

Prey availability affects daily torpor by free-ranging Australian owl-nightjars (*Aegotheles cristatus*)

Lisa I. Doucette · R. Mark Brigham ·
Chris R. Pavey · Fritz Geiser

Received: 16 January 2011 / Accepted: 22 November 2011 / Published online: 17 December 2011
© Springer-Verlag 2011

Abstract Food availability, ambient temperatures (T_a), and prevailing weather conditions have long been presumed to influence torpor use. To a large extent, this is based on measurements in the laboratory of animals placed on restricted diets and kept at low T_a . Information on the determinants of torpor employment in the field is limited. We assessed winter torpor by insectivorous, free-ranging Australian owl-nightjars (*Aegotheles cristatus*; 22 birds, 834 bird-days over six winters). Birds in three habitats were investigated to test whether torpor use is affected by annual T_a , rainfall, and arthropod abundance. Owl-nightjars entered daily torpor regularly at all sites. Torpor frequency, depth and bout duration were greatest during two periods with lower arthropod abundance, providing rare evidence of the link between food availability and torpor patterns of wild birds. Temporal organization of torpor was similar among sites, and nocturnal torpor was more frequent than previously reported. Our findings quantitatively demonstrate that reduced food resources

affect torpor usage independently from T_a , and support the view that food availability is a primary ecological determinant of torpor use in the wild.

Keywords Energetics · Food resources · Heterothermy · Temperature telemetry · Thermoregulatory strategy

Introduction

The energetic costs of maintaining elevated metabolic rates to compensate for increased heat loss at times of low ambient temperature (T_a) are substantial (Withers 1992). One physiological strategy that some species of birds use to reduce this cost is to enter daily torpor (McKechnie and Lovegrove 2002). Torpor in heterothermic birds and mammals is characterized by a controlled reduction of body temperature (T_b), metabolic rate (MR), and activity, and is especially employed by species that periodically face energetic constraints due to extreme climatic conditions and ephemeral food supplies (Geiser 2004). Torpor in mammals is known to be influenced by a multitude of factors including food and water availability, T_a , photoperiod, reproductive state, prevailing weather conditions, and circannual cycles (Csada and Brigham 1994; Song and Geiser 1997; Körtner and Geiser 2000a, b), but little data exist for determinants of torpor use in birds.

Historically, torpor was hypothesized to be used by birds only as a last resort to survive ‘energetic emergencies’, possibly due to limited knowledge of avian torpor in the wild (Lasiewski and Dawson 1964; Peiponen 1965). Torpor was thought to be induced when low T_a and seasonal or daily food shortages reduced energy reserves to a level that could not support endothermic heat production (Bartholomew et al. 1957; Calder 1973; Hainsworth et al. 1977).

Communicated by Oliver Love.

L. I. Doucette (✉) · F. Geiser
Centre for Behavioural and Physiological Ecology, Zoology,
University of New England, Armidale, NSW 2351, Australia
e-mail: lisadoucette@live.com.au

R. M. Brigham
Department of Biology, University of Regina,
Regina, SK S4S 0A2, Canada

C. R. Pavey
Biodiversity Conservation, NRETAS, PO Box 1120,
Alice Springs 0871, Australia

Present Address:

C. R. Pavey
CSIRO, PO Box 2111, Alice Springs 0871, Australia

Supporting evidence came from laboratory studies showing that birds (Hohtola et al. 1991), and more specifically Caprimulgiformes (Marshall 1955; Lasiewski and Dawson 1964; Peiponen 1965; Dawson and Fisher 1969), only entered torpor when deprived of food for several days. In contrast, field studies on a variety of species indicate that heterothermic responses may be a routine means of balancing energy supply and demand, and energy emergencies or deficits are not always necessary for torpor induction (Reinertsen 1983; Brigham 1992; Körtner et al. 2001; Turbill et al. 2003; Schleucher 2004). For instance, hummingbirds enter nocturnal torpor regularly during winter and while migrating, irrespective of T_a and nectar availability (Carpenter 1974). Nonetheless, to date, only frugivorous, nectarivorous, and insectivorous birds, those that would regularly experience seasonal food shortages, have been reported to employ deep torpor (reduction in T_b to $<30^\circ\text{C}$) (McKechnie and Lovegrove 2002). Aerial insectivores, including bats, swifts, swallows, and nightjars which rely on activity by their prey, may be among those most strongly affected by T_a -dependent food availability (Racey and Swift 1985). Torpor may also be employed by mammals during periods of prey shortage due to seasonal drought, even when not accompanied by low T_a (Bartels et al. 1998; Coburn and Geiser 1998). However, given the direct correlation between low T_a , drought and reduced arthropod abundance and activity (King 1974; Doucette 2008), it is difficult to separate the influence of these factors on torpor use by insectivores. Food availability declines with T_a , while energy requirements increase (Speakman and Thomas 2003). Currently, there is no evidence for wild, free-ranging birds that quantifies the effect of T_a and food availability on torpor use.

As an insectivorous bird that relies on activity to locate their prey, Australian owlet-nightjars (*Aegotheles cristatus*; 45 g) should be affected by decreases in insect abundance during cold or dry conditions (Racey and Swift 1985; Brigham et al. 2000; Lane et al. 2004). Owlet-nightjars are non-migratory, cavity roosting, nocturnal Caprimulgiformes which regularly use torpor in winter in parts of their range, and are found in a variety of habitats throughout Australia (Brigham et al. 2000; Doucette et al. 2011). The purpose of our study is to compare thermoregulatory behavior and daily torpor use of owlet-nightjars at three

sites: (1) a natural semi-arid desert habitat, (2) an irrigated semi-arid desert habitat, and (3) a cool, temperate, high-altitude eucalypt woodland.

Three main environmental factors differ between these habitats, all of which may influence torpor use: T_a , annual rainfall, and arthropod abundance. Due to lower levels of rainfall in the desert, arthropod abundance was expected to be lower. We predicted that torpor frequency, depth, and duration would be greater in the desert if torpor is strongly influenced by food availability. Mean winter minimum T_a (MIN T_a) is lower in the eucalypt woodland. If torpor use is determined by low T_a , its frequency, depth, and duration should be greater at this site. Torpor use was expected to be less at the irrigated desert site than at either of the other two sites due to high arthropod abundance and moderate T_a s. Furthermore, as T_a is the same at both desert sites, the irrigated area allows us to independently test for the influence of arthropod abundance on torpor use in the arid environment.

Materials and methods

Study sites

Our study was conducted at the three locations during six winters (May–September 1996, 1997, 1999, 2004, 2005 and 2006; Table 1). Two of these locations, Ormiston Gorge ($23^\circ38'S$, $132^\circ44'E$; 640 m elevation) and the Alice Springs Desert Park ($23^\circ43'S$, $133^\circ50'E$; 630 m elevation), are located in the semi-arid desert of central Australia in the West MacDonnell Ranges. For some analysis, data from these two sites are pooled and referred to as the “desert” sites. The two sites have similar vegetation (for details, see Doucette 2010), but the Desert Park has areas that are regularly irrigated. For this reason, Ormiston Gorge is designated as desert (D) site and the Desert Park is designated as the irrigated desert (ID) throughout. The mean MIN T_a and maximum T_a (MAX T_a) in Alice Springs for July are 4.0 and 19.9°C and the mean annual rainfall is 282 mm (1941–2007, Australian Bureau of Meteorology).

