy in many endotherms (Geiser 2004). To further explore the occurrence of torpor in owls, we investigated patterns of thermoregulation in free-living pearl-spotted owlets *Glaucidium perlatum* and African scops-owls *Otus senegalensis* in the Kalahari Desert of South Africa. The Kalahari Desert region is characterized by extremes of temperature, arid winters, and unpredictable precipitation during summer (Lovegrove 1993). Small owls inhabiting this area are thus likely to experience food shortages during cold and dry winter nights when the availability of arthropod prey is reduced.

Material and Methods

Study Site

Free-ranging pearl-spotted owlets and African scops-owls were studied in Molopo Nature Reserve (25°47'S, 22°56'E) at an elevation of approximately 1,000 m above sea level in the Northwest Province, South Africa, from June 1 to August 9, 2007 (austral winter). This reserve falls within the semiarid Kalahari Desert region, where the climate varies seasonally between dry and cool winters (May to August) with frequent subzero temperatures at night and hot summers (November to March) with spatially and temporally unpredictable patterns of rainfall (Lovegrove 1993). The mean \pm SD annual rainfall recorded in Molopo Nature Reserve over a 50-yr period was 332 ± 105 mm (Meyer et al. 2007). Our study took place in the southern part of the reserve, where the vegetation consisted mainly of mixed *Acacia* spp. and *Boscia albitrunca* savannah on deep red sand and scrub on irregular dry calcrete pans.

Air Temperature Recording

Air temperature (T_a) was measured in the study area using two temperature-sensitive data loggers (iButton Thermochron, Dallas Semiconductor, Dallas, TX). The iButtons were housed in ventilated polystyrene cups suspended in the shade about 2 m above the ground, at two sites about 6 km apart (<10 m difference in altitude). Before the study, the iButtons were calibrated in a temperature-controlled water bath (model ME, Julabo Labortechnik, Seelbach, Germany), using a mercury thermometer (resolution = 0.2°C) with an accuracy traceable to the U.S. National Bureau of Standards, over the approximate T_a range experienced at the study site during winter.

Capture of Birds

Eight pearl-spotted owlets (three males, five females) and four African scops-owl (all males) were caught during June and July 2007 using mist nets and call playback or spring traps baited with mealworms. Neither species displays sexual dimorphism in plumage coloration, but females can be distinguished by their softer and higher-pitched calls (Hockey et al. 2005). All four individual African scops-owls were caught in adjacent territories (~1.5 km apart) and gave low-pitched calls. They were also highly aggressive toward call playback, and we strongly suspect that all these individuals were males.

Skin Temperature Recording

Skin temperature (T_{skin}) was measured using temperature-sensitive VHF transmitters (2.5 g, model PD-2T, Holohil Systems, Carp, Ontario, Canada) emitting a frequency between 150.061 and 150.741 MHz. These transmitters were calibrated in a temperature-controlled water bath at temperatures between 5° and 45°C, using the mercury thermometer (resolution = 0.2°C). A broadband communications receiver (IC-R10, Icom, Bellevue, WA) was used to obtain signals from the transmitters during calibration. The relationships between pulse rate and temperature were best described by second-order polynomial regressions, with all r^2 values > 0.995. Shortly after each owl was captured, a transmitter was secured dorsally beneath the feathers in the interscapular region, using a harness constructed from clothing elastic inserted through a 6.5-mm Teflon ribbon (Telonics, Mesa, AZ), a design modified from Figure 18.2 of Kenward (2000), following McKechnie et al. (2007). This method has been widely used for the measurement of T_{skin} in free-ranging caprimulgids (Brigham 1992; Brigham et al. 2000; McKechnie et al. 2007), and loose harnesses can be readily detected from T_{skin} readings that vary unpredictably. Owls, however, are more likely to damage harnesses than are nightjars; if there were any indications that a harness had come loose, we excluded data from that individual.

