

## Torpor in Free-Ranging Tawny Frogmouths (*Podargus strigoides*)

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### ABSTRACT

Several small caprimulgid birds (<80 g) are known to enter torpor, apparently to cope with a fluctuating supply of insect prey. Since the large Australian tawny frogmouth (*Podargus strigoides*; 381–556 g) is also insectivorous, we investigated its thermoregulatory behaviour and thermal biology to determine whether this species is also heterothermic. In an open woodland at ~1,000 m altitude, we equipped eight free-ranging birds with external temperature-sensitive radio transmitters attached to an elastic harness to measure skin temperature ( $T_{\text{skin}}$ ). Core body temperature ( $T_{\text{b}}$ ) was measured in three of these birds fitted with an additional intraperitoneal transmitter.  $T_{\text{skin}}$  was closely correlated with  $T_{\text{b}}$ , although  $T_{\text{skin}}$  was usually several degrees below  $T_{\text{b}}$ . During the three coldest months of the year (June–August), shallow torpor with  $T_{\text{b}}$  as low as 29.1°C occurred frequently, whereas during spring and summer, torpor was not recorded. Torpor occurred either during the night and/or during the first half of the day. Night torpor bouts were initiated after a short activity period around dusk and lasted on average for about 7 h. Torpid birds always aroused before sunrise to either commence a second short foraging period or to fly directly to a day roost tree. After birds roosted,  $T_{\text{b}}$  fell again around sunrise, and birds occasionally entered a second dawn torpor bout; however, in most cases,  $T_{\text{b}}$  increased rapidly not long after entry, most likely due to passive heating by the sun. We conclude that despite their large body size and energetically conservative hunting strategy, tawny frogmouths, like several related caprimulgid species, frequently enter shallow torpor when low  $T_{\text{a}}$  demands high energetic costs for normothermic thermoregulation and likely reduces insect availability.

### Introduction

Endothermic mammals and birds can remain active at low ambient temperatures ( $T_{\text{a}}$ ) because they are able to produce sufficient endogenous heat to compensate for heat loss. While the high production of heat can be used to maintain a constant high body temperature ( $T_{\text{b}}$ ), it is energetically costly. Especially at low  $T_{\text{a}}$ , when endothermy provides most functional benefits, thermoregulation is energetically most expensive, and these costs are often accentuated by reduced food availability. Insectivorous endotherms, especially aerial feeders such as bats, swifts, swallows, and nightjars, which rely on activity by their prey, are among those most strongly affected by temperature-dependent food availability (Racey and Swift 1985). Because the energetic cost for living and thermoregulation in endotherms increases with decreasing body size while the ability to store fat declines (Calder 1984), energy limitations are an inverse function of size and disadvantage small species.

Apparently because of these energetic limitations, some small birds, notably aerial feeders, have evolved the ability to use torpor, especially during periods of inclement weather (Dawson and Hudson 1970; Reinertsen 1983; Prinzinger and Siedle 1988). Torpor is characterised by a controlled reduction of  $T_{\text{b}}$  and metabolic rate for energy conservation (Dawson and Hudson 1970; Geiser and Ruf 1995) and is employed by several members of the order Caprimulgiformes (nightjars and relatives; Jaeger 1948, 1949; Marshall 1955; Bartholomew et al. 1957, 1962; Lasiewski and Dawson 1964; Peiponen 1965; Dawson and Fisher 1969; Dawson and Hudson 1970; Withers 1977; Reinertsen 1983; Brigham 1992; French 1993). Although the ability to undergo torpor seems to be common in this order, torpor in the laboratory generally occurs only after substantial mass loss. It has therefore been proposed that torpor in most caprimulgid birds is an emergency measure, which may have limited relevance under natural conditions (Lasiewski and Dawson 1964).

Recent field studies on migratory Northern Hemisphere caprimulgiforms support this assumption for some species (Firman et al. 1993; Hickey 1993), whereas others, such as free-ranging poorwills (*Phalaenoptilus nuttallii*) in summer and Australian owl-nightjars (*Aegotheles cristatus*) in winter, enter torpor regularly (Brigham 1992; Brigham et al. 2000). Seasonal torpor in caprimulgiforms, therefore, may be more common and widespread than the summer studies on migratory species or laboratory studies suggest and may even include some larger species.