The third site is located in Imbota Nature Reserve ($30^\circ35'S$, $151^\circ45'E$; 1,000 m elevation), a cool, temperate eucalypt woodland in the Northern Tablelands of New

Table 1 Details of study sites

Site name	Site code	Climate	Vegetation	Years sampled
Ormiston Gorge	D	Semi-arid	<i>Acacia</i> sp. shrubland and riverine woodland	2004 and 2005
Desert Park	ID	Semi-arid, partially irrigated	<i>Acacia</i> sp. shrubland and riverine woodland	2004 and 2005
Imbota Nature Reserve	EW	Cool temperate	Eucalypt woodland	2006, 1996 ^a , 1997 ^a , 1999 ^a

^a Data from Brigham et al. (2000)

South Wales, 10 km southeast of Armidale (see Doucette 2010 for site description). The mean daily MIN T_a and MAX T_a for Armidale in July are 1.0 and 13.2°C (1857–1997, Australian Bureau of Meteorology). Mean annual rainfall is 790 mm and mean monthly rainfall in winter is 51.5 mm. This location was designated as the eucalypt woodland (EW) site.

The photoperiod amongst all sites was similar throughout the winter, with sunrise occurring ~30 min earlier at the EW site (sunrise = 0551–0719 hours depending on site and month).

Ambient temperature and rainfall

Small temperature data loggers (Thermochron iButtons®, Model DS1921, $\pm 0.5^\circ\text{C}$ resolution; Dallas Semiconductor, Dallas, TX, USA) were placed in the shade 1 m above the ground in a central position at each site to measure T_a hourly. Weather stations at the Ormiston Gorge ranger station and at the Alice Springs Desert Park provided daily rainfall data. Daily rainfall data for Armidale were used for the EW site (Australian Bureau of Meteorology).

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. Most birds were fitted with an external radio transmitter (model PD-2T; Holohil Systems, Carp, ON, Canada) to measure skin temperature (T_{skin} ; $n = 20$ birds). External transmitters were attached using a backpack-style harness made from elastic thread. The transmitters were placed underneath the bird's feathers and affixed so that the harness kept the temperature sensor in contact with the bird's skin in the interscapular region to record T_{skin} (Brigham 1992; Brigham et al. 2000; McKechnie et al. 2007; Doucette et al. 2011). Two birds in central Australia (one at each location) in 2004 and one at EW in 1999 were kept overnight to surgically implant internal transmitters (Sir-track, Havelock North, New Zealand) to measure core T_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 day roosts using 3-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 birds in their roosts. T_{skin} or T_b was

recorded every 10 min continuously when birds were 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 3- or 5-element Yagi antennae. Data were downloaded to a computer every 4–5 days. The custom-made data loggers measured the interval between two transmitter pulses, and the Lotek recorded T_b or T_{skin} when it detected four consecutive pulses. Pulse rates recorded on loggers were confirmed by collecting data manually several times daily by using a receiver and timing 10 pulse intervals using a stopwatch. T_{skin} or T_b was estimated from pulse intervals using the calibration curve previously determined for each transmitter.

Arthropod sampling

Pitfall and light traps were used to sample arthropods at all study sites. Pitfall traps (diameter = 68 mm, depth = 150 mm), each containing 50 ml of 50% ethanol, were placed in a grid pattern consisting of 12 traps per plot (three rows of 4 traps; Table 2). Traps were placed at 10-m intervals. Arthropods were sampled in three different locations at each of the two desert study sites (2004, 2005) and at two locations in the eucalypt woodland (EW) in 2006 only. Sampling locations were chosen to represent different habitats where owlet-nightjars were captured, and thus known to forage. As a result of differences in habitat variability between the desert sites and the eucalypt woodland, three locations were used at each of the two desert sites and two locations in the monotypic eucalypt woodland (Table 2; Doucette 2008). To sample nocturnal

Table 2 Details of arthropod sampling at the three study sites

	Desert (D)	Irrigated desert (ID)	Eucalypt woodland (EW)
Pitfall traps			
No. of locations	3	3	2
Traps per location	Grid of 12 (3 rows of 4 traps)	Grid of 12 (3 rows of 4 traps)	Grid of 12 (3 rows of 4 traps)
Sampling period	2 nights per fortnight	2 nights per fortnight	2 nights per fortnight
Light traps			
No. of locations	3	3	2
Traps per location	1	1	1
Sampling period	1 night per fortnight + 1 night on new moon at each location	1 night per fortnight + 1 night on new moon at each location	1 night per fortnight + 1 night on new moon at each location

Table 3 A comparison of measures of torpor by free-ranging owlet-nightjars (*Aegotheles cristatus*) at the irrigated desert site in 2004 and 2005 (ID-2004, ID-2005), the desert site in 2004 and 2005 (D-2004, D-2005), and the eucalypt woodland site from 1996 to 1999 and in 2006 (EW-96-99, EW-2006)

	ID-2004 (<i>n</i> = 5, <i>N</i> = 68)	D-2004 (<i>n</i> = 5, <i>N</i> = 70)	ID-2005 (<i>n</i> = 2, <i>N</i> = 21)	D-2005 (<i>n</i> = 3, <i>N</i> = 77)	EW-96-99 (<i>n</i> = 4, <i>N</i> = 142)	EW-2006 (<i>n</i> = 4, <i>N</i> = 57)	Test result	<i>P</i> value	Post hoc comparison, Tukey test <i>P</i> < 0.05
Torpor frequency (%)	31	27	46	61	48	55	$\chi^2_5 = 51.9$	<0.0001	2005 and EW > 2004 ^a
Torpor use (%)	2.3 ± 1.3	4.0 ± 1.9	9.6 ± 0.4	9.4 ± 4.7	5.5 ± 2.6	16.0 ± 3.3	$F_{5, 22} = 3.6$	<0.05	EW-2006 > 2004
Mean minimum T_{skin} (°C)	27.6 ± 0.4	28.4 ± 0.5	26.3 ± 0.1	25.1 ± 0.5	26.1 ± 0.8	24.5 ± 0.4	$F_{5, 18} = 7.9$	<0.005	2004 > EW-2006 and D-2005
Mean torpor bout length (min)	121 ± 18	120 ± 21	196 ± 13	211 ± 10	170 ± 19	252 ± 26	$F_{5, 20} = 6.0$	<0.005	EW-2006 > 2004
Minimum T_{skin} (°C)	21.8	21.7	21.5	18.6	19.4	20.6			
Maximum torpor bout length (min)	429	480	541	640	530	587			

Torpor frequency (%) is the percentage of days torpor occurred of the days data was recorded (Chi-square test). Torpor use (%) is the mean of the total number of minutes torpor was recorded as a percentage of the total number of minutes T_{skin} data was recorded each week. Values for minimum T_{skin} during torpor (°C) and torpor bout length (min) are given as mean ± SE for all torpor bouts (*N*) recorded (one-factor ANOVA using the mean value per individual); *n* = number of individuals. The presentation of only the year in comparison tests indicates that the difference was significant for both sites for that year

^a Results of post hoc 2 × 2 contingency table comparisons of combined site data for 2004 and 2005 and combined years for EW

arthropods each pitfall trap was uncovered at dusk and covered at dawn. Traps were opened for two nights fortnightly at each site. Arthropods were removed from traps post-sampling and stored in 70% ethanol.