The signals emitted by Holohil transmitters have been reported to drift, and they should be recovered after data collection and recalibrated (J. B. Williams, personal communication). We recovered transmitters from two African scops-owls 5 wk after they were tagged and recalibrated them at three temperatures (19°, 29°, and 39°C) in the water bath. At 39°C, the pulse rates of both transmitters were higher than they were during initial calibration (equivalent to a mean change in T_{skin} readings of 1.2°C), but at 19° and 29°C, the pulse rates were identical to initial calibration. Since we were not able to retrieve transmitters from any of the pearl-spotted owlets, we examined T_{skin} values of the pearl-spotted owlets to investigate whether there were any consistent changes in T_{skin} that might be the result of transmitter drift. We compared each individual's nighttime (1800 to 0500 hours) T_{skin} data recorded during the first 4 d to the last 4 d of data collection but found no significant differences.

We recorded T_{skin} from June 1, 2007, to August 9, 2007, in eight pearl-spotted owlets (data collection per individual of 39, 39, 36, 32, 20, 12, 11, and 3 d) and four African scops-owls (28, 22, 6, and 4 d of data collection). We used a broadband communications receiver (IC-R10, Icom, Bellevue, WA) to obtain signals from the transmitters. Readings from each transmitter were taken at 0.1–5-h intervals during the night and day. For each reading, the duration of a minimum of 20 pulse intervals was timed manually using a stopwatch to obtain T_{skin} estimations. Manual measurement of T_{skin} using a stopwatch is widespread in such studies and appears to be consistent with results obtained using digital data loggers (Rismiller and McKelvey 1996). We converted pulse intervals to T_{skin} values using the calibration curve previously determined for each

transmitter. While measuring T_{skin} , the modulation of pulses allowed us to assess whether an individual was active and moving about (Brigham et al. 1999, 2000).

One pearl-spotted owlet and two African scops-owls were held in a field laboratory for ~16 h before release to compare T_{skin} , T_b , and T_a gradients. T_{skin} and cloacal T_b were measured simultaneously at $5^\circ \leq T_a \leq 35^\circ\text{C}$. The owls were placed in 1.69-L plastic chambers within an insulated environmental chamber, which was constructed by lining the interior of a 66.2-L cooler box with copper tubing, through which water was pumped by a temperature-controlled circulator (model ME, Julabo Labor-technik, Seelbach, Germany). T_a within the plastic chamber was measured using a Cu-Cn thermocouple and a TC-1000 thermocouple meter (Sable Systems, Las Vegas, NV). T_b was measured using a lubricated fine-gauge Teflon-coated Cu-Cn thermocouple (IT-18, Physitemp, Clifton, NJ) inserted into the cloaca to a depth at which a slight withdrawal did not result in a change in the reading (~2 cm). The thermocouple was secured by attaching the thermocouple wire to the tail feathers immediately behind the cloaca, using adhesive tape and a wire paperclip. T_b data were discarded if the thermocouple became dislodged during measurements. All the thermocouples were previously calibrated in the temperature-controlled water bath. Data from the thermocouples were digitized using a Universal Interface II (Sable Systems, Las Vegas, NV) and recorded on a laptop computer using EXPEDATA software (Sable Systems). All procedures in this study were approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (clearance certificate 2007/31/01).

Data Analyses and Defining Departures from Normothermy

Values are presented as mean \pm SD for n = number of individuals and N = number of observations, unless stated otherwise. The relationships between T_{skin} , T_b , and T_a were described using the regression model that provided the best fit to each data set, identified following Song et al. (1997). Changes in T_{skin} and T_a were described using least squares linear regression models in STATISTICA, version 7.0 (StatSoft, Tulsa, OK).

Considerable debate surrounds the terminology used to refer to the downregulation of T_b and metabolic rate below normothermic levels and the approaches used to distinguish such states from normothermy (Barclay et al. 2001; Schleucher and Prinzinger 2006; Willis 2007). Rather than attempting to define torpor on the basis of behavioral criteria (which is rarely feasible in the field [Barclay et al. 2001]) or applying a specific T_b or T_{skin} threshold value, such as $T_{\text{skin}} = 30^\circ\text{C}$ (Brigham 1992; Brigham et al. 2000), we used a method modified from that of McKechnie et al. (2007) that identifies departures from normothermic T_b or T_{skin} by testing the fit of a normal distribution curve to the T_{skin} data of each individual. We used Kolmogorov-Smirnov tests to check the fit of a normal distribution curve to the normothermic T_{skin} data within each individual. We included T_{skin} data irrespective of time of day, since neither species exhibited clear circadian rhythms of normothermic T_{skin} . If

there was a significant fit of normality to the T_{skin} data for an individual, we concluded that it did not deviate from normothermy during the study period. However, if an individual's T_{skin} data were significantly nonnormal, then we estimated the normothermic T_{skin} range for that individual by fitting a normal distribution to the T_{skin} data that was greater than or equal to the upper modal T_{skin} , following McKechnie et al. (2007). For each individual, the lower 99% confidence limit (CL) of the normothermic distribution was then determined and the upper threshold T_{skin} for departures from normothermy was calculated by subtracting 3°C from the lower 99% CL of normal T_{skin} (Fig. 1) to account for the error associated with estimating T_b from T_{skin} measurements.