The largest members of the order Caprimulgiformes are the frogmouths (Podargidae). The tawny frogmouth (*Podargus strigoides*), a sedentary species distributed over the entire Austra-

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lian continent (Schodde and Mason 1980), is most likely to experience prolonged food shortages in areas where low  $T_a$  reduces insect activity (Statham 1982; Racey and Swift 1985) because they rely mainly on active ground-dwelling arthropods, which are caught by pouncing from a perch (Serventy 1936; Coleman 1946; Rose and Eldridge 1997). Prewinter fat storage in frogmouths (McCulloch 1975) suggests that they are not able to balance their energy expenditure throughout winter even with an energetically conservative hunting strategy and a low metabolic rate (Lasiewski and Bartholomew 1966; McNab and Bonaccorso 1995; Bech and Nicol 1999). However, body fat stores can provide only a limited energy supply for a 500-g species, and thus it seems unlikely that they would be able to bridge energy bottlenecks over the entire winter without entering torpor. Nevertheless, the prediction that torpor may be used by frogmouths (Gould 1865; McCulloch 1975; Rose 1976) is not supported by captive studies (McNab and Bonaccorso 1995; Bech and Nicol 1999). The aim of our study was therefore to investigate whether and when in the year free-ranging tawny frogmouths would use torpor.

### Material and Methods

The study was conducted between April and December 1997 and between June and August 1999 in the Imbota Nature Reserve (formerly Eastwood State Forest; 30°35'S, 151°44'E; altitude ca. 1,000 m) about 10 km east of Armidale on the Northern Tablelands of New South Wales, Australia. Spotlight surveys were conducted regularly from a vehicle along established tracks. When a bird was spotted, a raptor trap (Cam 1985) was placed close to the bird. During autumn/winter 1997 and 1999, eight birds were trapped (body mass  $453 \pm 64$  g; individual details in Table 1). Seven of these birds were members of resident pairs. Bird 180 was light, showed extensive movements between the territories of at least three resident pairs, always roosted alone, and was probably a dispersing subadult.

All captured frogmouths were fitted with external, long-range, temperature-sensitive radio transmitters. The transmitters had

been calibrated against a mercury thermometer (traceable to a standard) to the nearest 0.1°C in a water bath and were attached using an elastic harness (Brigham 1992). Each transmitter (Sir-track; dimensions without antenna,  $2.5 \times 1.3 \times 0.7$  cm; mass, ca. 5 g; battery life, up to 1 yr) was placed underneath the feathers in contact with the skin of the upper back to obtain an estimate of  $T_{\text{skin}}$ . To estimate core  $T_b$  from  $T_{\text{skin}}$  measurements, one bird in 1997 and two birds in 1999 were fitted with both external and internal transmitters. Although the small loop antennae of the internal transmitters reduced the reception range considerably, we were able to collect sufficient data, including several torpor bouts for two individuals, to allow for a direct comparison of core  $T_b$  and  $T_{\text{skin}}$ . Following Hudson and Scott (1979), we defined torpor in frogmouths as a reduction of  $T_b$  by 5°C (i.e.,  $T_b < 34^\circ\text{C}$  from a nocturnal resting value of about 39°C). While this value may appear high, it seems an appropriate definition for this species for the following reasons. First, the  $T_b$  reduction usually occurred during the activity phase, unlike during "rest phase hypothermia" (Prinzinger et al. 1991; Reinertsen 1996). Second, the minimum of the average day  $T_b$  was 34°C. Third, the minimum  $T_b$  for both night and dawn torpor was below 30°C, defined as "torpor" by Reinertsen (1996), and although  $T_b$  did not fall below 30°C during all bouts, the similarity of  $T_b$  patterns suggests that all bouts represent the same physiological state.

After the position of the day roost area had been determined for a bird, a receiver/logger (Körtner and Geiser 1998) was deployed, preferably at an elevated location where signals from the roost area could be detected. One logger/bird was usually sufficient to receive signals from external transmitters, but for the highly mobile, solitary bird, two or three units were employed. Likewise, internal transmitters required several recording units.  $T_{\text{skin}}$  and  $T_b$  were recorded every 10 min, and data were downloaded at 1–2-wk intervals. The location of birds was checked regularly in the morning and sometimes during the night to ensure that they roosted within receiver/logger range. We noted when huddling or separate roosting by individuals of a pair occurred.

Table 1: Details of frogmouths used in the study

Bird Number	Sex	Body Mass (g)	Recording Period	
			External	Internal
180	Female, subadult	381	4/15/97–6/6/97	...
560 <sup>a</sup>	Female, adult	430	4/7/97–4/28/97	...
920	Male, adult	407	5/27/97–12/31/97	...
940	Male, adult	556	5/27/97–12/31/97	...
960	Male, adult	416	7/21/97–12/31/97	7/21/97–7/26/97
980	Male, adult	539	3/28/97–12/31/97	...
280	Male, adult	471	6/6/99–8/31/99	6/6/99–8/31/99
440	Male, adult	416	6/21/99–8/31/99	6/21/99–8/31/99

<sup>a</sup> Bird lost transmitter before winter, and no torpor was recorded for this individual.