Nocturnal aerial arthropods were sampled in the same plots using an ultra-violet light trap (Australian Entomological Supplies, Coorabell, NSW, Australia) suspended 0.5–1 m above the ground. At the desert sites, the traps were placed in patches of *Acacia* sp. woodland where the owlet-nightjars foraged, thus the visibility of light traps in the desert was comparable to those in the open woodland.

Each of the locations was sampled for aerial and terrestrial arthropods every fortnight. Additionally, each site was sampled using light traps for aerial arthropods during the new moon, as studies have shown that light traps are more effective during this period (Bowden and Church 1973). All light and pitfall trap samples were dried at 60°C for at least 12 h and weighed to determine dry biomass (±0.01 g) using a Mettler AE 260 balance (Mettler Instrumente, Switzerland). Arthropods <3 mm long or >11 mm diameter were excluded from analysis as these are not normally consumed by nightjars (Jackson 2000; Jetz et al. 2003).

Data analysis

Mean ± SE active T_{skin} for owlet-nightjars with external transmitters was 37.2 ± 0.1°C. We considered owlet-

nightjars to be torpid when T_{skin} fell below 30°C for 20 min or more (see also Reinertsen 1996; Brigham et al. 2000). Mean active core T_b of owlet-nightjars with implanted transmitters was 39.4 ± 0.2°C, and birds were defined as having entered torpor when T_b fell below 33°C for 20 min or more. Brigham et al. (2000) compared T_{skin} and T_b of an owlet-nightjar in captivity with both an external and internal transmitter attached and found the difference to be 3.0 ± 0.8°C. For comparison of minimum T_{skin} (MIN T_{skin}) during torpor amongst birds, 3°C was subtracted from the minimum T_b of birds with internal transmitters to estimate T_{skin} . Days or nights from which T_{skin} or T_b data were missing for more than a 3-h period were excluded from the analysis. Torpor-days are defined as days when an individual used at least one bout of torpor in a 24-h period. Torpor use (%) is defined as the number of minutes torpor was used as a percentage of total minutes T_{skin} was recorded each week for all birds. This measure takes into account the number of birds using torpor, the number of torpor bouts, and the duration of those bouts.

Torpor frequency, defined as the percentage of days torpor was used, was compared for each site/year using Chi-square tests (χ^2 ; Table 3). Post hoc two-way contingency tables were used to compare pairs of sites. Yates correction for continuity was used for all χ^2 tests with 1 degree of freedom to correct for bias (Zar 1998). The means for torpor use, torpor bout length, and MIN T_{skin}

Table 4 Correlation matrix showing Spearman rank order correlation coefficients (r_s) and P values for weekly means of minimum ambient temperature (T_a , °C), rainfall (mm), total arthropod biomass (g), torpor use (%), minimum T_{skin} during torpor (°C), and torpor bout duration (min) for each site and year

	Year	Minimum T_a (°C)	Rain (mm)	Arthropod biomass (g)	Torpor use (%)	Torpor bout length (min)	Minimum T_{skin} (°C)
Site	0.45 $P = 0.003$	-0.25 $P = 0.13$	0.50 $P < 0.001$	-0.50 $P < 0.001$	0.41 $P = 0.009$	0.32 $P = 0.07$	-0.35 $P = 0.05$
Year		-0.72 $P < 0.0001$	0.25 $P = 0.11$	-0.52 $P < 0.0001$	0.42 $P = 0.007$	0.51 $P = 0.003$	-0.61 $P < 0.0001$
Minimum T_a			-0.81 $P = 0.62$	0.28 $P = 0.08$	-0.20 $P = 0.11$	-0.44 $P = 0.01$	0.40 $P = 0.02$
Rain				-0.14 $P = 0.39$	0.18 $P = 0.27$	0.33 $P = 0.07$	-0.36 $P = 0.04$
Arthropod biomass					-0.61 $P < 0.0001$	-0.54 $P < 0.002$	0.54 $P < 0.002$
Torpor use						0.71 $P < 0.0001$	0.58 $P < 0.0001$
Torpor bout length							-0.84 $P < 0.0001$

Torpor use (%) is the number of minutes torpor was recorded as a percentage of the total number of minutes T_{skin} was recorded each week. Data for EW 96–99 are excluded as no arthropod data was recorded for those years. $n = 21$ birds, $N = 40$ observations (weeks). An alpha value of $P < 0.002$ indicates a significant correlation ($P < 0.05$ with Bonferroni Correction) (Curtin and Schulz 1998)

during torpor for each bird were compared amongst sites and years using a one-way analysis of variance (ANOVA). Due to natural outliers in the climate and arthropod biomass data (e.g., days with high rainfall and high arthropod biomass due to mass hatchings), the variables were not normally distributed and were compared amongst sites and years using Kruskal–Wallis ANOVAs (K–W ANOVA). The efficiency of the Kruskal–Wallis non-parametric ANOVA compared to the parametric equivalent is 95.5% (Siegel and Castellan 1988). Tukey Tests or Dunn’s Method was used for post hoc analysis.

Arthropod biomass was sampled weekly or fortnightly at each site throughout the study, not each night. To enable comparison of the effects of the environmental variables on torpor, weekly data were used (total arthropod biomass, total rainfall and average minimum T_a) and compared to weekly torpor data for all individuals combined (torpor use, average torpor bout length; average of minimum T_{skin} during torpor). For several of the pairs of variables, the joint distribution was not bivariately normal (Quinn and Keough 2002). Transforming the data was not a practical option due to negative T_a values that would have been excluded if the data were logarithmically or square-root transformed. Thus, pairs of variables were compared using a Spearman rank order correlation, which is 91% as powerful as a Pearson product moment correlation (Lehner 1996). A Bonferroni correction was used to adjust the significance of the P value of the tests based on the number

of comparisons. The correlation was considered to be significant if $P < 0.002$ (28 comparisons). The comparison revealed strong correlation between site and rainfall/arthropod abundance and year and T_a /arthropod abundance (Table 4).

Modeling was used to determine which variables (MIN T_a , rainfall and arthropod abundance) best predict the torpor use, bout length, and MIN T_{skin} . Quinn and Keough (2002) recommend omitting predictor variables if they are highly correlated with other predictor variables that are to remain in the model. Multiple predictor variables that are measuring similar biological entities represent redundant information. In this case, the strong collinearity between site and year and the environmental variables meant that the categorical variables for site and year had to be omitted from the models (Quinn and Keough 2002). All variables that remained in the models were continuous. We used multiple linear regression analysis to create models that included rainfall, MIN T_a , and/or arthropod abundance and selected the model with the smallest Bayesian Information Criteria (BIC; Quinn and Keough 2002). BIC adjusts for sample size and number of predictors, penalizing the models with a greater number of predictors. The top three models were considered useful for making inferences. The model weight (w_i) indicates the probability that a model is the best approximating model among the candidate models (Table 5).

