

# Roost type influences torpor use by Australian owlet-nightjars

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**Abstract** Australian owlet-nightjars (*Aegotheles cristatus*; ~50 g) are one of only a few avian species that roost in cavities year-round and regularly enter torpor. Cavity roosts act as thermal buffers, and roost type likely affects energy expenditure of small birds. We used radiotelemetry to locate diurnal winter roost sites of owlet-nightjars in central Australia and to measure body ( $T_b$ ) and skin ( $T_{skin}$ ) temperature. We also recorded ambient temperature inside ( $T_{IN}$ ) and outside roosts. Individual owlet-nightjars used one to seven different roosts (tracking time 3–10 weeks), selecting either rock crevices (four birds) or tree hollows (four birds), or switching between the two roost types (seven birds). Rock crevices ( $T_{IN}$  +9°C to +33°C) were warmer and thermally more stable than tree hollows ( $T_{IN}$  -4.0°C to +37°C). Torpor, often expressed by a reduction of  $T_{skin}/T_b$  by >10°C for 3–4 h at dawn, was influenced by roost selection; torpor use in tree hollows was almost twice that in rock

crevices. Despite the potential energy savings accrued from roosting in well-insulated cavities, owlet-nightjars roosted in tree hollows more often (65% bird days,  $n=398$ ) than in rock crevices (35% bird days,  $n=211$ ). Lower costs of arousal from torpor via passive rewarming and basking and decreased risk of predation are two possible explanations for the preference to roost in tree hollows. We provide the first evidence for the influence of cavity roost selection on torpor use in a free-ranging bird and show that roost selection and thermal biology are strongly interrelated in determining energy expenditure.

**Keywords** *Aegotheles* · Cavities · Desert · Roost selection · Thermal buffering · Thermoregulation

## Introduction

Cavity roosts are typically buffered against extremes in ambient temperature ( $T_a$ ) and offer birds and mammals that inhabit them substantial energy savings (Kendeigh 1961; Walsberg 1986; Chruszcz and Barclay 2002; Lausen and Barclay 2006). During cold conditions, birds may experience significant thermoregulatory stress during their resting phase when they are inactive. Nocturnal insectivores concentrate their foraging effort at dusk, when prey are most active, during periods of cold weather, and spend much of the night and early morning roosting. Cavity roosts may be vital for some species in reducing the energy expended to maintain high body temperatures ( $T_b$ ) during such food shortages. For birds roosting in cavities or domed nests, nocturnal energy consumption may be reduced by up to 43% compared to birds roosting in exposed sites (Walsberg 1985). The retention of metabolically produced heat by a bird within cavities roost further enhances energy savings

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(White et al. 1975, 1978; but see Walsberg 1986). However, this benefit is greatest for colonial roosting species, such as swifts (Bartholomew et al. 1957) and nuthatches (Knorr 1957), which use clustering for warmth. For solitary roosting birds the relative importance of roost thermal microclimate becomes especially critical as they must rely solely on roost insulation for a thermal advantage to reduce energy costs.

Birds of the order Caprimulgiformes use torpor regularly (McKechnie and Lovegrove 2002; Brigham et al. 2006) but most roost in the open. The Australian owlet-nightjar (*Aegotheles cristatus*) is the only Caprimulgiform that regularly roosts in cavities (Holyoak 2001). The small body size (40–50 g) of this species makes it more susceptible to predation (Brigham et al. 1999), and appropriate cavity roosts may be crucial for both insulation and protection. Australian owlet-nightjars are insectivorous birds that would be greatly affected by decreased insect abundance and activity during cold periods and are likely energetically stressed during adverse conditions (Brigham et al. 2000; Woods 2002; Lane et al. 2004). In a eucalypt woodland on the temperate Northern Tablelands of New South Wales, Australian owlet-nightjars frequently employ daily torpor during winter (Brigham et al. 2000). Their use of torpor in winter (Brigham et al. 2000; Doucette 2007), small size and obligate use of cavities makes them an ideal species to evaluate the effects of cavity thermal buffering on torpor use.

The use of well-insulated roost cavities has important implications for avian thermal physiology, and roosts that remain warmer than outside  $T_a$  may reduce the requirement for frequent use of deep torpor. Considerable research on the ecologically similar, heterothermic, insectivorous bats that live in cold climates has identified roost thermal microclimate as important in roost selection (Kerth et al. 2001; Sedgeley 2001; Chruszcz and Barclay 2002; Turbill et al. 2003; Smith and Racey 2005; Lausen and Barclay 2006; Solick and Barclay 2006). Bats tend to select roosts that are warmer at night and thermally stable, such as deep rock crevices (Lausen and Barclay 2003), warm buildings (Lausen and Barclay 2006) or tree cavities with stable microclimates (Sedgeley 2001; Willis and Brigham 2007). By roosting in warmer locations, these bats lowered their costs for normothermic thermoregulation and did not employ torpor as often (Lausen and Barclay 2006). However, Australian long-eared bats (*Nyctophilus geoffroyi*) that express torpor even in summer, preferred poorly insulated roosts that allowed for passive rewarming (Turbill et al. 2003). Passive rewarming can reduce arousal costs by up to 85% in small mammals (Geiser et al. 2004) and Lovegrove et al. (1999) suggested that nocturnal animals should be specific in their choice of refugia as the thermal buffering capacity of refugia will impact on the ability to passively rewarm.

The desert region of central Australia is characterised by unpredictable rainfall, variable arthropod availability and large daily fluctuations in  $T_a$  during winter (−5°C to +30°C). We found that owlet-nightjars in central Australia regularly roosted in both rock crevices and tree hollows. The thermoregulatory behaviour and thermal biology of free-ranging birds that use rock crevices as thermal refugia in comparison to those that use trees hollows has not been quantified. If, as expected, rock crevices and tree cavities differ in thermal buffering capability and stability, we predict that thermoregulatory patterns and use of torpor will differ for birds using the two roost types. We specifically predict that rock crevice roosts would be more thermally stable than tree cavities and individuals roosting in rock crevice would use torpor less frequently than those roosting in tree roosts.