In both years,  $T_a$  was measured hourly with data loggers placed at two locations in the woodland (in 1997, at roost sites for the most distant pairs; Körtner and Geiser 1998). The average  $T_a$  for the two locations was used in our analysis because the measurements were similar. Due to the predominantly dry and sunny weather conditions,  $T_a$  fluctuated by 10°–20°C on most days (Fig. 1). In 1997, the lowest  $T_a$  occurred between mid-June and August (Fig. 1).  $T_a$ 's in the winter of 1999 were similar, but July was considerably warmer than in 1997. Although frost was commonly observed in the surrounding farmland,  $T_a$  fell below 0°C only occasionally within the woodland.

Regressions were calculated using the method of least squares (Zar 1996). As a single linear regression did not appear to describe appropriately the relationship of  $T_b$  versus  $T_{skin}$  of two individuals and to allow for a better day-night comparison, values were fitted by two linear regressions by determining the smallest sum of the residual sum of squares (Yeager and Ultsch 1989). The average, minimum, and maximum  $T_a$  on nights when birds entered torpor were compared to those nights when none of the birds became torpid using a two-sample *t*-test (Zar 1996). The minimum  $T_b$  and torpor bout duration during the day and night were compared for individuals that entered at least three torpor bouts using a repeated-measures *t*-test (i.e., one-sample *t*-test). Data are presented as the mean  $\pm$  SD, and significance was assumed at a 5% level; *n* represents the number of data points, whereas *N* is the number of individual birds.

## Results

The  $T_b$ 's during the day measured using implanted transmitters (bird 280:  $37.0^\circ \pm 2.4^\circ\text{C}$ ; bird 440:  $36.7^\circ \pm 1.5^\circ\text{C}$ ; bird 960:  $36.7^\circ \pm 1.0^\circ\text{C}$ ) were on average lower (*t*-test,  $P < 0.005$ ; bird 280: *df* = 6,284; bird 440: *df* = 1,393; bird 960: *df* = 104) than at night (bird 280:  $37.5^\circ \pm 1.3^\circ\text{C}$ ; bird 440:  $37.0^\circ \pm 2.5^\circ\text{C}$ ; bird 960:  $37.1^\circ \pm 0.6^\circ\text{C}$ ). Although these means differed by only about 0.5°C, pronounced daily fluctuations of up to 10°C were recorded (Fig. 2). During both day and night,  $T_b$  fell occasionally below 30°C, with the lowest recorded readings being 29.1° and 29.7°C for night and day, respectively. At dusk, the main activity period of frogmouths,  $T_b$  remained relatively stable, and most  $T_b$ 's were between 38° and 40°C. Even during the middle of the night, when frogmouths were often inactive,  $T_b$  remained above 36°C during 59% of all nights (Fig. 3C).

Torpor in frogmouths commenced either during the night and ended before sunrise (night torpor) or began after the normal activity phase shortly before sunrise (dawn torpor). Night torpor and dawn torpor were always separated by an arousal, and two successive torpor bouts on a day were not unusual (Fig. 2).

### Night Torpor

After a more or less extended period of activity, birds often entered shallow torpor when  $T_a$  was below approximately 9°C.

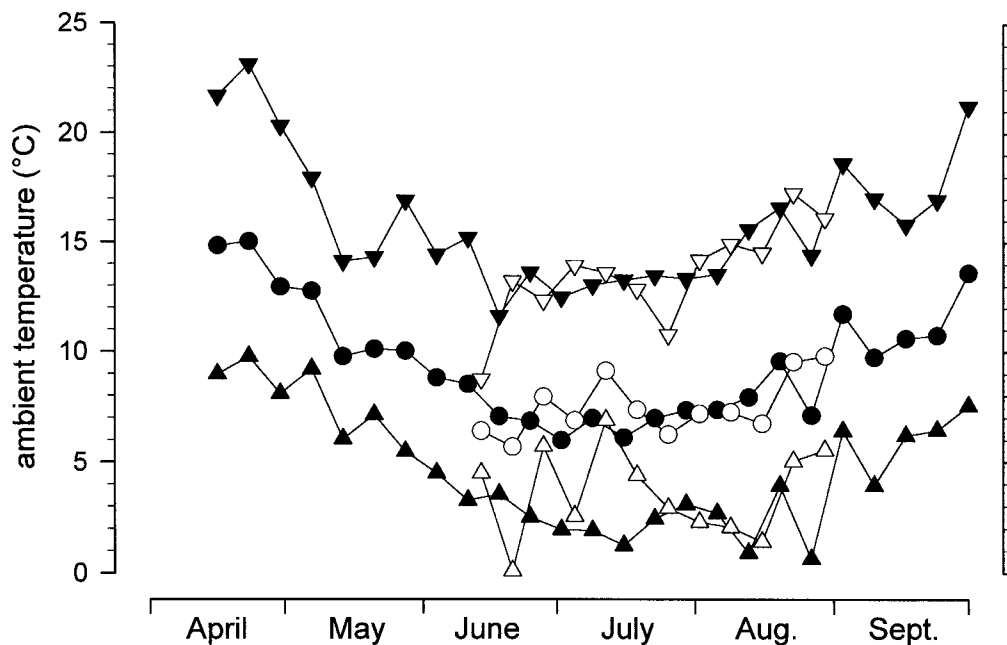


Figure 1. Weekly average of daily minimum, maximum, and average  $T_a$  at Imbota Nature Reserve between April and October 1997 (filled symbols) and between June and August 1999 (open symbols).