Our initial statistical analysis revealed no significant difference in dependent torpor variables between the sites

Table 5 Multiple linear regression models of the effect of predictor environmental variables [arthropod biomass (g), minimum T_a ($^{\circ}\text{C}$), rainfall (mm)] on torpor use (%), torpor bout length (min) and minimum T_{skin} during torpor ($^{\circ}\text{C}$)

Model	n	p	P value	BIC	Δ_i	w_i
Torpor use						
Arthropod biomass	40	1	0.029	180.7	0	0.44
Arthropod biomass \times rain	40	2	0.032	182.0	1.33	0.23
Rain	40	1	0.113	183.1	2.38	0.14
Torpor bout length						
Min T_a	32	1	0.015	274.5	0	0.47
Min $T_a \times$ arthropod biomass	32	2	0.023	276.0	1.56	0.22
Arthropod biomass	32	1	0.083	277.7	3.20	0.10
Minimum T_{skin}						
Min T_a	32	1	0.025	47.87	0	0.50
Min $T_a \times$ arthropod biomass	32	2	0.045	49.88	2.01	0.18
Arthropod biomass	32	1	0.120	50.65	2.78	0.13

Data are based on weekly mean values for each site and year. Bayesian Information Criteria (BIC) were used to select the best fitting models. Only the best three models for each measure of torpor are presented. p is the number of parameters in the model, Δ_i is the difference in BIC value between the i th and top-ranked model, and w_i is the weight (probability that the i th model is actually the best approximating model among the candidate models)

in the desert whilst the difference between the dry and wet years was significant. Thus, for some analysis the irrigated desert and the non-irrigated desert sites were combined for clarity. Data are presented as means \pm SE of the number of individuals measured (n). N = the number of observations recorded. An alpha value of 0.05 was used for all tests except for the Spearman rank correlation (Table 4). Minitab 13.1 was used for ANOVAs, Spearman rank correlations, and multiple linear regressions. Chi-squared tests were performed using Statistix 1.6.

Results

Climate

Mean winter (May–September) MIN T_a s for each year (1996, 1997, 1999 and 2006) in EW were significantly lower than the desert in 2004 and 2005 (K–W ANOVA: $H_5 = 231.14$, $P < 0.00001$; Fig. 1). MIN T_a did not differ between years in the desert. Mean MIN T_a in the desert during winter averaged $7.2 \pm 0.4^{\circ}\text{C}$, which was $5.3 \pm 0.3^{\circ}\text{C}$ greater than Mean MIN T_a in EW. Winter temperatures in the EW in 2006 (mean 2.4°C) approximated the long-term average (2.1°C); however, the coldest

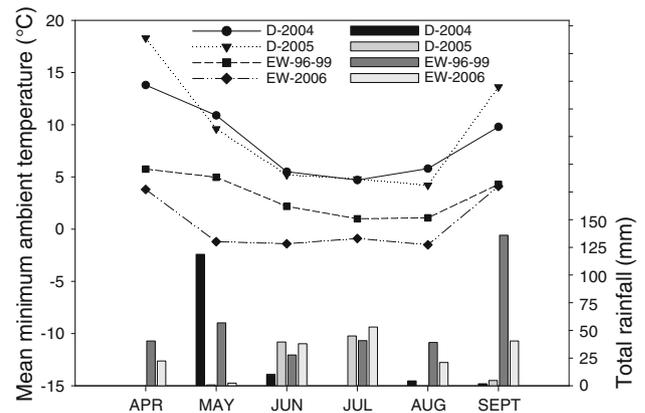


Fig. 1 Mean monthly ambient temperatures ($^{\circ}\text{C}$) and total rainfall (mm) for the desert in 2004 and 2005 and the eucalypt woodland (EW) site in 1996–1999 and 2006

temperatures ever recorded in Armidale occurred this year (-10.8°C) with several nights $< -10^{\circ}\text{C}$ and many nights $< -7^{\circ}\text{C}$ (Australian Bureau of Meteorology). MIN T_a in 2006 was lower than in the milder winters of 1996, 1997 and 1999 (Fig. 1).

Average winter (May–September) rainfall in Alice Springs is 66.3 mm (1940–2007, Australian Bureau of Meteorology), which is substantially less than in the EW (251 mm; 1857–2007, Australian Bureau of Meteorology). In both 2004 (120 mm) and 2005 (85 mm), above average winter rain occurred in central Australia; however, it is the timing of rainfall that appears to have the greatest effect on the overall arthropod abundance throughout the winter months. Heavy rains (120 mm) in mid-May 2004 (Fig. 1), preceded by a wetter than average year (420 mm), caused the usually dry Ormiston Creek to flow from 22 May 2004 until mid-June 2004, and small pools persisted in the river channel until the end of August 2004. In contrast, between June 2004 and May 2005, only 72 mm of rain fell, making for dry conditions in winter 2005. From mid-June to mid-July 2005, 85 mm of rain fell. Overall, there was no significant difference in rainfall between the winters of 2004 and 2005 at the desert sites (Dunn's Test, $P < 0.05$) even though in 2005 the creek remained dry and the permanent waterhole in Ormiston Gorge was less than one-quarter the size of 2004. The irrigated site at the Alice Springs Desert Park experienced similar low rainfall between 2004 and 2005. However, regular irrigation likely meant less impact on arthropod availability at this site. EW received significantly more rain than the desert from 1996 to 1999 ($H_7 = 147.2$, $P < 0.00001$). The winter of 2006 was a dry year with only 163 mm of rain. This is almost half the winter average (251 mm, 1857–2007). In contrast, winters from 1996–1999 had above average rainfall (280 to 428 mm; Australian Bureau of Meteorology).

Arthropod biomass

Aerial and terrestrial arthropod biomass was significantly lower at the EW site in 2006 compared to both desert sites in 2004 and ID-2005 (K–W ANOVA: Aerial: $H_4 = 23.3$, $P < 0.001$; Terrestrial: $H_4 = 330.36$, $P < 0.0001$; Fig. 2). Although the difference between years was less at ID, arthropod biomass was lower in dry 2005 compared to wet 2004. D-2005 did not differ significantly from EW for aerial or terrestrial biomass. Arthropod abundance was greater at ID compared to D in both years. However, the difference between years overshadowed the difference between sites overall with significantly greater arthropod biomass in wet 2004 than in dry 2005 and the EW site in 2006 (K–W ANOVA: Aerial: $H_2 = 27.3$, $P < 0.00001$; Terrestrial: $H_2 = 148.4$, $P < 0.00001$).

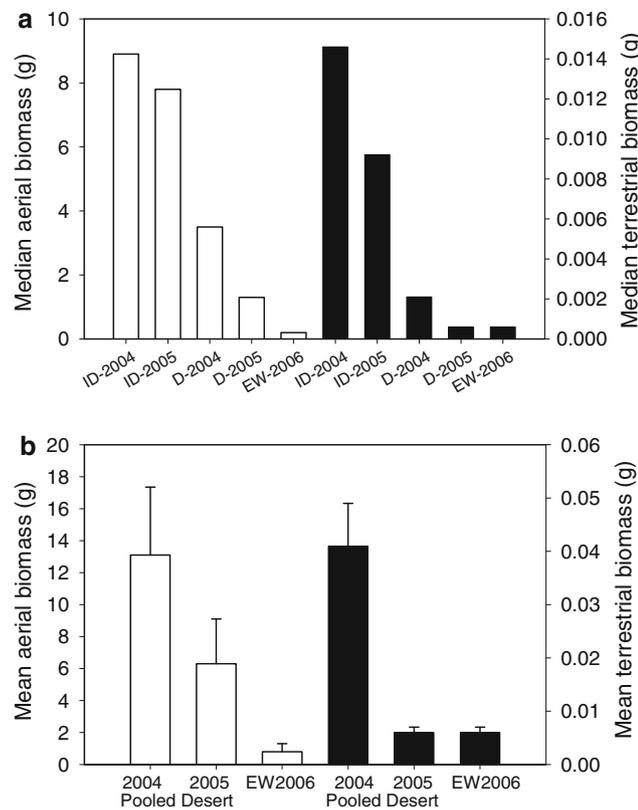


Fig. 2 Median (a) and mean \pm SE (b) aerial (white bars) and terrestrial (black bars) arthropod biomass (g) collected in light and pitfall traps during winter (June–September) for the irrigated desert (ID) in 2004 and 2005, desert (D) in 2004 and 2005, and the eucalypt woodland (EW) in 2006. Due to high variation between samples, median values are a better representation of the data than means. Aerial and terrestrial arthropod biomass was significantly lower at EW site in 2006 compared to both desert sites in 2004 and ID-2005 ($P < 0.001$). The difference between years overshadowed the difference between sites overall with significantly greater arthropod biomass in wet 2004 than in dry 2005 and EW in 2006 (Aerial $P < 0.00001$; Terrestrial $P < 0.00001$), thus the two desert sites are pooled in (b) to simplify the comparison