Results

Mean M_b was 79.5 ± 5.4 g ($n = 8$) for pearl-spotted owlets and 60.6 ± 3.6 g ($n = 4$) for African scops-owls. Air temperature during the study period (May 31–August 9, 2007) ranged from -7.0° to 33.1°C , with a mean daily minimum and maximum T_a of $2.7^\circ \pm 3.8^\circ\text{C}$ and $24.4^\circ \pm 3.0^\circ\text{C}$, respectively, and an overall mean air temperature of 12.7°C (Fig. 2A).

T_{skin} was predictably related to T_b in the one pearl-spotted owlet and two African scops-owls in which T_{skin} and T_b were simultaneously measured in the field laboratory (Fig. 1). All birds remained normothermic during simultaneous measurements of T_{skin} and T_b . The relationships between $T_b - T_{\text{skin}}$ and $T_b - T_a$ were best described using polynomial regression models, where $T_b - T_{\text{skin}} = -0.0057(T_b - T_a)^2 + 0.4894(T_b - T_a) - 7.3559$ ($r^2 = 0.949$) in the pearl-spotted owlet and $T_b - T_{\text{skin}} = -0.0009(T_b - T_a)^2 + 0.1537(T_b - T_a) - 2.2295$ ($r^2 = 0.955$) in African scops-owls ($n = 2$; Fig. 1). At low T_a values, T_{skin} typically remained within 3° and 2°C of T_b for the pearl-spotted owlet and the African scops-owls, respectively (Fig. 1). At $T_a > 25^\circ\text{C}$, T_{skin} overestimated T_b by similar magnitudes in the two species.

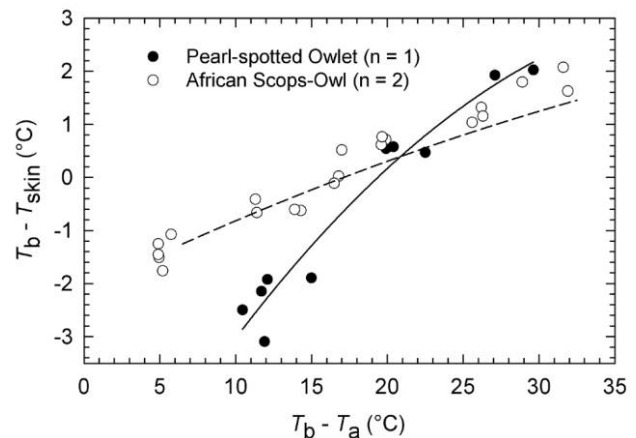


Figure 1. Simultaneous measurements of skin temperature (T_{skin}), body temperature (T_b), and air temperature (T_a) in a single pearl-spotted owlet (filled circles) and two African scops-owls (open circles) held in a field laboratory.