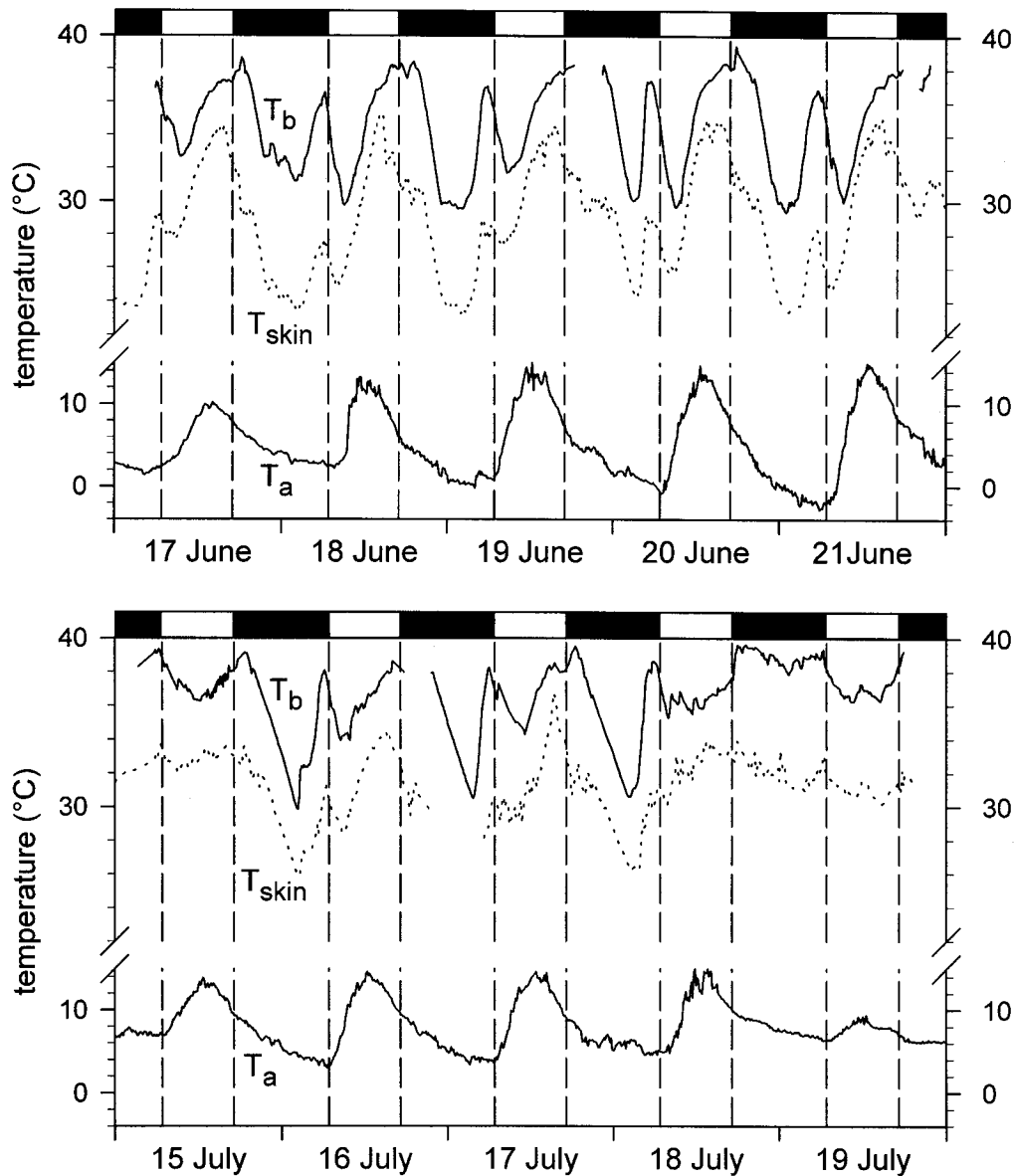


Figure 2. Record of  $T_b$ ,  $T_{skin}$ , and  $T_a$  for one tawny frogmouth (280) over 10 d in winter illustrating night and dawn torpor. Dark bars indicate scotophase.