Owlet-nightjar captures

Data were collected for 10 owlet-nightjars in the desert in 2004 (5 ID and 5 D), including data for one bird with an internal transmitter at each site. In 2005, only 5 owlet-nightjars were caught (2 ID and 3 D) due to dry conditions and low bird abundance. Data were collected at EW for 2 birds in 1996, 3 in 1997, 1 in 1999 (internal transmitter; Brigham et al. 2000), and 4 in 2006. Body mass at capture ranged from 38.9 to 58.1 g (mean = 46.5 g), and was within the normal range for the species (40–60 g; Holyoak 2001). There was no relationship between owlet-nightjar body mass and torpor frequency (linear regression; $F_{1,15} = 0.82$, $P = 0.38$), torpor bout length ($F_{1,15} = 0.19$, $P = 0.67$) or minimum torpid T_{skin} ($F_{1,15} = 0.05$, $P = 0.83$).

Torpor use

Torpor bouts were recorded in the desert between 18 May and 13 Sept 2004 and 3 June to 16 August 2005. Eight of the 10 birds in the desert in 2004 entered torpor at least once for a total of 138 torpor bouts (121 torpor-days), occurring on 29% of the 418 bird-days that T_{skin} or T_b was recorded (Table 3). Torpor frequency was greater in dry 2005, and all five desert birds entered torpor for a total of 98 torpor bouts (77 torpor-days), resulting in torpor occurrence on 57% of the 136 bird-days that T_{skin} was recorded (Fig. 3). Torpor bouts were recorded at EW from 8 May until 8 September. Seven of the eight radio-tagged birds at EW entered torpor for a total of 199 torpor bouts (140 torpor-days); resulting in torpor occurring on 50% of the 280 bird-days of monitoring.

Torpor frequency differed significantly amongst sites/years ($\chi^2_5 = 51.9$, $P < 0.0001$; Table 3), but did not differ between the two desert sites in either year (2004: $\chi^2 = 0.4$, $P = 0.52$; 2005: $\chi^2 = 1.8$, $P = 0.18$). Torpor frequency was greater in D-2005 than D-2004 ($\chi^2 = 0.326$, $P < 0.0001$), but did not differ between years for the irrigated desert ($\chi^2 = 2.5$, $P = 0.11$). Torpor use at EW was similar to both desert sites in dry 2005 ($\chi^2_2 = 3.9$, $P = 0.14$), but greater than wet 2004 ($\chi^2_2 = 32.2$, $P < 0.0001$).

In all sites/years, birds most frequently entered torpor in the morning between 0600 and 1200 hours ($N = 317$, 72.9% of torpor-days; Fig. 4). The mean time of torpor entry was 90 ± 16 min after sunrise (0551–0719 hours depending on the day and site). When afternoon bouts occurred (1200–1800 hours; mean start time: desert = $13:36 \pm 14$ min, EW = $13:42 \pm 8$ min) they always followed an earlier morning bout in the desert ($N = 16$) and on 98% of occurrences ($N = 43$) at EW. Night torpor bouts occurred on 28% of bird-nights ($N = 21$) in the EW, and 6% ($N = 8$) and 27% ($N = 17$)

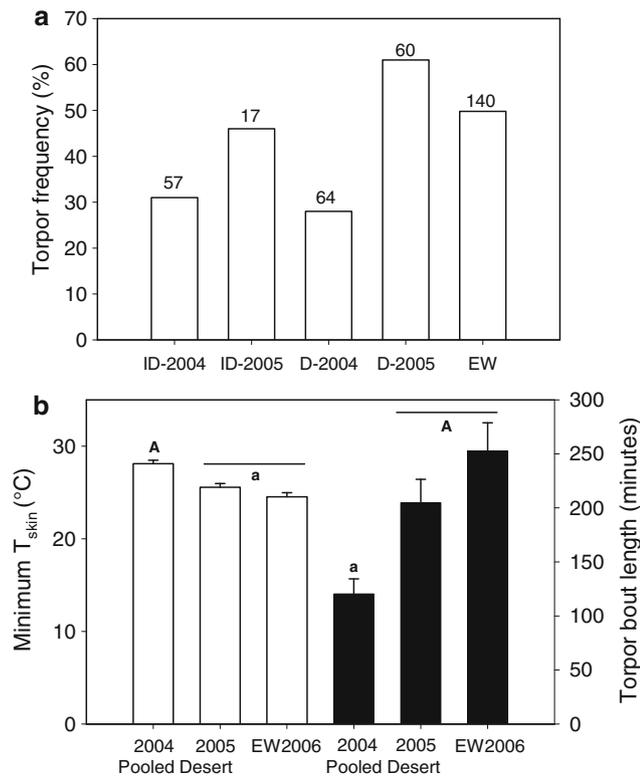


Fig. 3 **a** Torpor frequency of owllet-nightjars (*Aegotheles cristatus*) as a percentage of the number of bird-days of data collected. The x-axis labels are for the irrigated desert (ID) in 2004 and 2005, desert (D) in 2004 and 2005, and the eucalypt woodland (EW) site. Torpor frequency differed significantly amongst sites/years ($P < 0.0001$), but did not differ between the two desert sites in either year. Torpor use at EW was similar to both desert sites in dry 2005 but greater than wet 2004 ($P < 0.0001$). Numbers above the bars represent the total number of torpor days. **b** Mean \pm SE minimum T_{skin} (°C; white bars) during torpor and torpor bout length (min; black bars) by owllet-nightjars at the irrigated desert and desert sites pooled for each year (wet 2004 and dry 2005) and in the eucalypt woodland (EW) in 2006. Letters indicate significant differences with bars labeled *a* having values significantly less than *A*. Torpor bout length was significantly shorter (ANOVA: $F_{2,15} = 18.3$, $P < 0.001$) and Minimum T_{skin} during torpor higher ($F_{2,20} = 8.2$, $P < 0.005$) in wet 2004 than in dry 2005 and EW 2006. Sample sizes of individual birds (n) are given in Table 3

of bird-nights in the desert in 2004 and 2005, respectively. Bird-days on which more than one torpor bout occurred were significantly more common in the desert in 2005 ($N = 13$, 16%) and EW ($N = 50$, 18%), than the desert in 2004 ($N = 7$, 3%; $\chi^2_{0.05,2} = 30.9$, $P < 0.0001$).