## Materials and methods

### Study sites

Our study was conducted during two winters (May to October 2004–2005) at two sites in semi-arid central Australia in the West MacDonnell Ranges near Alice Springs, Northern Territory. Ormiston Gorge (23°37'S, 132°43'E) is located ~150 km west of Alice Springs. The Alice Springs Desert Park (23°37'S, 132°43'E) is located 7 km west of Alice Springs at the base of Mt. Gillen. Both sites sit at the base of cliffs 200–400 m in height. Geologically, the West MacDonnell mountain range is complex, but mainly consists of metamorphic quartzite rock containing a multitude of rock crevices. The two sites have similar vegetation associations that include eucalypt woodland dominated by river red gums (*Eucalyptus camaldulensis*) and open mulga shrubland (*Acacia aneura*) with a ground storey dominated by spinifex grasses (*Triodia brizoides*, *Triodia longiceps*). The upper slopes of the ranges support hummock grassland (*Triodia* spp.) with emergent trees and shrubs including ghost gum (*Eucalyptus papuana*), desert bloodwood (*Corymbia opaca*) and corkwood (*Hakea suberea*). The Desert Park has areas that are regularly irrigated to encourage vegetation growth. Both sites support a multitude of hollow bearing trees and hollow stumps.

Average yearly rainfall in the West MacDonnell Ranges is 277 mm (1941–2006, Bureau of Meteorology, Alice Springs Airport), with high variability between years (lowest=82 mm (1965); highest=783 mm (1974)) and a tendency for summer rainfall (January and February). Seasonal fluctuations in  $T_a$  are marked. Mean minimum and maximum  $T_a$  are 4.0°C and 19.9°C (July) and 21.4°C and 36.4°C (January). Daily  $T_a$  fluctuations average 16°C in both summer and winter.

## Telemetry

Owlet-nightjars were caught by broadcasting taped calls to lure individuals into mist nets. Following capture, we measured body mass and placed an alloy band (Australian Bird and Bat Banding Scheme Project 1418–8) on the right leg. No external characteristics are known which can reliably be used to distinguish the *g* of owlet-nightjars. The sex of birds caught in 2005 was determined through DNA analysis using the shaft of feathers pulled from the chest area (Genetic Science Services, Fitzroy, VIC, Australia). As birds caught in 2004 were not sampled for DNA, results were not analyzed by sex. However, results from another study have shown that torpor occurs in both sexes, and there is no apparent difference in MIN  $T_{\text{skin}}$  between genders (Doucette 2007).

Most birds were fitted with an external radio transmitter (model PD-2T, Holohil Systems, Carp, ON, Canada) to measure skin temperature ( $T_{\text{skin}}$ ;  $n=13$ ). External transmitters were attached using a backpack-style harness made from elastic thread. The transmitters were affixed to sit underneath the bird's feathers so that the harness kept the temperature sensor in contact with the bird's skin in the interscapular region to record  $T_{\text{skin}}$  (Brigham 1992; Brigham et al. 2000; McKechnie et al. 2007). Two birds, one at each location, in 2004 were kept overnight to surgically implant internal transmitters (Sirtrack Ltd., Havelock North, New Zealand) to measure core  $T_{\text{b}}$ . Internal transmitters were implanted intraperitoneally under isoflurane (0.5–4% in oxygen) anaesthesia. Following surgery, birds were held for 24 h before being released at the site of capture. All transmitters were calibrated to the nearest 0.1°C before attachment/implantation.

Birds were tracked to diurnal roosts using three-element Yagi antennae and Merlin (Custom Electronics, Urbana, IL, USA) or Icom (IC\_R10, Icom, Bellevue, WA, USA) receivers. Remote receiver/data logging stations were set up on high ground and/or by placing antennae in trees to receive the signal from the bird in its roost.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was recorded every 10 min 24 h a day when the bird was in range of the receiver. Data were recorded using custom-made data loggers (Körtner and Geiser 1998) or a Lotek SRX\_400 receiver/logger (Lotek Engineering, Aurora, ON, Canada) attached to a three- or five-element Yagi antennae. Data were downloaded to a laptop computer every 4–5 days. Pulse rates recorded on loggers were confirmed by collecting data manually several times daily by using a receiver and timing ten pulse intervals using a stopwatch.  $T_{\text{skin}}$  or  $T_{\text{b}}$  was calculated from pulse intervals using the calibration curve previously determined for each transmitter.

## Roost temperature

Roosts were found by tracking radio-tagged birds to their respective roosts each morning and recording the position using a GPS. Wherever possible, small temperature data loggers (Thermochron iButtons®, Model DS1921,  $\pm 0.5^\circ\text{C}$ , Dallas Semiconductor Corp., Dallas, TX, USA, 13-mm diameter) were placed in the roosts to record the internal roost temperature ( $T_{\text{IN}}$ ) each hour. For rock crevice roosts iButtons were tied to a stick and placed as far into the roosts as possible (usually 50 to 80 cm). In some cases, these iButtons may not have been situated in the crevice as deeply as the birds could access due to constraints such as sharp bends in the orientation of the crevice. Placement of iButtons was always conducted when the bird was either roosting in a different cavity or not present while foraging at night.

Substitute tree hollows were used to measure the  $T_{\text{IN}}$  of tree roosts rather than putting iButtons directly in roosts. Substitute hollows were of the same diameter, with the same opening aspect, and were within 20 m of the actual roost but were generally lower in the tree (2.8 to 5 m). Specifically designed holders with iButtons attached were tied to a piece of cord and dropped as far into the hollow as possible (40 to 180 cm). These depths may not always resemble the precise places within the tree that the birds could potentially access but were the best possible approximation. Actual tree roosts were not used for  $T_{\text{IN}}$  measurements as they were typically too high to reach safely (i.e. >10 m) and due to the risk of the bird becoming entangled in the cord holding the iButton. Results of a trial at Ormiston Gorge to determine the influence of height (0 to 18 m) on  $T_{\text{IN}}$  of tree hollows revealed height had no influence on  $T_{\text{IN}}$  for hollows higher than 2 m (Doucette 2007). Ecological parameters and corresponding impacts on  $T_{\text{IN}}$  for tree hollows and rock crevices are presented elsewhere (Doucette 2007).