The frequency of night torpor bouts between June and August was  $50\% \pm 7\%$  in 1997 ( $N = 5$  total, four birds per month), and for the two birds measured during the warmer 1999 winter, the frequency was 28% and 25%, respectively. During these 3 mo, the minimum  $T_a$  and the average  $T_a$  for the night were significantly lower on days when shallow torpor was used by one or more individuals than on days when no bird entered torpor ( $t$ -test; torpor: average night  $T_a = 4.4^\circ \pm 1.9^\circ\text{C}$ ; no tor-

por: average night  $T_a = 7.0^\circ \pm 1.6^\circ\text{C}$ ;  $P < 0.001$ ,  $df = 171$ ; 1997 and 1999 data pooled). In May and early September, torpor was rare (<10%), and torpor was not recorded in April and between late September and December, which is the breeding season of frogmouths at the study site (Körtner and Geiser 1999a).

The mean duration of all night torpor bouts was  $418 \pm 71$  min (range = 170 to 660 min,  $n = 204$ ,  $N = 7$ , mean of mean

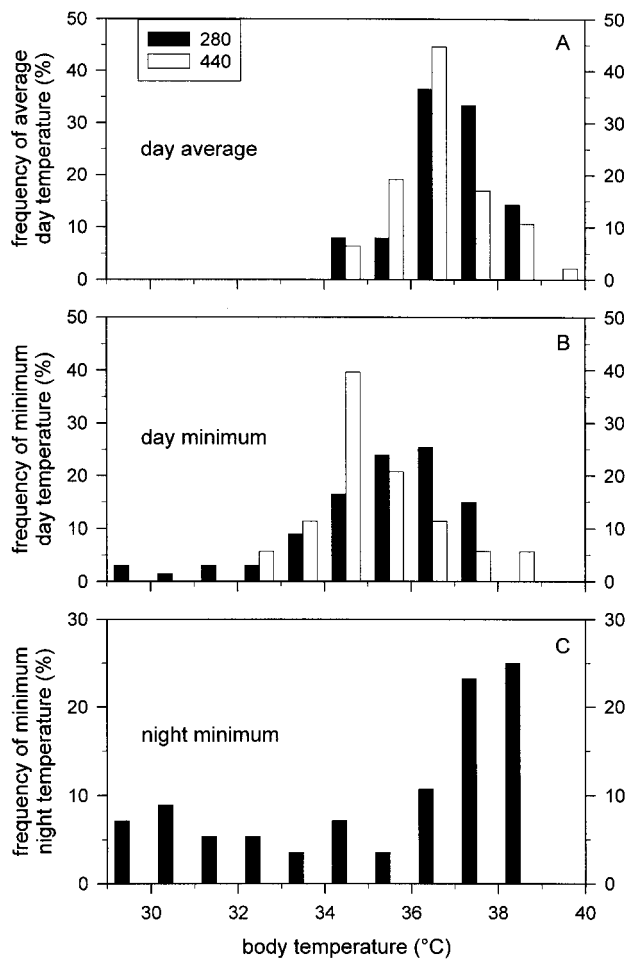


Figure 3. Frequency distribution of (A) the average day  $T_b$ , (B) the minimum day  $T_b$ , and (C) the minimum night  $T_b$  for two tawny frogmouths. Only days or nights with a complete data set were included in the analysis, which means that the upper range for the minimum night  $T_b$  is probably underestimated because the birds were more likely to leave the reception range on nights when they were active and maintained a high  $T_b$ . Not enough complete-night data sets were available for bird 440.

for each individual over the whole recording period). The lowest recorded minimum  $T_b$  during night torpor for the two birds in 1999 was 29.4° and 29.1°C (mean of all bouts: 31.1° ± 1.4°C,  $n = 24$ ,  $N = 2$ ; mean of the mean = 31.2°C).  $T_{skin}$  minima were generally several degrees lower than  $T_b$ , but  $T_b$  and  $T_{skin}$  minima during torpor were closely correlated ( $T_b = 0.53T_{skin} + 17.5$ ,  $r^2 = 60\%$ ,  $P < 0.001$ ). The mean of the lowest  $T_{skin}$  minima recorded during night torpor for each individual was 22.5° ± 1.3°C ( $N = 7$ ; calculated  $T_b = 29.4^\circ\text{C}$ ), and the average for all torpor bouts was 25.7° ± 1.8°C ( $n = 204$ ,  $N = 7$ ; calculated  $T_b = 31.1^\circ\text{C}$ ).

Bout duration was correlated with both minimum  $T_{skin}$  and

minimum  $T_b$  (duration [min] =  $-20.1T_{skin} + 967$ ,  $r^2 = 7.6\%$ ,  $P < 0.001$ ; duration [min] =  $-63.8T_b + 2,427$ ,  $r^2 = 54.5\%$ ,  $P < 0.001$ ). Night  $T_a$  (minimum and average) was significantly correlated with both torpor bout duration as well as  $T_{skin}$  minima. Although these correlations indicate that torpor is longer and deeper during colder nights, the low  $r^2$  values derived from the regressions suggest that other environmental and physiological variables were involved and that  $T_a$  by itself has limited predictive value.