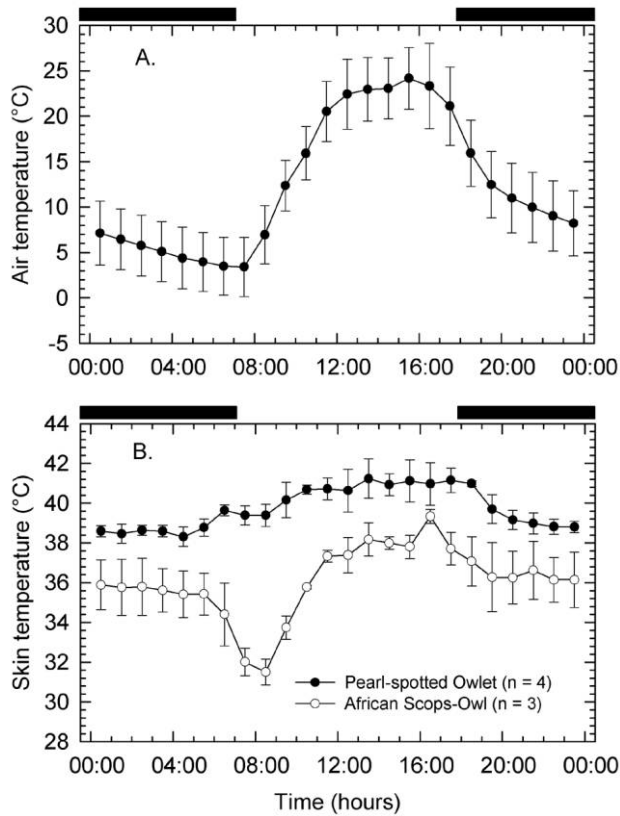


Figure 2. Mean \pm SD hourly air temperature (T_{air} ; A) and mean \pm SD hourly skin temperature (T_{skin} ; B) in four pearl-spotted owlets and three African scops-owls recorded from May 31 to August 9, 2007, in Molopo Nature Reserve. Each datum represents mean T_{a} or T_{skin} for a species pooled to the nearest half an hour (e.g., 6:30 for 6:00 to 7:00). The black bars at the top of the figure indicate nighttime.

Pearl-Spotted Owlets

Pearl-spotted owlets were active and heard calling during the day and night while they were radio tracked, with the highest activity levels occurring around sunset and sunrise. We obtained reliable T_{skin} traces from four pearl-spotted owlets. T_{skin} in these individuals typically peaked at 38.5° to 42.5°C between 1200 and 1800 hours and was subsequently maintained at 38° to 39°C (mean nighttime $T_{\text{skin}} = 39.7^{\circ} \pm 1.0^{\circ}\text{C}$, $n = 4$, $N = 850$; Fig. 2B).

The pearl-spotted owlets showed significantly normal distributions of T_{skin} , which was typically maintained between 36.5° and 41°C (Fig. 4). At no time during the study did pearl-spotted owlets exhibit torpor, and the lowest T_{skin} we observed was 35.6°C.

African Scops-Owls

African scops-owls were active only at night and typically returned to the same roosting sites about 30 min before sunrise while radio tracked. We obtained reliable T_{skin} traces from three African scops-owls. Only 9 h of data were obtained from the fourth individual since it moved to an inaccessible site shortly

after it was released. T_{skin} typically peaked an hour before sunset at 38° to 39°C and was subsequently maintained between 34° and 38°C during the night (mean nighttime $T_{\text{skin}} = 36.0^{\circ} \pm 1.2^{\circ}\text{C}$, $n = 3$, $N = 328$; Fig. 2B). After sunrise, the African scops-owls reduced T_{skin} below 34°C for 1.5–5 h (pooled mean duration of complete bouts = 2.8 ± 0.8 h, $n = 3$, $N = 30$) every day during the study period (Fig. 3).

Reductions in T_{skin} (mean nighttime T_{skin} minus minimum T_{skin}) shortly after sunrise ranged from 3.3° to 8.6°C (pooled mean = $5.3^{\circ} \pm 1.1^{\circ}\text{C}$, $n = 3$, $N = 36$), and minimum T_{skin} (pooled mean of lowest daily T_{skin} readings) averaged $30.5^{\circ} \pm 0.8^{\circ}\text{C}$ in three individuals (Fig. 2). Circadian fluctuations in T_{skin} (maximum T_{skin} minus minimum T_{skin}) ranged from 5.8° to 12.0°C. Minimum daily T_{skin} was reached at approximately 0830 hours and was maintained for 0.5 to 2 h before the onset of rewarming (Fig. 2). There was no relationship between the minimum T_{skin} and minimum T_{a} values recorded on the same day during the study period ($F_{1,38} = 0.036$, $P = 0.85$). Three African scops-owls reduced T_{skin} below 30°C (mean absolute lowest $T_{\text{skin}} = 29.0^{\circ} \pm 0.1^{\circ}\text{C}$, $n = 3$) during the study period (Fig. 3, data from one bird). We recorded eight bouts where T_{skin} was reduced $<30^{\circ}\text{C}$ and another seven bouts where $T_{\text{skin}} = 30^{\circ}\text{C}$. This minimum T_{skin} was usually maintained for less than 30 min.