Each iButton placed inside a cavity to measure  $T_{\text{IN}}$  was paired with one placed outside the roost (outside temperature ( $T_{\text{OUT}}$ )). This iButton was folded in a sheet of A4 paper, placed in a waterproof plastic bag and tied to vegetation at the opening of rock crevices and on the outside of the branch containing the roost entrance for tree roosts.  $T_{\text{a}}$  was measured in the shade 1 m above the ground in a central location in each of the two study sites.

## Data analysis

Microclimate was compared between rock and tree roosts using several measures of temperature: minimum daily (24 h) temperature (MIN  $T_{\text{IN}}$ ), maximum daily (24 h) temperature (MAX  $T_{\text{IN}}$ ) and range of roost temperature (the maximum minus the minimum tempera-

ture for a particular day; RANGE  $T_{IN}$ ). Kruskal–Wallis analyses of variance on ranks with a Dunn's post hoc pairwise comparison were used to compare particular cavities on the same days. Roost types were compared for each temperature measure using an ANCOVA with the relevant  $T_a$  measure as a covariant. RANGE  $T_{IN}$  was  $\log_{10}$  transformed to achieve equality of variance between the two roost types.

Mean  $\pm$  SE active  $T_{skin}$  for owlet-nightjars tagged with external transmitters was  $37.9 \pm 0.1^\circ\text{C}$ . Birds were considered torpid when  $T_{skin}$  fell below  $30^\circ\text{C}$  for birds with external transmitters for 20 min or more (Reynolds and Lee 1996; Brigham et al. 2000). Mean active  $T_b$  of owlet-nightjars with internal transmitters implanted was  $40.0 \pm 0.2^\circ\text{C}$  and birds were considered torpid when  $T_b$  fell below  $33^\circ\text{C}$  for 20 min or more. These thresholds exceed the recommended  $T_b$  reduction of  $>5^\circ\text{C}$  from normothermia to define torpor use in birds (Schleucher 2004). Brigham et al. (2000) compared  $T_{skin}$  and  $T_b$  of a captive owlet-nightjar with both an external and internal transmitter attached and found the difference to be  $3.0 \pm 0.8^\circ\text{C}$ . For comparison of minimum  $T_{skin}$  (MIN  $T_{skin}$ ) amongst birds,  $3^\circ\text{C}$  was subtracted from the minimum  $T_b$  (MIN  $T_b$ ) of birds with internal transmitters to calculate MIN  $T_{skin}$ . Days in which  $T_{skin}$  or  $T_b$  data were missing for  $>3$  h period during daylight hours (sunrise to sunset) were excluded from our analysis. Torpor days are defined as days on which at least one bout of torpor occurred.

A one-factor adjusted means ANCOVA with  $T_a$  as a covariant was used to determine if the daily Minimum  $T_a$  influenced the Minimum  $T_{skin}$  during torpor and the duration of a torpor bout on any given day. Differences in torpor frequency of birds for each roost type were determined using two-way contingency tables (Quinn and Keough 2002). Yates correction factor was used for all  $\chi^2$  tests with 1° of freedom (Zar 1998). For two birds, which entered torpor in both roost types, the mean MIN  $T_{skin}$  and bout duration was calculated separately for torpor use in rock crevices and tree hollows.

Rates of passive rewarming from torpor bouts were calculated from the 25 morning torpor bouts in rock crevices with the lowest MIN  $T_{skin}/T_b$  and a random selection of 25 morning torpor bouts in tree roosts from the comparable MIN  $T_{skin}/T_b$  range ( $21.5^\circ\text{C}$  to  $28.5^\circ\text{C}$ ). The overall slope of the arousal stage of the torpor bout was calculated from the first point after the MIN  $T_{skin}/T_b$  to the MAX  $T_{skin}/T_b$  at the end of the bout.

Numerical values are presented as means  $\pm$  SE for  $n$  = number of individuals and  $N$  = number of days of observations recorded. An alpha value of 0.05 was used for all tests.

## Results

### Owlet-nightjar captures

Sixteen owlet-nightjars were captured, and data were collected for 14 individuals. One bird was caught twice in 2004. This bird originally had an internal transmitter but was fitted with an external transmitter when recaptured. Because of the different transmitter types and timing of data collection (early versus late winter), we analyzed the data from this individual as being from two separate birds (thus data were recorded from  $n=15$  birds).

### Roost selection

Telemetry data were recorded for a total of 609 bird days with a mean of 40 days per individual (range 12 to 72 days). Individual birds used between one and seven different roosts (tracking time 3–10 weeks), but the number of roosts used was independent of the time tracked. Half of the birds used either rock crevices ( $n=4$ ) or tree hollows ( $n=4$ ) exclusively and the rest used both rock crevice and tree roosts ( $n=7$ ). With the exception of two birds that used rock and tree roosts equally, the other five birds that used both rock and tree roosts generally preferred one type and spent only a few days in the other.

Tree hollows were used as roosts on 398 days (65%), and rock crevices were used on 211 days (35%). A total of 23 rock crevice roosts and 22 tree hollow roosts were identified. Tree hollow and rock crevice roosts appeared to be available in excess at both sites. Birds at the Desert Park (irrigated) roosted in rock crevices more often (57%) than at Ormiston (20%; non-irrigated), which could reflect a preference for specific characteristics of available roosts (Doucette 2007). However, as the frequency of torpor use was the same for both sites, the data for the two sites were combined. Birds roosted in rock crevices less in 2004 (32%) than in 2005 (42%); however, torpor use in each roost type followed the same pattern each year.