Torpor bout length was significantly greater in the EW in 2006 than at both desert sites in wet 2004 (Table 3; Fig. 3b). The duration of the longest torpor bout was 640 min (10.7 h), which occurred at night (beginning at 1936 hours) on 7 July 2005 (Fig. 4). Mean MIN T_{skin} during torpor was higher in the desert in 2004 than in 2005 or at EW in 2006 (Table 3; Fig. 3b). The lowest MIN T_{skin}

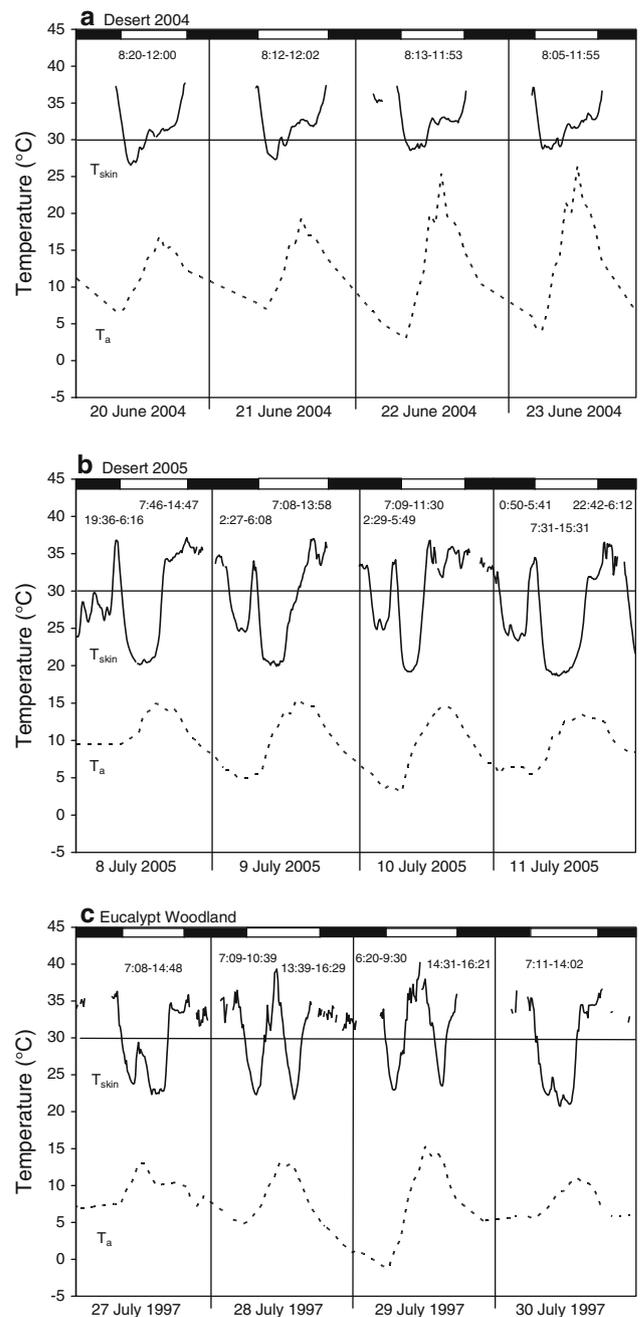


Fig. 4 Examples of torpor bout patterns used by individual owllet-nightjars in the desert in wet 2004 (**a**) and dry 2005 (**b**) and the eucalypt woodland (EW) site in 1997 (**c**) showing T_{skin} (solid line) and T_a (dotted line). Torpor bouts in the desert were longer and deeper in 2005 than in 2004 and the occurrence of more than one bout per day was more frequent. The same pattern of multiple, deep, frequent torpor bouts occurred at EW. Start and end times of torpor bouts are labeled above each bout. Dark and light bars at the top of each figure correspond to scotophase (night) and photophase (day)

during a torpor bout was 18.6°C, which occurred at 0731 hours on 11 July 2005 when MIN T_a was a relatively warm 7°C (Fig. 4b). The lowest unadjusted T_b measured for a bird with an internal transmitter was 19.4°C (EW-

2006). Minimum torpid T_{skin} was negatively correlated with torpor bout length ($y = -0.013x + 28.22$, $r^2 = 0.37$, $P < 0.0001$, $N = 408$).

Effects of climate and arthropod abundance on torpor

The Spearman rank correlation matrix comparing site, year, mean weekly environmental parameters and mean weekly physiological parameters indicated that several factors were correlated (Table 4). Arthropod biomass was highly correlated with torpor use, bout length and MIN T_{skin} ($P < 0.002$; Table 4). Minimum T_a and rainfall were not strongly correlated with any of the torpor measures. Year had a strong correlation with MIN T_{skin} , MIN T_a , and arthropod biomass. Site had no correlation with any torpor measures, but was strongly correlated with rainfall and arthropod abundance. The collinearity of site and year with environmental variables prevented the use of site and year in the multiple linear regression analysis (Quinn and Keough 2002).

Forward and backward stepwise regressions of the data produced the same “best fit” models as the BIC method for all torpor measures. The top three models selected using the BIC approach for each torpor measure are presented in Table 5. BIC selected a model for torpor use with just one predictor variable: arthropod abundance. This model has a 44% probability of being the best approximating model among the 7 candidate models tested. The second and third best models to predict torpor use included rainfall as a predictor variable. MIN T_a alone was the best predictor variable for torpor bout length and MIN T_{skin} . This simple model had a 47% (bout length) and 50% (minimum T_{skin}) probability of being the best approximating model (Table 5). The second and third best models for torpor bout length and MIN T_{skin} included arthropod abundance as a predictor variable.

Discussion

Food availability, T_a , microclimate and prevailing weather conditions are presumed to influence torpor use. However, this assumption is largely based on laboratory measurements of birds placed on restricted diets and kept at low T_a (Marshall 1955; Lasiewski and Dawson 1964; Peiponen 1965; Dawson and Fisher 1969; Ligon 1970; Calder and King 1974). Information on the determinants of torpor use in the field is limited. Our study contributes substantially to the scarce data on the link between environmental conditions and torpor in free-ranging birds. It shows that daily torpor is frequently used by owlet-nightjars at different sites, and its occurrence appears to be strongly influenced by arthropod biomass. The use of torpor appears vital to owlet-nightjar survival in habitats with cold winter T_a and low arthropod abundance.

Arthropod abundance was low at EW, likely due to lower winter T_a , but biomass was similar to that recorded by an earlier study at a nearby location in the region using the same trapping methodology (Lowman 1982). The biomasses of aerial and terrestrial arthropods sampled at the desert sites are comparable to arthropod biomass previously sampled at Ormiston Gorge during winters 1991–1993 (Gilfillan 2001) and elsewhere in the Australian arid zone (Drake and Farrow 1985; Read 1987). Rainfall early in the winter of 2004 (May) resulted in a pulse of resource availability including a relatively high arthropod abundance. In the desert in 2005, despite mid-winter rains, there was no detectable resource pulse, availability of standing water was reduced compared to 2004, and arthropod abundance was lower. Thus, although arthropod abundance differed between irrigated and non-irrigated sites in the desert, the difference between years was greater. A valid comparison of the relationship between torpor use, T_a and arthropod availability was best established by comparing years in the desert and the EW.

Torpor frequency, depth, and bout length were greater during the two periods with the lowest arthropod biomass (2005 and EW-2006; Fig. 3). The strong correlation between arthropod biomass and measures of torpor suggest arthropod biomass is a primary determinant of torpor (Table 4). The selection of the best fit model from multiple linear regressions analysis for torpor use is consistent with the hypothesis that the total time birds spent in torpor was directly related to arthropod biomass (Table 5). As this measure was inclusive of the number of birds using torpor each week and the frequency of torpor bouts, the results indicate that the likelihood of a bird entering torpor is dependent on the arthropod biomass at the site. A difference in arthropod abundance also explains the disparity in torpor use between the 2 years in the desert despite no difference in T_a .