The three African scops-owls from which we obtained reliable data showed multiple peaks in T_{skin} distributions and the range in T_{skin} was $\geq 10^{\circ}\text{C}$ (Fig. 4). Although only two individuals showed T_{skin} distributions that were significantly nonnormal, that all three African scops-owls showed similar extended ranges and patterns of T_{skin} supports the conclusion that they all deviated from normothermy. The mean T_{skin} threshold for torpor was $33.7^{\circ} \pm 1.4^{\circ}\text{C}$ ($n = 3$) and 31% of all T_{skin} measurements ($n = 3$, $N = 358$) fell below the respective thresholds, indicating the frequent use of heterothermy by these individuals (Fig. 4).

The mean rewarming rate of the African scops-owls was $0.05^{\circ} \pm 0.00^{\circ}\text{C min}^{-1}$ ($n = 3$, $N = 22$), and this rate varied between 0.02° and 0.12°C min⁻¹. These rewarming rates were equivalent to only 3%–25% of the allometrically predicted endogenous rewarming rates for a 58- to 66-g bird (McKechnie and Wolf 2004a). Such low rewarming rates are usually the result of passive rewarming in the sun (McKechnie and Wolf 2004b), but we could not confirm whether the African scops-owls in this study were exposed to solar radiation during rewarming. One individual with $T_{\text{skin}} = 31^{\circ}\text{C}$ was approached at its roost site 2 h after sunrise. It was roosting in the shaded canopy of a *Boscia albitrunca* tree and responded to the disturbance by rewarming at a rate of $0.35^{\circ}\text{C min}^{-1}$, that is, three times faster than the maximum rewarming rate observed in undisturbed individuals.

Discussion

Our data reveal divergent winter thermoregulation patterns in two small, sympatric owl species. Measurements of T_{skin} confirmed the use of short, shallow bouts of torpor in African

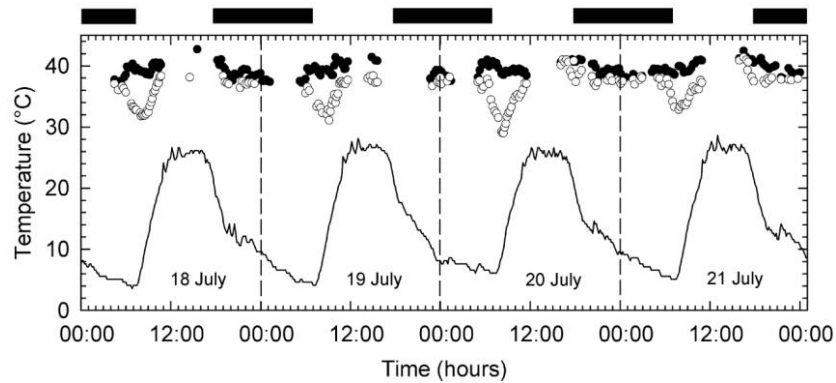


Figure 3. Skin temperature (T_{skin}) in a single pearl-spotted owl (filled circles) and African scops-owl (open circles) on four consecutive days during July 2007. Air temperature (T_a) is indicated by a solid line. The black bar at the top of the figure indicates nighttime. The pearl-spotted owl typically remained homeothermic, whereas the African scops-owl showed shallow bouts of torpor every morning after sunrise. After sunrise on the morning of July 20, the African scops-owl reduced T_{skin} to 29.0°C.

scops-owls, whereas torpor was absent in pearl-spotted owlets during the study period.

We are confident that the reductions in T_{skin} in African scops-owls were not artifacts of loose transmitters, since (1) T_{skin} often remained constant despite rapid T_a cooling during the night, (2) decreases in T_{skin} often occurred during periods of steady or increasing T_a in the morning, and (3) the timing of T_{skin} reductions in individuals was predictable among days (Fig. 3). If the T_{skin} fluctuations had been the result of loose harnesses, then reductions in T_{skin} would have occurred in an unpredictable fashion during activity, as was seen in a few pearl-spotted owlets in this study for which harnesses were pulled loose (B. Smit, personal observations).