#### Dawn Torpor

Dawn torpor was usually initiated after the birds had settled in their day roost before sunrise, which was often the coolest part of the day. Minimum daytime  $T_a$  was 3.4°C lower on days when dawn torpor was observed in at least one individual than on days when none of the birds was torpid ( $t$ -test: torpor  $T_a = 1.9^\circ \pm 2.3^\circ\text{C}$ ; no torpor:  $T_a = 5.3^\circ \pm 2.1^\circ\text{C}$ ;  $P < 0.001$ ,  $df = 140$ ; 1997 and 1999 pooled). Dawn torpor was used less often than night torpor. During 1997, only four individuals used dawn torpor between June and August, and three of them used it only infrequently (<6 bouts per individual; torpor frequency: 5% ± 7%,  $N = 3$ ). Likewise, in 1999, dawn torpor was less often observed than night torpor. Dawn torpor was as common as night torpor for only one individual in 1997 (torpor frequency June–August: 51% of 92 d). This bird, unlike the others studied, occupied a territory on a steep slope with a westerly aspect, and consequently, sun exposure occurred later in the day.

Dawn torpor bouts were also shorter on average than night torpor bouts (210 ± 71 min, range = 81 to 491 min,  $n = 100$ ,  $N = 7$ , mean of the mean for each individual; repeated-measures  $t$ -test,  $P < 0.01$ ,  $df = 5$ ). The lowest recorded  $T_b$ 's during dawn torpor for the two birds with internal transmitters were 29.7° and 32.4°C, respectively (mean for all bouts 32.5° ± 1.4°C,  $n = 19$ ,  $N = 2$ ; mean of the mean = 32.6°C). Again,  $T_b$  and  $T_{skin}$  were highly correlated ( $T_b = 0.78T_{skin} + 10.7$ ,  $r^2 = 75.8\%$ ,  $P < 0.001$ ). The mean of lowest recorded  $T_{skin}$  minima for each bird during dawn torpor bouts was 25.0° ± 2.0°C ( $N = 7$ ; calculated  $T_b = 30.2^\circ\text{C}$ ), and the mean for all torpor bouts was 26.7° ± 1.7°C ( $n = 100$ ,  $N = 7$ , calculated  $T_b = 31.6^\circ\text{C}$ ). Night torpor  $T_b$  was, on average, 0.8° ± 0.7°C lower than dawn torpor  $T_b$  (repeated-measures  $t$ -test,  $P < 0.05$ ,  $df = 5$ ).

Unlike at night, dawn torpor bout duration and  $T_b$  minimum were not correlated. Bout duration was also not correlated with any of the  $T_a$  parameters of the previous night nor with the minimum day  $T_a$  but was inversely related to maximum day  $T_a$ , although the low  $r^2$  (7%) again indicates limited predictive value. However, both the minimum  $T_b$  and  $T_{skin}$  during dawn torpor were correlated with the minimum day  $T_a$  (usually early morning;  $T_b = 0.29T_a(\text{minimum}) + 31.9$ ,  $r^2 = 22.3\%$ ,  $P < 0.05$ ;  $T_{skin} = 0.19T_a(\text{minimum}) + 26.3$ ,  $r^2 = 11\%$ ,  $P < 0.001$ ).

## Discussion

Our study shows that free-ranging tawny frogmouths regularly enter shallow torpor for several hours, with  $T_b$  falling below 30°C during cold winter nights or mornings. These observations substantially increase the size range for birds known to enter torpor and demonstrate that daily torpor is not restricted to species weighing <100 g. Considering how frequently torpor was employed by this 500-g species, it appears likely that the use of avian torpor for energy conservation is more common than is presently believed (Körtner et al. 2000) and is likely to play an important role in the survival of birds in the wild.

The terminology used for defining torpor differs widely among authors. We believe that the pronounced pattern of  $T_b$  fluctuations observed here is adequately described by the term “shallow torpor” rather than “rest phase hypothermia” for several reasons: (i) most of our torpor bouts were observed at night, the normal activity phase of nocturnal frogmouths; (ii) the drop of  $T_b$  by more than 5°C in frogmouths agrees with the definition of torpor for mammals (Hudson and Scott 1979), whereas during “rest phase hypothermia,” the reduction of  $T_b$  is usually less than 5°C (Reinertsen 1996); (iii) the minimum  $T_b$  of frogmouths is close to that predicted for an avian daily heterotherm of its body mass (Geiser and Ruf 1995); (iv) the frequency distribution for night  $T_b$  minima, which is distinctly left skewed (Fig. 3), suggests a lower threshold for normothermic  $T_b$  as high as 36°C; and (v) two published articles suggest that normothermic  $T_b$  of frogmouths is above 37°C (McNab and Bonaccorso 1995; Bech and Nicol 1999).