Many laboratory studies have reported that periods of fasting and mass loss were required to ‘force’ birds to use torpor (Marshall 1955; Lasiewski and Dawson 1964; Peiponen 1965; Dawson and Fisher 1969; Ligon 1970; Calder and King 1974; Prinzinger et al. 1981). A restricted diet, associated in some cases with a substantial loss of body mass, typically results in increased torpor frequency, depth, and duration in both mammals and birds. However, severe food shortages or periods of fasting were not required to stimulate torpor in free-ranging owlet-nightjars. One owlet-nightjar was captured in June 2006 at EW with a body mass of 51.3 g. It had previously been captured in February 2006 (52.5 g) and was captured again in September 2006 (51.5 g). This individual used torpor on 93% of bird-days during June–July 2006 despite its high body mass. Several other bird species readily enter torpor during favorable environmental conditions and without an acute reduction in

food availability (Carpenter 1974; Carpenter and Hixon 1988; Brigham 1992; Merola-Zwartjes and Ligon 2000; Körtner et al. 2001; Lane et al. 2004).

Direct evidence for the effect of food availability on torpor use in free-ranging birds is scarce. We know of only two studies that have experimentally examined the response of birds to reduced food abundance; however, both relied strongly on artificial conditions in field situations. Bech et al. (1997) caught three species of hummingbirds at artificial feeders and deprived them of food for varying periods until sunset, then kept them in cages overnight to examine torpor use. All three species entered torpor, but torpor frequency and duration were positively related to the duration of the fasting time before sunset. Secondly, Woods and Brigham (2004) used artificial lighting to investigate the effect of aerial insect abundance on the use of torpor by common poorwills (*Phalaenoptilus nuttalli*). They found that torpor frequency decreased by 38% at the site with supplemental illumination. However, poorwills and other Caprimulgiformes are known to increase activity during periods with increased lunar light (i.e. full moon) irrespective of prey density (Jetz et al. 2003; Woods and Brigham 2008). Thus, the effect of increased light and activity levels leading to decreased torpor employment could not be excluded.

Although arthropod biomass was more strongly correlated with torpor bout duration and MIN T_{skin} (Table 4), the best fit model suggests that the depth and duration of torpor are influenced more by MIN T_a , potentially combined with arthropod biomass (Table 5). The much lower $T_{a,s}$ at the EW site, and the correspondingly longer torpor bouts and lower MIN T_{skin} at this site, likely contributed substantially to this result. Low $T_{a,s}$ are known to influence torpor bout length and depth (e.g., Geiser and Brigham 2000; Turbill and Geiser 2008); however, the correlation between torpor duration and T_a is variable within and among species (Geiser and Broome 1993; Turbill and Geiser 2008). The mechanism that controls torpor in birds in relation to T_a is poorly understood (McKechnie and Lovegrove 2002).

The temporal pattern and periodicity of torpor were similar between sites and years. At all sites and under all conditions, birds never remained in torpor past sunset, when insect availability is expected to be highest (Racey and Swift 1985). However, owlet-nightjars used torpor at night more frequently (up to 27% of bird-nights) than previously observed (Brigham et al. 2000). Night torpor was rarely used in the desert in 2004 (6% of bird-nights) when prey abundance was higher.

While the most common torpor pattern for owlet-nightjars was a single morning bout, a bi-modal pattern of two torpor bouts per day, or at least a lowering of T_{skin} twice per day with a midday arousal, occurred in both

habitats. Synchronizing arousal with the warmest part of the day should greatly reduce the cost of arousing from torpor (Körtner and Geiser 2000a; Schmid 2000; Geiser and Drury 2003; Doucette et al. 2011). However, the bimodal pattern includes one active arousal and suggests that it is not passive re-warming with T_a that always mandates arousal. One possibility is that, once the critical T_b set point is reached, the metabolic rate increases and metabolic processes stimulate arousal (Geiser and Kenagy 1988). Unlike for many other species, T_{skin}/T_b for owlet-nightjars often did not reach steady state as it did not flatten at the lowest T_b , and arousal generally commenced immediately following the point when the lowest T_b occurs (Fig. 4). A second possibility, therefore, is that there is a trade-off between torpor duration and the risk of predation (Welton et al. 2002). Owlet-nightjars may use shorter daytime bouts to remain alert and reduce predation risk. Although rates of re-warming were highly variable amongst individuals (Doucette 2008), owlet-nightjars rewarm more slowly than most other birds (McKechnie and Wolf 2004), and would presumably be unable to react to a predator when at low T_b or be able to arouse quickly (Carpenter and Hixon 1988).

Obviously, winter in the colder parts of Australia is energetically challenging for a small, nocturnal bird dependant on a fluctuating food source. Our results demonstrate a clear link between prey availability and the frequency of torpor use in free-ranging birds independently of T_a . Birds with reduced food resources were able to increase the frequency of torpor use to balance energy supply and demand, offering support for the concept that food availability is a primary ecological determinant of torpor use in the wild.

Acknowledgments Thanks to Fred Harvey for field assistance. This study was funded by the University of New England, the National Science and Engineering Council of Canada, and the Australian Research Council. Small grants were provided by Birds Australia, the Royal Zoological Society of New South Wales, and the Australian Bird Study Association. Permits for the research were issued by the University of New England Animal Ethics Committee, the Northern Territory Parks & Wildlife Commission, the New South Wales National Parks & Wildlife Service, and the Australia Bird & Bat Banding Scheme. This research complies with the current laws of Australia.

References

- Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal the northern blossom-bat *Macroglossus minimus* (Megachiroptera). *J Comp Physiol B* 168:233–239
- Bartholomew GA, Howell TR, Cade TJ (1957) Torpidity in the white-throated swift, Anna's hummingbird, and poor-will. *Condor* 59:145–155
- Bech C, Abe AS, Steffensen JF, Berger M, Bicudo J (1997) Torpor in three species of Brazilian hummingbirds under semi-natural conditions. *Condor* 99:780–788