### Cavity thermal buffering capacity

Rock crevice roosts generally had excellent thermal insulation capabilities and consistently maintained higher MIN  $T_{IN}$  and lower MAX  $T_{IN}$  than tree roosts (Table 1; Fig. 1).  $T_{IN}$  of 13 rock crevices (measured on 492 days), indicated that they were never colder than  $+9^\circ\text{C}$  or warmer than  $+33^\circ\text{C}$  (Table 1). In contrast, tree hollows had MIN  $T_{IN}$  as low as  $-4^\circ\text{C}$  and MAX  $T_{IN}$  up to  $+37^\circ\text{C}$  (11 roosts; 374 days). The overall RANGE  $T_{IN}$  was  $24^\circ\text{C}$  in rock crevices and  $41^\circ\text{C}$  in tree hollows. There was a strong

**Table 1** Mean±SE and range of values for each of the thermal measures for rock crevice and tree hollow roosts (13 rock roosts measured on 492 days; 11 tree roosts measured on 374 days)

Variable	$T_{IN}$ (°C)		$T_{OUT}$ (°C)		$T_a$ (°C)	
	Mean±SE	Range	Mean±SE	Range	Mean±SE	Range
Rock						
MIN	20.0±0.9	9.0–26.5	13.0±0.6	0.0–24.0	8.1±1.1	–3.4–20.0
MAX	24.0±0.6	16.0–33.0	33.3±2.3	18.0–51.5	25.3±0.8	15.0–35.0
Tree						
MIN	13.2±1.8	–4.0–26.0	10.4±1.7	–5.0–21.5	10.9±1.5	–1.5–21.5
MAX	24.9±1.9	10.5–37.0	31.1±2.1	13.0–44.5	26.2±1.7	13.0–39.0

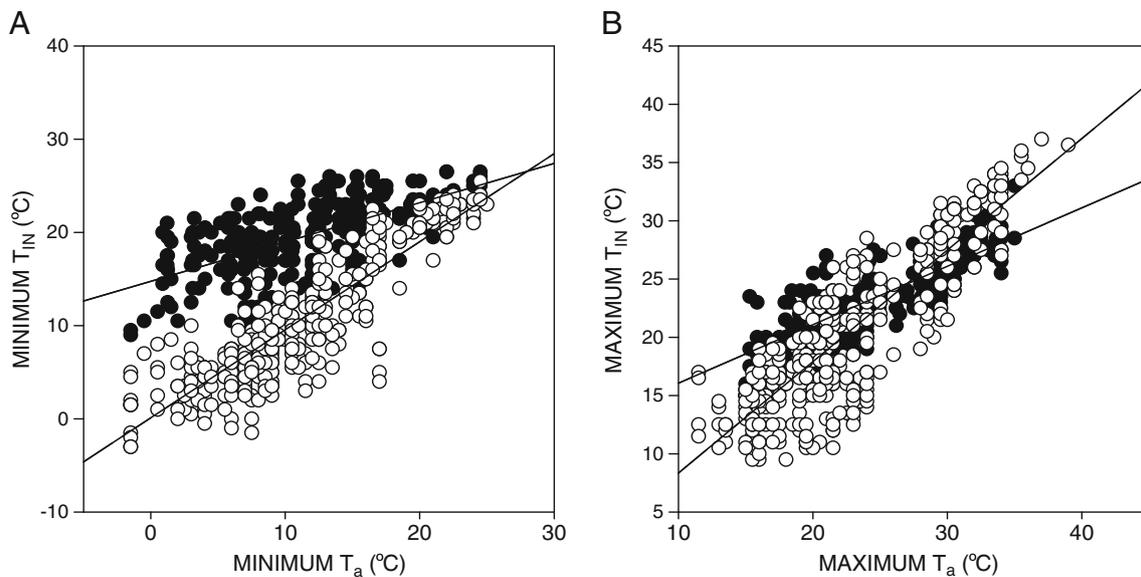
$T_{IN}$ =temperature in cavity,  $T_{OUT}$ =temperature immediately outside cavity,  $T_a$ =ambient temperature in shade at the site

interaction between roost type and  $T_a$  for most measures (Table 2); however rock crevices exhibited less temperature fluctuation with  $T_a$  than tree hollows (Fig. 2). For MAX  $T_{IN}$ , rock crevices were consistently warmer than tree roosts below MAX  $T_a$  of 28°C but remained cooler than tree roosts above this threshold (Fig. 1). Results comparing  $T_{IN}$  to  $T_{OUT}$  indicate that the cliff faces in which the rock crevice roosts were located radiated considerable amounts of heat. MAX  $T_{OUT}$  reached 51.5°C with a mean 24 h MAX  $T_{OUT}$  of 32.5°C (Table 1).  $T_{OUT}$  was typically higher than site  $T_a$  for rock crevices due to solar heat absorbed by the dark red rocks that was radiated throughout the day and night, and because they were located higher on the ranges (Table 1; Fig. 3b). In contrast, tree roost  $T_{OUT}$  was typically lower than site  $T_a$  as trees were located lower in dry creek beds and gullies.

#### Torpor use

Owlet-nightjars entered torpor about twice as often when roosting in tree hollows than when roosting in rock crevices (Fig. 4) in 2004 ( $\chi^2=12.87$ ,  $n=10$ ,  $N=418$ ,  $P<0.0001$ ) and 2005 ( $\chi^2=5.75$ ,  $n=5$ ,  $N=136$ ,  $P<0.05$ ) and in both years combined ( $\chi^2=15.47$ ,  $n=15$ ,  $N=554$ ,  $P<0.0001$ ). Data on torpor use for the 2 years were combined for all subsequent analysis of the effects of roost type. Birds consistently used torpor more when roosting in tree hollows throughout the winter, irrespective of month (Fig. 5).