### $T_{skin}$ versus $T_b$

External transmitters measuring  $T_{skin}$  have been successfully employed to assess the use of torpor and to estimate core  $T_b$  in several species of small mammals and birds (Brigham 1992; Audet and Thomas 1996; Barclay et al. 1996; Körtner and Geiser 1998, 2000). In our study, the external transmitter arrangement maximised the reception range and allowed an almost continuous record of  $T_{skin}$ ; therefore, it was best suited to assess torpor frequency. The advantage of data collected from implanted transmitters is the precise measure of core  $T_b$ ; however, data were often discontinuous despite the use of several receiver/loggers. The large size of frogmouths allowed a comparison of the two transmitter types,  $T_b$  versus  $T_{skin}$ , on the same individual in the field, and, unlike in some small species (<50 g), which show  $T_b - T_{skin}$  differentials of <2°C (Brigham 1992; Barclay et al. 1996), frogmouths revealed a temperature gradient of several degrees. Solar radiation during the day occasionally reversed the thermal gradient, with  $T_{skin}$  exceeding  $T_b$ . This complicated the assessment of  $T_b$  via  $T_{skin}$  and appears to be the reason for the different relationship between  $T_b$  and  $T_{skin}$  during day and night (Fig. 4). Overall, our study suggests that, with current transmitter technology,  $T_{skin}$  measurements provide a better es-

timate of torpor frequency and timing because the superior transmitter range yields a more continuous data set, although the assessment of the exact  $T_b$  is, of course, less accurate.

### Thermoregulation and Torpor

Although avian diversity is more than twice that of mammals, and, on average, birds are smaller than mammals, the literature suggests that torpor is much more commonly used by mammals (Dawson and Hudson 1970; Reinertsen 1983; Geiser and Ruf 1995). Under laboratory conditions, substantial drops in  $T_b$  have been recorded only in small birds and, in some of these, only after severe starvation (Marshall 1955; Lasiewski and Dawson 1964; Peiponen 1965; Dawson and Fisher 1969). When studied in the field, however, some species will frequently undergo torpor, sometimes even under apparently favourable environmental conditions (Brigham 1992; Brigham et al. 2000; Geiser et al. 2000). In frogmouths, even normothermic thermoregulation differs between the laboratory and the field. In comparison with other Caprimulgiformes, which show pronounced daily fluctuations in  $T_b$  (Bartholomew et al. 1957; Lasiewski and Bartholomew 1966; Dawson and Fisher 1969; Lasiewski et al. 1970), captive frogmouths regulate  $T_b$  between 37° and 38°C even at low  $T_a$  (McNab and Bonaccorso 1995; Bech and Nicol 1999). In contrast, in free-ranging frogmouths, core  $T_b$  fell below 37°C ( $N = 2$ ) during 85%–90% of all days recorded, and  $T_{skin}$  readings for the remaining birds revealed a similar pattern. This discrepancy in thermoregulation and torpor between field and laboratory suggests that frogmouths, and probably birds in general, are more susceptible to captivity-induced stress than mammals. In particular, birds that can store substantial amounts of body fat, such as many Caprimulgiformes (Marshall 1955; McCulloch 1975), could resist entering torpor for prolonged periods. Thus, the scarcity of reports on torpor in captive birds may partly reflect their reluctance to enter torpor when stressed, possibly because they avoid entering a physiological state that reduces their alertness.

The reduction of  $T_b$  in torpid frogmouths is not as substantial as in smaller Caprimulgiformes. The minimum  $T_b$  reached in species entering daily torpor exclusively (nonhibernators) is a direct function of body mass (Geiser and Ruf 1995). Consequently, nightjars (70–90 g), with the exception of the hibernating poorwill, seem to attain  $T_b$  between 15° and 20°C (Marshall 1955; Lasiewski and Dawson 1964; Peiponen 1965), close to the minimum  $T_b$  predicted for a 70-g bird during daily torpor (Geiser and Ruf 1995). For 500-g frogmouths, this relationship predicts a  $T_b$  during torpor of 28.5°C, which is only slightly below the minimum value observed here (29.1°C).

Frogmouths entered torpor during both the day and night. Night torpor bouts were always terminated by arousal before dawn and were occasionally followed by one torpor bout during the daytime. In a similar fashion, starved European nightjars (*Caprimulgus europaeus*) undergo a successive series of