- Bowden J, Church BM (1973) The influence of moonlight on catches of insects in light-traps in Africa. Part II. The effect of moon phase on light-trap catches. *Bull Entomol Res* 63:129–142
- Brigham RM (1992) Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol Zool* 65:457–472
- Brigham RM, Körtner G, Maddocks TA, Geiser F (2000) Seasonal use of torpor by free-ranging Australian owl-nightjars (*Aegotheles cristatus*). *Physiol Biochem Zool* 73:613–620
- Calder WA (1973) Microhabitat selection during nesting of hummingbirds in the rocky mountains. *Ecology* 54:127–134
- Calder WA, King JR (1974) Thermal and caloric relations of birds. In: Farner D, King J, Parkes K (eds) *Avian biology volume IV*. Academic, New York, pp 259–413
- Carpenter FL (1974) Torpor in an Andean hummingbird: its ecological significance. *Science* 183:545–547
- Carpenter FL, Hixon MA (1988) A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 90:373–378
- Coburn DK, Geiser F (1998) Seasonal changes in energetics and torpor patterns in the subtropical blossom-bat *Syconycteris australis* (Megachiroptera). *Oecologia* 113:467–473
- Csada RD, Brigham RM (1994) Reproduction constrains the use of daily torpor by free-ranging common poorwills (*Phalaenoptilus nuttallii*) (Aves, Caprimulgidae). *J Zool* 234:209–216
- Curtin F, Schulz P (1998) Multiple correlations and Bonferroni's correction. *Biol Psychiatry* 44:775–777
- Dawson WR, Fisher CD (1969) Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* 71:49–53
- Doucette LI (2008) Behavioural ecology and thermal physiology of the Australian Owllet-nightjar (*Aegotheles cristatus*). PhD dissertation, University of New England, Armidale
- Doucette LI (2010) Home range and territoriality of Australian owl-nightjars *Aegotheles cristatus* in diverse habitats. *J Ornithol* 151:673–685
- Doucette LI, Brigham RM, Pavey CR, Geiser F (2011) Roost type influences torpor use by Australian owl-nightjars. *Naturwissenschaften* 98:845–854
- Drake VA, Farrow RA (1985) A radar and aerial-trapping study of an early spring migration of moths (Lepidoptera) in inland New South Wales. *Aust J Ecol* 10:223–235
- Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274
- Geiser F, Brigham RM (2000) Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). *J Comp Physiol B* 170:153–162
- Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. *J Comp Physiol B* 163:133–137
- Geiser F, Drury RL (2003) Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *J Comp Physiol B* 173:55–60
- Geiser F, Kenagy GJ (1988) Duration of torpor bouts in relation to temperatures and energy metabolism in hibernating ground squirrels. *Physiol Zool* 61:442–449
- Gilfillan SL (2001) An ecological study of a population of *Pseudantechinus macdonnellensis* (Marsupialia: Dasyuridae) in central Australia. I. Invertebrate food supply, diet and reproductive strategy. *Wildl Res* 28:469–480
- Hainsworth FR, Collins BG, Wolf LL (1977) The function of torpor in hummingbirds. *Physiol Zool* 50:215–222
- Hohtola E, Hissa R, Pyörnilä A, Rintamäki H, Saarela S (1991) Nocturnal hypothermia in fasting Japanese quail: the effect of ambient temperature. *Physiol Behav* 49:563–567
- Holyoak DT (2001) *Nightjars and their allies: the Caprimulgiformes*. Oxford University Press, Oxford
- Jackson HD (2000) Prey size in relation to mouth size of nightjars in Zimbabwe. *Ostrich* 71:436–437
- Jetz W, Steffen J, Linsenmair KE (2003) Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* 103:627–639
- King JR (1974) Seasonal allocation of time and energy resources in birds. In: Paynter R (ed) *Avian energetics*. Nuttall Ornithological Club, Cambridge, pp 4–85
- Körtner G, Geiser F (1998) Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* 113:170–178
- Körtner G, Geiser F (2000a) The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. *Chronobiol Int* 17:103–128
- Körtner G, Geiser F (2000b) Weather patterns and daily torpor in free-ranging animals. In: Heldmaier G, Klingenspor M (eds) *Life in the cold: 11th international hibernation symposium*. Springer, Berlin, pp 103–110
- Körtner G, Brigham RM, Geiser F (2001) Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). *Physiol Biochem Zool* 74:789–797
- Lane JE, Brigham RM, Swanson DL (2004) Daily torpor in free-ranging whip-poor-wills (*Caprimulgus vociferus*). *Physiol Biochem Zool* 77:297–304
- Lasiewski RC, Dawson WR (1964) Physiological responses to temperature in the common nighthawk. *Condor* 66:477–490
- Lehner PN (1996) *Handbook of ethological methods*, 2nd edn. Cambridge University Press, Cambridge
- Ligon JD (1970) Still more responses of the poor-will to low temperatures. *Condor* 72:496–498
- Lowman MD (1982) Seasonal variation in insect abundance among three Australian rainforests, with particular reference to phytophagous types. *Aust J Ecol* 7:353–361
- Marshall JT (1955) Hibernation in captive goatsuckers. *Condor* 57:129–134
- McKechnie AE, Lovegrove BG (2002) Avian facultative hypothermic responses: a review. *Condor* 104:705–724
- McKechnie AE, Wolf BO (2004) The energetics of the rewarming phase of avian torpor. In: Barnes BM, Carey HV (eds) *Life in the cold: evolution, mechanisms, adaptation, and application*. Twelfth International Hibernation Symposium. Institute of Arctic Biology, University of Alaska, Fairbanks, pp 265–273
- McKechnie AE, Ashdown RAM, Christian MB, Brigham RM (2007) Torpor in an African caprimulgid, the freckled nightjar *Caprimulgus tristigma*. *J Avian Biol* 38:261–266
- Merola-Zwartjes M, Ligon JD (2000) Ecological energetics of the Puerto Rican Tody: heterothermy, torpor, and intra-island variation. *Ecology* 81:990–1003
- Peiponen VA (1965) On hypothermia and torpidity in the nightjar (*Caprimulgus europaeus* L.). *Ann Acad Sci Fenn* 87:1–15
- Prinzinger R, Göppel R, Lorenz A, Kulzer E (1981) Body temperature and metabolism in the red-backed mousebird (*Colius castanotus*) during fasting and torpor. *Comp Biochem Physiol* 69A:689–692
- Quinn GP, Keough MJ (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge
- Racey PA, Swift SM (1985) Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. 1. Foraging behaviour. *J Anim Ecol* 54:205–215
- Read DG (1987) Diets of sympatric *Planigale gilesi* and *P. tenuirostris* (Marsupialia: Dasyuridae): relationships of season and body size. *Aust Mammal* 10:11–21
- Reinertsen RE (1983) Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res* 1:269–284
- Reinertsen RE (1996) Physiological and ecological aspects of hypothermia. In: Carey C (ed) *Avian energetics and nutritional ecology*. Chapman & Hall, New York, pp 125–157

- Schleucher E (2004) Torpor in birds: taxonomy, energetics, and ecology. *Physiol Biochem Zool* 77:942–949
- Schmid J (2000) Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: energetic consequences and biological significance. *Oecologia* 123:175–183
- Siegel S, Castellan JJ (1988) Nonparametric statistics for the behavioral sciences, 2nd edn. McGraw-Hill, New York
- Song X, Geiser F (1997) Daily torpor and energy expenditure in *Sminthopsis macroura*: interactions between food and water availability and temperature. *Physiol Zool* 70:331–337
- Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 430–490
- Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. *J Comp Physiol B* 178:597–605
- Turbill C, Law BS, Geiser F (2003) Summer torpor in a free-ranging bat from subtropical Australia. *J Therm Biol* 28:223–226
- Welton NJ, Houston AI, Ekman J, McNamara JM (2002) A dynamic model of hypothermia as an adaptive response by small birds to winter conditions. *Acta Biotheor* 50:39–56
- Withers PC (1992) *Comparative animal physiology*. Saunders College, Fort Worth
- Woods CP, Brigham RM (2004) The avian enigma: “hibernation” by common poorwills (*Phalaenoptilus nuttallii*). In: Barnes BM, Carey HV (eds) *Life in the cold: evolution, mechanisms, adaptation, and application*. Twelfth International Hibernation Symposium. Institute of Arctic Biology, University of Alaska Fairbanks, USA, pp 129–138
- Woods CP, Brigham RM (2008) Common poorwill activity and calling behavior in relation to moonlight and predation. *Wilson J Ornithol* 120:505–512
- Zar JH (1998) *Biostatistical analysis*, 4th edn. Prentice-Hall, Upper Saddle River