Thirteen of the 15 radio-tagged birds entered torpor at least once for a total of 231 torpor bouts (199 torpor days), comprising 36% of the 554 bird days that  $T_{skin}$  or  $T_b$  was successfully recorded. Torpor bouts were recorded between 18 May and 13 September 2004 and 3 June to 16 August



**Fig. 1** Plots of MIN  $T_{IN}$  and MAX  $T_{IN}$  in rock crevices (black circles) and tree hollows (white circles) compared to the temperatures at the site. Results and  $R^2$  for each ANCOVA model are given in Table 2. Linear regressions are **A** rock, MIN  $T_{IN}=14.75+0.42$  (MIN  $T_a$ ); tree,

MIN  $T_{IN}=0.11+0.94$  (MIN  $T_a$ ); **B** rock, MAX  $T_{IN}=11.05+0.50$  (MAX  $T_a$ ); tree, MAX  $T_{IN}=-1.23+0.96$  (MAX  $T_a$ ). All linear regressions are significant ( $P<0.0001$ )

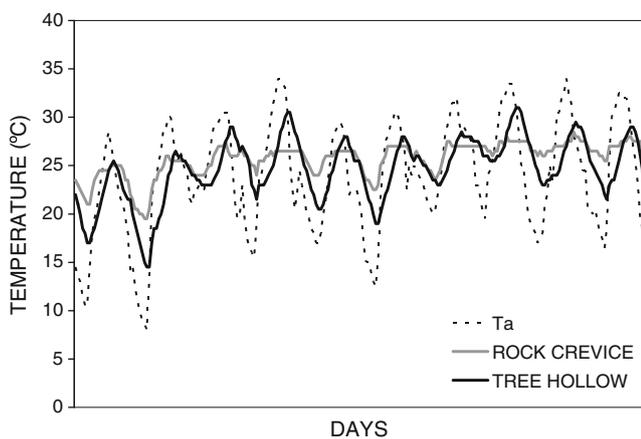
**Table 2** Results of ANCOVA models describing temperature inside ( $T_{IN}$ ) owl-nightjar roosts

	Source	$F$	$P$	$R^2$
MIN $T_{IN}$	Roost type	$F_{1,625}=357.61$	<0.0001	0.90
	MIN $T_{OUT}$	$F_{1,625}=2,107.69$	<0.0001	
	Roost type $\times T_{OUT}$	$F_{1,625}=85.10$	<0.0001	
MAX $T_{IN}$	Roost type	$F_{1,626}=41.58$	<0.0001	0.45
	MAX $T_{OUT}$	$F_{1,626}=263.89$	<0.0001	
	Roost type $\times T_{OUT}$	$F_{1,626}=40.16$	<0.0001	
MIN $T_{IN}$	Roost type	$F_{1,621}=768.42$	<0.0001	0.82
	MIN $T_a$	$F_{1,621}=1,045.15$	<0.0001	
	Roost type $\times T_a$	$F_{1,621}=153.17$	<0.0001	
MAX $T_{IN}$	Roost type	$F_{1,621}=144.55$	<0.0001	0.76
	MAX $T_a$	$F_{1,621}=1,243.85$	<0.0001	
	Roost type $\times T_a$	$F_{1,621}=121.36$	<0.0001	
Log range $T_{IN}$	Roost type	$F_{1,597}=5.83$	<0.05	0.53
	Log range $T_a$	$F_{1,597}=100.16$	<0.0001	
	Roost type $\times T_a$	$F_{1,597}=19.42$	<0.0001	

Roost type (rock or tree) was a categorical variable and ambient temperature ( $T_a$ ) was included as a covariant in all ANCOVA models. Model  $R^2$  is given for each model

2005 within tracking periods of 10 May to 6 October 2004 and 1 June to 5 September 2005. The average torpid MIN  $T_{skin}$  was 26.5°C, and the lowest torpid MIN  $T_{skin}$  was 18.6°C, which occurred on 11 July 2005 when the MIN  $T_a$  was a relatively warm 7°C (Fig. 3a). The lowest  $T_b$  measured for a bird with an internal transmitter was 24.8°C. The duration of the longest bout of torpor was 640 min (10.7 h) for a bird roosting in a tree hollow.

Roost type and MIN  $T_a$  did not significantly affect duration of torpor bouts (ANCOVA, roost type,  $F_{1,228}=0.09$ ,  $P=0.76$ ; MIN  $T_a$ ,  $F_{1,228}=1.35$ ,  $P=0.25$ ; Fig. 6). MIN  $T_{skin}$  reached during torpor bouts was related to MIN  $T_a$

**Fig. 2** Plot of temperature in a rock crevice and in a tree hollow and ambient temperature ( $T_a$ ) for 10 days during August 2005