Although our limited laboratory data suggest that T_{skin} was a reliable predictor of T_b , the relationship between the latter two variables may well be modified by the more complex thermal environments experienced by free-ranging birds. The only data on T_b - T_{skin} gradients from small birds under natural conditions of which we are aware involved a single Australian owl-nightjar, *Aegotheles cristatus*, kept in an outdoor aviary, in which T_{skin} generally underestimated T_b by $3.0^\circ \pm 0.8^\circ\text{C}$ (Brigham et al. 2000). In addition, although the harnesses we used kept the transmitters in close contact with the owls' skin, we cannot rule out the possibility of variation in T_{skin} due to such factors as a thin layer of air between the transmitter and the skin. Because of these potential sources of error and the slight drift observed in two transmitters that were recovered, we used a threshold T_{skin} value for each bird that was equivalent to 3°C below the lower 99% CL for normothermic T_{skin} , and we are confident that our conservative approach to identifying departures from normothermy minimized the effects of T_b - T_{skin} gradients. Moreover, the major conclusions of our study are based on changes in T_b and are not dependent on the measurement of precise absolute values.

The reductions in T_{skin} in African scops-owls are, to the best of our knowledge, the most pronounced T_{skin} reductions yet observed in owls and are below the T_{skin} threshold for torpor of 30°C used in studies on caprimulgids (Brigham 1992;

Brigham et al. 2000; Lane et al. 2004). However, the heterothermic bouts we observed in African scops-owls were not as pronounced as those recorded in caprimulgids of similar M_b (Brigham et al. 2000; Lane et al. 2004). We consider the T_{skin} reductions below normothermic limits in African scops-owls to represent shallow torpor, following Körtner et al. (2001). Although the depth of the heterothermic bouts in African scops-owls varied between 3° and 9°C, the patterns were highly consistent, suggesting that these bouts represented a common physiological response. Moreover, the shallow torpor bouts in African scops-owls were more similar to the torpor bouts recorded in caprimulgids (Brigham et al. 2000; Körtner et al. 2001; Fletcher et al. 2004) than the patterns of rest-phase hypothermia (T_b reductions <5°C) typically observed in passerines (Reinertsen 1996; McKechnie and Lovegrove 2003).

T_{skin} patterns in African scops-owls closely resembled the torpor bouts recorded around sunrise in Australian owl-nightjars, common nighthawks *Chordeiles minor* and whip-poor-wills *Caprimulgus vociferus* (Brigham et al. 2000; Fletcher et al. 2004; Lane et al. 2004). Like many caprimulgids, African scops-owls are likely to undergo periods of energetic stress during cold winters when the availability of food resources (mainly arthropods) is reduced. African scops-owls at our study site were significantly heavier by, on average, 13%, during summer ($n = 7$) compared with winter ($n = 7$; B. Smit and A. E. McKechnie, unpublished data). These winter reductions in M_b are consistent with the Dehnel effect observed in small mammals, which involves winter M_b and basal metabolic rate reductions that are mediated by seasonal endogenous leptin cycles (Mezhzherin 1964; Lovegrove 2005). However, it is noteworthy that the seasonal M_b changes in African scops-owls at our study site coincided with an 85% decrease in the abundance of nocturnal, terrestrial arthropods during winter (B. Smit and A. E. McKechnie, unpublished data). Terrestrial arthropods are a primary source of food for African scops-owls (Kemp 2005a), and it is not surprising in the light of these large seasonal reductions in food availability that African scops-owls used torpor to reduce energy demands during winter in the Kalahari Desert.

