Daily Torpor in a Free-ranging Goatsucker, the Common Poorwill (Phalaenoptilus nuttallii)

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Abstract
Numerous laboratory studies show that common poorwills (Caprimulgidae: Phalaenoptilus nuttallii) are capable of entering daily torpor when deprived of food. Using temperature-sensitive radio transmitters, I measured the skin temperature of free-ranging birds under natural conditions to test three hypotheses about the use of torpor by poorwills. I predicted that (1) poorwills would enter torpor only in “energy emergencies” (defined as birds with low body mass), (2) only the non-incubating or brooding member of a pair would use torpor during the breeding season, and (3) poorwills would be less likely to enter torpor on moonlit nights when longer periods of activity can be sustained. My results show that adult poorwills of both sexes enter torpor regularly in April, May, and September, but not during the breeding season. I found no evidence that torpor was used only in energy emergencies or that the lunar cycle influenced the use of torpor. Skin temperatures regularly dropped below 10°C and in one instance fell below 3°C. On one occasion an individual bird remained torpid for at least 36 h. I found limited evidence suggesting that the temperature at twilight, but not insect abundance, can be used to predict whether birds will remain active or enter torpor.

Introduction

The high metabolic rate of homeothermic animals has favored the evolution of a number of ways to minimize energy expenditure and cope with periods of food shortage. Torpor, which allows the reduction of metabolic rate and consequently body temperature ($T_b$), is one physiological means used by some homeotherms to “escape” conditions of extreme cold or food shortage. In birds and mammals, torpor is characterized by a periodic, facultative lowering of $T_b$ resulting in a hypometabolic state (Wang 1989). Depending

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on the species, environmental conditions, and ecological situation, $T_b$ may drop $4^\circ-35^\circ$C below normal, and torpor may last from hours to weeks (Wang 1989).

Torpor in birds and mammals is polyphyletic (see Dawson and Hudson [1970] and Wang [1989] for reviews) and represents an advanced form of thermoregulation rather than a reversion to primitive poikilothermy. However, because hypometabolism has been studied almost exclusively in mammals (Heller 1989), the use of torpor by birds is interesting from a comparative standpoint. Dawson and Hudson (1970) and Reinertsen (1983) reviewed the occurrence of facultative torpor in birds and listed eight orders in which the phenomenon has been found. Torpor in birds typically lasts less than 24 h and has been characterized as taking two forms. Nocturnal hypothermia (see, e.g., Reinertsen and Haithorn 1983) occurs when individuals show shallow depressions ($5^\circ-10^\circ$C) in $T_b$ and return to normal by dawn, whereas daily torpor typically involves depression of $T_b$ by more than $10^\circ$C. It is likely that these two physiological states represent a continuum and cannot be clearly differentiated, as my arbitrary temperature ranges suggest. Many hummingbirds (Trochilidae; Krüger, Prinzinger, and Schumann 1982) and goatsuckers (Caprimulgidae; Bartholomew, Howell, and Cade 1957) enter daily torpor under laboratory conditions. One species that might not fit this classification is the common poorwill (Caprimulgidae: Phalaenoptilus nuttallii), the only bird thought to be capable of entering long-term torpor or hibernation (Jaeger 1948, 1949; Brauner 1952).

Studies of daily torpor in hummingbirds (Lasiewski 1963; Lasiewski and Lasiewski 1967; Hainsworth, Collins, and Wolf 1977; Withers 1977; Krüger et al. 1982) and goatsuckers (Marshall 1955; Bartholomew et al. 1957; Howell and Bartholomew 1959; Bartholomew, Hudson, and Howell 1962; Peiponen 1966; Austin and Bradley 1969; Dawson and Fisher 1969; Ligon 1970; Withers 1977) are almost exclusively laboratory investigations. This is probably due to the small size of these birds and their inaccessibility under field conditions. In one of the few field studies, Calder and Booser (1973) used thermistors implanted in synthetic eggs and found that incubating female broad-tailed hummingbirds (Selasphorus platycercus) entered torpor on only two of 161 nights. On the two nights, the use of torpor was correlated with a reduced opportunity for feeding.