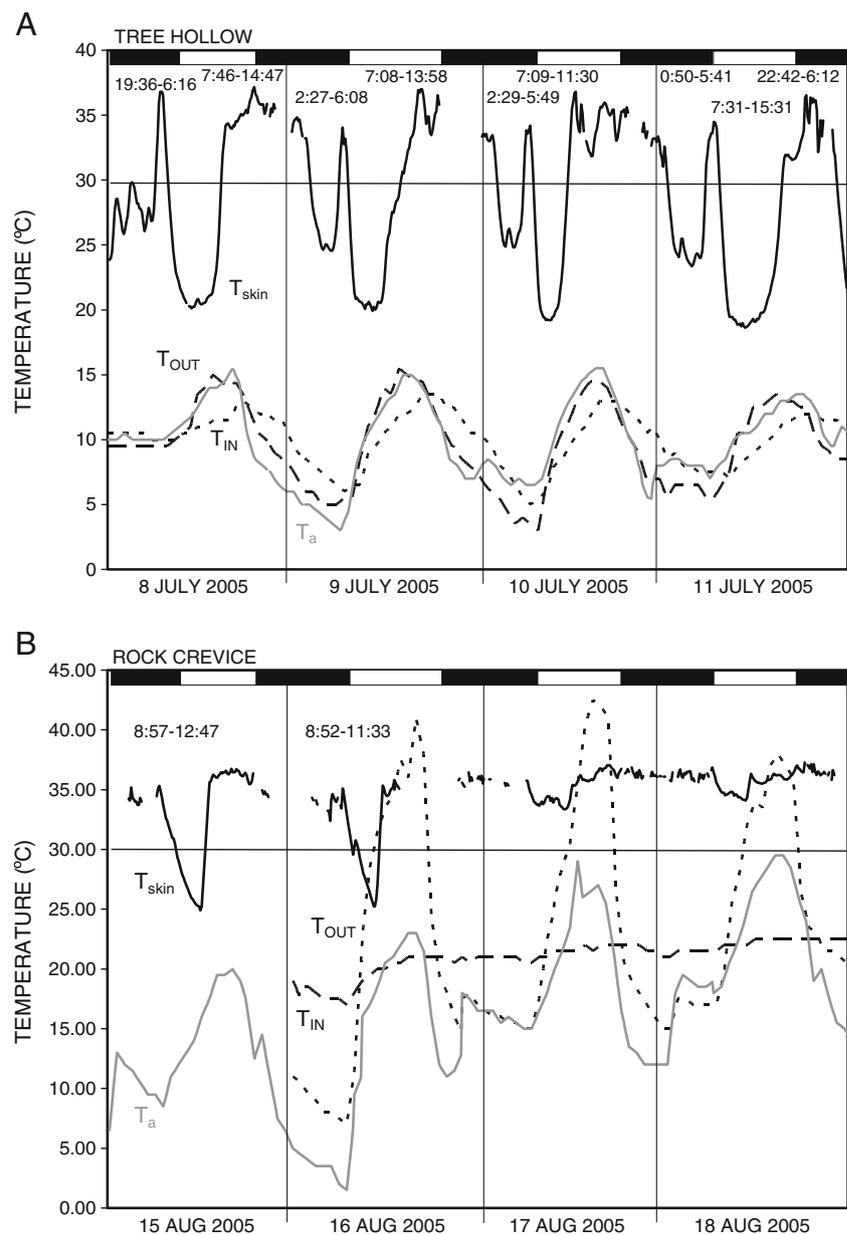
(ANCOVA,  $F_{1,230}=4.84$ ,  $P<0.05$ ) but was not influenced by roost type ( $F_{1,230}=0.67$ ,  $P=0.41$ ). The mean MIN  $T_{skin}$  during torpor for each individual was significantly negatively related to the mean duration of torpor bouts ( $F_{1,14}=31.47$ ,  $P<0.001$ ,  $R^2=0.71$ , MIN  $T_{skin}=30.51-0.02$  (torpor duration)).

Typically, birds entered torpor once on any given day (single bout=87%) for several hours. Occasionally, birds entered torpor twice daily (double bout=12%,  $n=9$ ,  $N=28$ ), entering torpor either at dawn and again in the afternoon, or at night (i.e. 0100–0200 hours) and at dawn (Fig. 3). Based on the number of bird days that owl-nightjars used respective cavities, the use of double bouts did not differ between the two roost types (tree hollows,  $n=6$ ,  $N=18$ , 4.9% bird days; rock crevices,  $n=4$ ,  $N=9$ , 4.8% bird days). However, double torpor bouts in tree hollows usually consisted of a night and a morning bout (59%), whereas in rock crevices they consisted of a morning and afternoon bout (80%).

Torpor was employed most frequently in the morning between 0600 and 1200 hours ( $N=182$ , 78.8%; mean start time 0739 hours). Arousals from morning torpor bouts coincided with the time of increasing  $T_a$  (1021 hours). Afternoon torpor bouts (1200–1800 hours; mean start time=1336 hours) occurred on 15 occasions and almost always followed a morning torpor bout ( $n=8$ ,  $N=14$ ). Birds entered torpor more often in the afternoon when they were roosting in rock crevices ( $n=3$ ,  $N=8$ , 4.3% of bird days) than in tree hollows ( $n=5$ ,  $N=7$ ; 2.0% of bird days). Afternoon (double) torpor bouts occurred on days with lower MIN  $T_a$  ( $2.1\pm 0.8^\circ\text{C}$ ,  $N=15$ ), than on days when only morning torpor bouts occurred (MIN  $T_a=4.8\pm 0.3^\circ\text{C}$ ,  $N=151$ ). Five individuals entered torpor at night (1800–0600 h) on a total of 32 occasions (13.9%). Night torpor bouts occurred on days with a mean MIN  $T_a$  of  $3.1\pm 0.6^\circ\text{C}$ . As four of the five birds that used night torpor typically used only one type of roost (either rock or tree) as a day roost, we assume they were using that roost type when they entered night torpor. Based on this assumption, birds that roosted in trees entered torpor at night more often ( $n=3$ ,  $N=25$ , 6.8% of bird days) than those that roosted in rock crevices ( $n=2$ ,  $N=7$ , 3.7% of bird days).

Eighty percent of all torpor bouts occurred on days when the MIN  $T_a$  was below 6.8°C (the median MIN  $T_a$  for the period during which data were recorded). However, torpor occurred even when MIN  $T_a$  was as high as 14.5°C. Seven birds used both tree hollows and rock crevices as roosts and the MIN  $T_a$  on a given day had no effect on their selection of roost type. Birds used tree hollows twice as often as rock crevices irrespective of MIN  $T_a$  ( $\chi^2=0.03$ ,  $P=0.87$ ; Fig. 5). However, when  $T_a$  was  $<6.8^\circ\text{C}$ ,