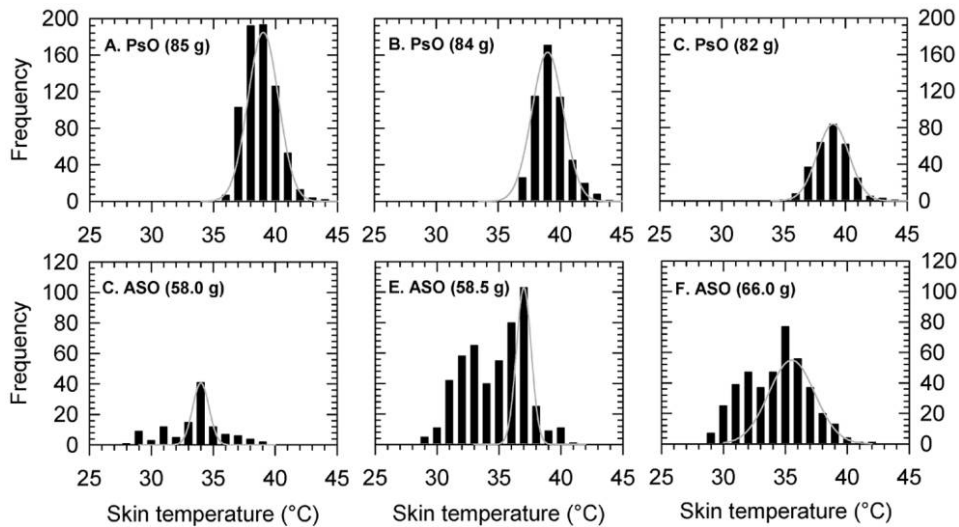


Figure 4. Frequency distributions of skin temperature (T_{skin}) in three pearl-spotted owlets (*PsO*; A–C) and three African scops-owls (*ASO*; D–F) monitored during June and July 2007. Each panel shows the T_{skin} data for one individual. The gray line represents a normal distribution of T_{skin} in each pearl-spotted owl (Kolmogorov Smirnov, $P > 0.05$), or the calculated normothermic T_{skin} distribution in each African scops-owl.

Pearl-spotted owlets, however, differ considerably from African scops-owls and caprimulgids in terms of their foraging behavior and diet (Kemp 2005b). Whereas both African scops-owls and most caprimulgids are exclusively nocturnal, pearl-spotted owlets show considerable flexibility in their activity pattern and often hunt during the day (Maclean 1993; Kemp 2005b). Foraging opportunities of pearl-spotted owlets for arthropods are therefore not restricted to the nighttime, as in African scops-owls. Moreover, pearl-spotted owlets are powerfully built, with large, strong feet that enable them to include mammals, birds, and reptiles of almost double their own M_b in their diet (Kemp 2005b). In contrast to the seasonal M_b changes recorded in African scops-owls, winter ($n = 6$) pearl-spotted owlets were 9.2% heavier than summer ($n = 5$) birds, although this difference was not significant (B. Smit and A. E. McKechnie, unpublished data). Pearl-spotted owlets are in all likelihood less energy limited than African scops-owls during winter in the Kalahari Desert, which potentially explains why the former species did not exhibit heterothermic responses during our study.

We have documented the occurrence of shallow torpor in African scops-owls but cannot exclude the possibility that this species employs more pronounced torpor. Many studies on caprimulgids have reported considerable interindividual variability in torpor use, with only small proportions of populations using pronounced torpor (Fletcher et al. 2004; Lane et al. 2004; McKechnie et al. 2007). One source of uncertainty is that we obtained data from only male African scops-owls. In both Puerto Rican todies (Merola-Zwartjes and Ligon 2000) and freckled nightjars *Caprimulgus tristigma* (McKechnie et al. 2007), only females reduced T_b below 25°C. In mammals, testosterone inhibits torpor use in males (Hall and Goldman 1980; Lee et al. 1990; Barnes 1996; Mzilikazi and Lovegrove 2002),

but this has not been established in birds (McKechnie and Lovegrove 2002). Another factor that possibly selects against the use of torpor is predation risk. During the study, we observed a pair of gabar goshawks *Melierax gabar* flushing and attempting to kill a single African scops-owl at its roost early one morning. If such predation events are a common threat to African scops-owls in the Kalahari Desert, then pronounced torpor with reduced responsiveness would presumably be selected against.

Our study reiterates the importance of thermoregulatory data from wild, free-ranging populations when assessing the occurrence of torpor in birds (Brigham et al. 2000; Fletcher et al. 2004; Lane et al. 2004; Cooper et al. 2008). That at least one owl species exhibits qualitatively similar patterns of heterothermy to caprimulgids provides further insight into the phylogenetic distribution of this phenomenon within the order Strigiformes. Before our study, the lack of evidence for torpor in owls led to the hypothesis that this trait evolved early in the suborder Caprimulgi (Lane et al. 2004). However, our data reveal that owls likely share a physiological capacity for heterothermic responses with their close relatives, the caprimulgids, providing further evidence that avian torpor represents a monophyletic, plesiomorphic trait, as hypothesized by Malan (1996).

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