On the basis of laboratory studies, many authors claim that torpor in birds occurs only when the animal is energetically stressed (Calder and King 1974; Hainsworth et al. 1977; Hainsworth and Wolf 1978; Hudson 1978). In both hummingbirds and goatsuckers, torpor under laboratory conditions has been associated with a prior depletion of energy in the form of reduced body mass (Marshall 1955; Hainsworth et al. 1977; although see Jaeger 1948;
Ligon 1970). Recently however, Carpenter and Hixon (1988) found a wild, healthy, energetically unstressed rufous hummingbird (*Selasphorus rufus*) in torpor. This is counter to the prediction of the “energy emergency” hypothesis. There are no field data on the use of torpor by goatsuckers under natural conditions that allow for an evaluation of this hypothesis.

Heterothermic bats (e.g., vespertilionids and rhinolophids) are ecologically similar to goatsuckers in that they feed on flying insects captured during crepuscular or nocturnal activity periods. Both laboratory (reviewed in McNab [1982]) and field studies (Racey and Swift 1981; Audet and Fenton 1988) show that insectivorous bats use torpor in situations other than energy emergencies (defined by reduced body mass). However, pregnant and lactating bats, like nesting hummingbirds (Calder and Booser 1973), enter torpor only under extreme conditions. For bats, the explanation for this is that it delays parturition and inhibits lactation (Racey 1973; Racey and Swift 1981; McNab 1982; Audet and Fenton 1988).

The purpose of this study was to determine, with temperature-sensitive radio transmitters, when or if free-ranging poorwills enter torpor. If poorwills enter torpor only in energy emergencies, then torpor should occur rarely and only in birds with low body masses. If poorwills behave like insectivorous bats (see, e.g., Audet and Fenton 1988), then I predict that they will enter torpor regularly during periods of low nocturnal temperatures and low insect abundance but not, or only rarely, during the incubating or brooding period, since this may result in hatching delay or the death of embryos or chicks (Hafthorn 1988). If torpor occurs during the nesting period, I predict that it will only be used by the nonincubating or nonbrooding member of the pair. Finally, since some goatsuckers, including poorwills, forage more during moonlit periods of the night (Mills 1986; Brigham and Barclay, in press), torpor, if used, should occur less often on “light” nights when birds have more time available for foraging.

**Material and Methods**

*Study Site*

The study was conducted in September 1988 and from April to September in 1989 and 1990 in the Okanagan Valley of south-central British Columbia (49°18'N, 119°31'W), near the northern limit of the species' breeding range, where they do not overwinter (Cannings, Cannings, and Cannings 1987). Therefore, my observations represent characteristics of torpor and not hibernation. The southern Okanagan Valley comprises a series of lakes linked by the Okanagan River. On the side hills of the valley, where the activities
of *Phalaenoptilus nuttallii* are centered, the vegetation consists of open conifer forest dominated by *Pinus ponderosa* (Cannings et al. 1987). In 1988 and 1989, I captured individuals on the eastern side of the valley near Vaseaux Lake. In 1990, I trapped individuals on the western side, 8 km NW of the town of Oliver. The two study areas were separated by less than 10 km. I captured poorwills in mist nets set in foraging areas (usually across gravel roads) or by luring birds into nets using song playbacks. I distinguished males from females by the presence and length of white tips on the rectrices (Chapman 1925). Females had buff-colored tail tips about half the length of males’ tail tips (J. T. Marshall, personal communication). All individuals included in the analysis were at least 1 yr old.

**Telemetry**

I used temperature-sensitive radio transmitters (model PD-2T, Holohil Systems, Woodlawn, Ontario) to measure the temporal patterns of activity by poorwills and to ascertain when they entered torpor. Transmitters (average mass 2.4 g) were affixed to the birds with an elastic harness slipped over the wings (Brigham 1989). The effective range of signal reception varied from 1 to 4 km depending on terrain. I classified individuals as either moving or stationary at 5-min intervals using a Merlin 12 telemetry receiver (Custom Electronics, Urbana, Ill.) and a five-element Yagi antenna. During each measurement, a minimum of 20 pulses were monitored and any change in either the direction or strength of the signal was defined as a movement.