**Fig. 3** Examples of torpor bout patterns of owlet-nightjars using rock crevice and tree hollow roosts. Each plot shows skin temperature ( $T_{\text{skin}}$ , solid line), temperature inside the roost ( $T_{\text{IN}}$ , dotted line), temperature immediately outside the roost ( $T_{\text{OUT}}$ , dashed line) and the ambient temperature at the site ( $T_{\text{a}}$ , grey solid line). Data were recorded for each bird at Ormiston during 4 days in winter 2005. Dark and light bars at the top of each figure represent photophase (day) and scotophase (night). Times indicate the start and end of each torpor bout. **A** Owlet-nightjar in tree hollow roost. Each day illustrates a double torpor bout, with a bout occurring at night followed by another bout at dawn. The lower range in daily  $T_{\text{IN}}$  compared to  $T_{\text{OUT}}$  illustrate the nominal buffering capacity of tree roosts. **B** Owlet-nightjar in rock crevice roost. The first 2 days show a single torpor bout with no torpor used on the later 2 days. The position of the roost high on a north-westerly facing a cliff resulted in high temperatures outside the roost ( $T_{\text{OUT}}$ ), with  $T_{\text{IN}}$  remaining stable

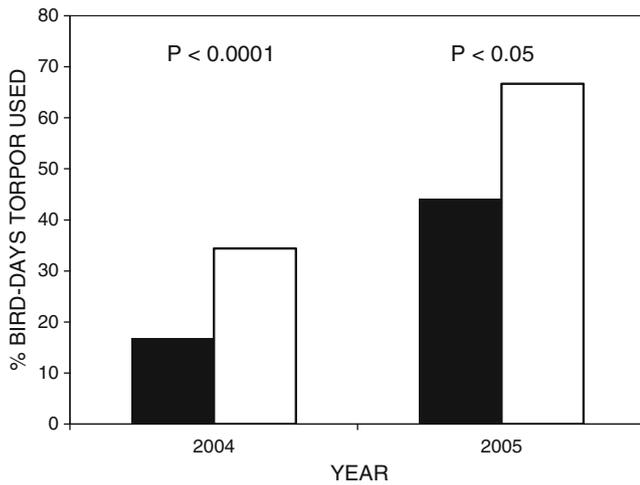


birds roosting in rock crevices were less likely to enter torpor ( $\chi^2=9.04$ ,  $P<0.01$ ). When  $\text{MIN } T_{\text{a}}$  was  $>6.8^\circ\text{C}$ , birds entered torpor less frequently, but there was no significant difference in torpor use between the two roost types ( $\chi^2=0.40$ ,  $P=0.53$ ).

Owlet-nightjars roosting in tree hollows rewarmed significantly faster ( $0.08\pm 0.009^\circ\text{C min}^{-1}$ ) than those roosting in rock crevices ( $0.04\pm 0.005^\circ\text{C min}^{-1}$ ), but rewarming rates and  $\text{MIN } T_{\text{a}}$  (roost type,  $F_{1,47}=8.34$ ,  $P<0.01$ ;  $\text{MIN } T_{\text{a}}$ ,  $F_{1,47}=0.62$ ,  $P=0.43$ ;  $R^2=0.18$ ) or  $\text{MIN } T_{\text{skin}}/T_{\text{b}}$  (roost type,  $F_{1,47}=8.86$ ,  $P<0.01$ ;  $\text{MIN } T_{\text{skin}}/T_{\text{b}}$ ,  $F_{1,47}=0.00$ ,  $P=0.95$ ; model  $R^2=0.17$ ) were not related.

## Discussion

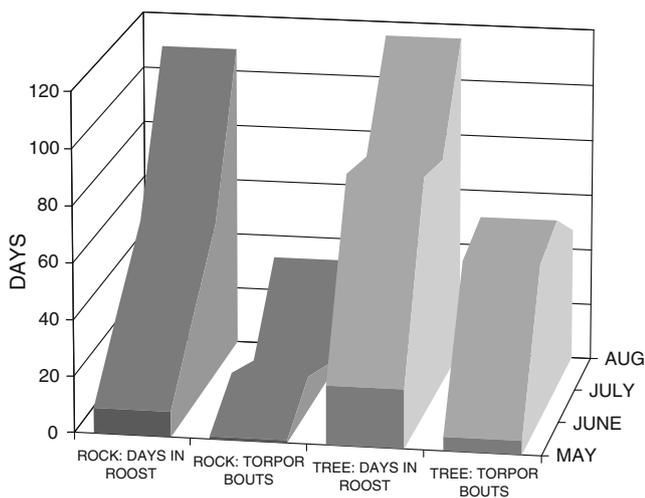
Our study provides the first data on the relationship between cavity roost selection and torpor use for a wild bird and is the first to describe thermoregulation in birds that regularly roosts in both trees and rock crevices. Owlet-nightjars entered torpor less often when roosting in more thermally stable and consistently warmer rock crevices. The use of these well-insulated roosts likely reduced the amount of energy required for owlet-nightjars to maintain high  $T_{\text{b}}$  and decreased the need to use torpor to conserve energy. Despite these energy savings, owlet-nightjars roosted in tree



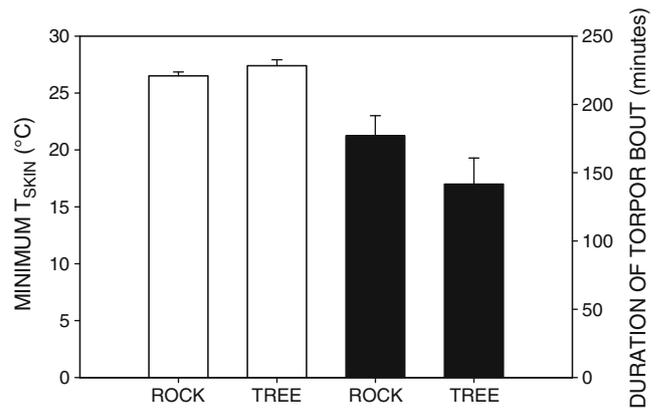
**Fig. 4** Owlet-nightjars entered torpor nearly twice as often when roosting in tree hollows (white bars;  $n=11$ ,  $N=366$ ) than when in rock crevices (black bars;  $n=10$ ,  $N=188$ ).  $P$  values are based on chi-square analysis

hollows more often (65% bird days) than rock crevices (35% bird days). Cool, poorly insulated tree hollows would facilitate the use of torpor during cold mornings and may allow for the use of passive rewarming or basking during the arousal phase. Increased protection from predators, especially during sun basking, may offer further explanation for the preference of roosts in tree hollows.