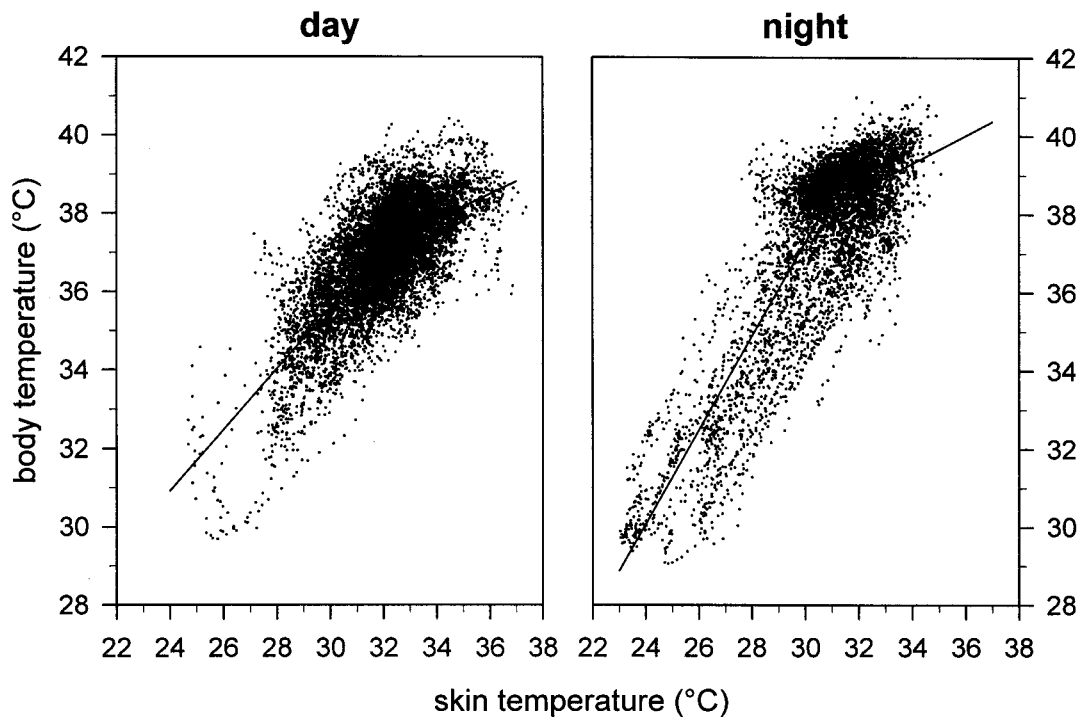


Figure 4. Core  $T_b$  as function of  $T_{skin}$  for two tawny frogmouths. Day and night data sets are shown separately and were fitted with two linear regressions each as described in "Material and Methods"; *day*: transition at  $T_{skin} = 29.9^\circ\text{C}$ ,  $T_b = 1.29 + 1.20T_{skin}$  (below),  $T_b = 27.11 + 0.36T_{skin}$  (above), and  $T_b = 9.06 + 0.93T_{skin}$  (all data); *night*: transition at  $T_{skin} = 31.9^\circ\text{C}$ ,  $T_b = 12.23 + 0.78T_{skin}$  (below),  $T_b = 26.79 + 0.33T_{skin}$  (above), and  $T_b = 18.36 + 0.58T_{skin}$  (all data).

torpor bouts, which are interrupted twice daily by arousals around sunrise and sunset. Therefore, the daily organization of torpor appears to reflect the normal bimodal activity patterns at dawn and dusk of nightjars and frogmouths (Peiponen 1965, 1966).

Night torpor in tawny frogmouths occurred at low  $T_a$ , when the activity of arthropods also declines (Statham 1982; Frey 1991). It appears that torpor is employed at night when energy costs for foraging are likely to exceed energy gained by food uptake. Although torpor at night will reduce energy expenditure, lack of feeding will result in an overall energy loss. Frogmouths, which frequently employ night torpor, therefore must rely on stored fat during winter and may be able to survive without eating for several days.

In contrast to entering torpor at night, torpor bouts during the day do not curtail foraging in nocturnal birds. It is therefore surprising that frogmouths used dawn torpor less frequently than night torpor. Since frogmouths roost on and actively select sun-exposed branches (Körtner and Geiser 1999b), dawn torpor was almost always terminated before midday, and it appears that the thermal environment of day roosts affects the timing and frequency of torpor during the day. Solar heating may limit

day torpor, and the only individual that used dawn torpor as frequently as night torpor occupied an area with delayed morning sun exposure. However, passive heating could reduce costs for arousal (Lovegrove et al. 1999), and basking may reduce daily energy expenditure, particularly at low  $T_a$  (Huertas and Díaz 2001).

When  $T_a$  exceeds thermoneutral conditions, the low metabolic rate of frogmouths and the ability to dissipate heat across their large, moist oral cavity at low energetic cost allows them to withstand midday sun exposure even under tropical conditions (Bartholomew et al. 1962; Lasiewski and Dawson 1964; Dawson and Fisher 1969; Lasiewski 1969; Lasiewski et al. 1970). This heat tolerance allows them to exploit solar heating during the morning to reduce energy expenditure without being adversely affected by heat when radiation levels are high.

Shallow torpor in frogmouths was restricted to winter, as in many heterothermic mammals and birds. It is therefore not surprising that most other Caprimulgiformes, in which torpor has been studied during their summer breeding season, were less likely to enter torpor. Thus, only more fieldwork at different seasons and on a wide variety of taxa is likely to reveal the extent and pattern of torpor use in birds.

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