Most animals spend the majority of their time at rest, and an energy saving strategy, such as selecting a thermally insulated roost, can significantly affect an organism's total energy budget (Kurta 1985). Patterns of torpor use suggest that birds roosting in the warmer, constant microclimate of rock crevices use less energy to maintain high  $T_b$  and need



**Fig. 5** Owlet-nightjars roosted in both rock crevices and tree hollows throughout the winter months. Torpor use was consistently more frequent in tree hollows compared to rock crevice roosts for each month. Data for 2004 and 2005 combined



**Fig. 6** The mean  $\pm$  SE torpid MIN  $T_{skin}$  (°C, white bars) ( $t$  test,  $t_{13}=-1.26$ ,  $P=0.23$ ) and duration of torpor bouts (minutes, black bars) ( $t$  test,  $t_{13}=1.34$ ,  $P=0.20$ ) did not differ significantly between birds roosting in rock crevices and tree hollows

to enter torpor less frequently than those roosting in tree hollows. By using warmer roosts within their thermoneutral zone, ecologically similar microbats can lower their thermoregulatory costs and do not need to enter torpor as often (Lausen and Barclay 2006) and can passively maintain warm, stable  $T_b$  (Speakman and Thomas 2003). Sedgeley (2001) found that tree hollows used by the bat *Chalinobius tuberculatus* that were 0.5°C warmer than unused cavities led to a 1.1% to 7.3% reduction in energy expenditure depending on the time of day and cavity structure. On average, the  $T_{IN}$  for rock crevices was 6.7°C warmer than tree hollows which, based on the relationship between resting metabolic rate and  $T_a$ , would enable a 27% energy savings for owlet-nightjars (Doucette and Geiser 2008). Warmer roosts minimize the cost of resting while remaining normothermic, and animals can avoid the energetically expensive process of arousal from torpor. An earlier study of thermoregulation by owlet-nightjars in a habitat where only tree roosts were used found that torpor use and the use of two torpor bouts per day was much more frequent (Brigham et al. 2000).

Normothermy is most energetically expensive when the  $T_a$  is lowest and morning torpor bouts appear to be the most common type in nocturnal heterotherms (Audet and Fenton 1988; Brigham et al. 2000; Geiser et al. 2000; Turbill et al. 2003).  $T_{IN}$  of both roost types was lowest near dawn and morning torpor bouts were the most common for nocturnal owlet-nightjars. Thermally stable rock crevices remained relatively warm in the morning; however,  $T_{IN}$  of tree roosts was generally >10°C lower than in the afternoon. Birds also entered torpor at night more often in trees than in rocks crevices. If conditions are adverse and not favourable for foraging, birds may return to their roosts earlier. Night torpor bouts occurred on cold nights (mean  $T_a=3.1^\circ\text{C}$ ) when foraging may not have been energetically feasible due

to low insect abundance (Doucette 2007; Stawski and Geiser 2010). In these adverse conditions birds are likely to experience low energy reserves and the cooler  $T_a$  in tree hollows may facilitate the use of torpor to maximize energy conservation. This may partially explain why owlet-nightjars roosted in tree hollows more often (65% bird days) than in rock crevices (35% bird days) during winter.

The minimal thermal buffering offered by tree hollows also offers an advantage in that animals can benefit from maximum heating over the  $T_a$  cycle (Lovegrove et al. 1999; Kerth et al. 2001; Turbill et al. 2003). Rewarming rates during arousal were twice as fast for owlet-nightjars roosting in tree roosts than in rock crevices irrespective of MIN  $T_{skin}$  or MIN  $T_a$ . Radiant heating of tree roosts could help birds to arouse passively at much lower energetic costs than active arousal. Tree hollows also allow for greater behavioural thermoregulation as the bird can select from a variety of thermal microclimates within a single tree. Furthermore, the height of hollow entrances offers good sun exposure, increasing opportunities for basking with a reduced risk of predation compared to basking at ground level. Owlet-nightjars were regularly observed basking in tree hollows (Doucette 2007). The energetic savings of passive rewarming with increasing  $T_a$  or basking can be substantial (Lovegrove et al. 1999; Geiser et al. 2002; Geiser and Drury 2003).

Another possible explanation for owlet-nightjars selecting tree roosts more often may be that they offer better protection from predators. Although owlet-nightjars typically experience predation while foraging outside the roost (Brigham and Geiser 1997), monitor lizards (Broadbent 1910), large snakes, foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) represent potential terrestrial predators that could access birds in shallow rock crevices. Owlet-nightjars in tree hollows can take refuge deep inside the tree trunk at great heights where they may be less accessible to many terrestrial predators. Rates of nest predation on cavity-roosting birds are greater for nests closer to the ground (Nilsson 1984; Rendell and Robertson 1989). Additionally, rock roosts were generally exposed, with little to no vegetation outside the roost. Birds would be vulnerable to predation when leaving the roost with no immediate refugia to offer protection. Owlet-nightjars wait until near total darkness before exiting roosts (Doucette 2007), likely missing a profitable foraging period, suggesting that the predation risk during roost departure is significant.

The MIN  $T_{skin}$  of owlet-nightjars was inversely related to the duration of torpor bouts, and bout duration and MIN Torpid  $T_{skin}$  did not differ for the two roost types (Fig. 6). Thus, MIN  $T_{skin}$  and bout duration appear to be unrelated to roost type and may be relatively fixed or directed by other factors, such as prey abundance (Doucette 2007). While owlet-nightjars were capable of reducing their MIN  $T_{skin}$

during torpor to below 20°C, they usually kept MIN  $T_{skin}$  at around 25°C in both roost types. This  $T_{skin}$  may represent the preferred threshold for owlet-nightjars that conserves energy but from which rewarming is facilitated.

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