Transmitters were affixed so that the harness kept the temperature sensor in contact with the bird’s skin on the back between the wings (interscapular region). Thus, I measured skin temperature (*Tsk*) in a manner analogous to that of Audet and Fenton (1988). Transmitters were calibrated to measure temperature from 0° to 40°C (±0.5°C). I determined *Tsk* by averaging three timings of the interval required for 10 transmitter pulses and then using the calibration curves prepared for each transmitter by the manufacturer. This was done every 20 min during nightly activity periods and opportunistically during the daytime. Because of the transient fluctuations in avian *Tb*’s (Reinertsen and Hafthorn 1983) and the fact that the *Tb* of active poorwills varies between 35° and 44°C under laboratory conditions (Bartholomew et al. 1962), I followed Hudson (1978) and operationally defined poorwills as having entered torpor when *Tsk* fell below 30°C. In this study, birds with skin temperatures below 30°C were never found or measured to be active.

Thirteen adult birds (six females, seven males) were captured and outfitted with transmitters. I monitored individual birds carrying transmitters for 165 bird-nights. On 108 of these nights, I monitored movements and the *Tsk*
of the individual all night (from approximately sunset until activity ceased at dawn).

Environmental and Lunar Conditions

I measured the minimum nightly temperature ($T_{\text{min}} \pm 0.5^\circ$C), using a Taylor maximum-minimum thermometer mounted 1 m above the ground. In both years the thermometer was placed within 1 km of the day roost or nest locations of birds carrying transmitters. There was a significant correlation in both 1989 and 1990 ($r^2 = 0.73$ and $P < 0.05$ in both years) between $T_{\text{min}}$ and the minimum temperature measured at the Penticton airport, located 15 km north of the study area. As a relative indication of twilight temperatures ($T_{\text{tw}}$) I used measurements from Penticton. At the same time that I measured $T_{\text{sk}}$, I used a Taylor laboratory thermometer at the tracking position to measure ambient temperature ($T_a$) to the nearest 2°C.

Nightly lunar conditions were grouped into five categories based on the percentage of the moon face illuminated (%MFI) at midnight (0%, 1%–25%, 26%–50%, 51%–75%, 76%–100%; Mills 1986). Values of %MFI were taken from tables published in the Astronomical Almanac (e.g., Anawalt and Boksenberg 1987). The times of sunset, nautical twilight, and sunrise were calculated for the study site by the Dominion Astrophysical Observatory, Victoria, British Columbia. I used the end of nautical twilight (when the sun is 12° below the horizon) as the time delineating dusk or dawn from true night (Mills 1986). Cloud cover was not taken into account, since it was rarely cloudy in the study area and because Mills showed it did not influence activity by whippoorwills ($Caprimulgus$ $vociferus$).

In 1989, I assessed the influence of insect abundance on the use of torpor by poorwills. Four sticky traps (coated with Tangletrap; Southwood 1978; Kunz 1988) were suspended approximately 1, 2, 3, and 5 m above a gravel road where poorwills commonly foraged. On nights when birds were tracked, the traps were hung at sunset and collected at sunrise. I recorded the total number of insects captured, identified each insect to order, and characterized them as large (>4 mm) or small (≤4 mm) in body length.

Results

On 16 occasions I measured $T_{\text{sk}}$ while simultaneously measuring cloacal temperature ($T_c$), using a quick-registering thermometer inserted 1 cm into the cloaca. There was a highly significant relationship between $T_{\text{sk}}$ and $T_c$ ($T_c = 1.58 + 0.9598 T_{\text{sk}}$; $r^2 = 0.99$, $P < 0.01$; fig. 1). This illustrates the
reliability of using $T_{sk}$ to assess $T_b$. Generally, $T_c$ was between 1° and 2°C higher than $T_{sk}$ (intercept = 1.58).

Individual poorwills entered torpor on 29 of the 165 bird-nights. Ten of the 13 birds that carried transmitters (six males, four females) used torpor. Twelve of the 13 birds carrying transmitters participated in at least one nesting attempt. One male apparently did not acquire a mate and did not nest. The incidence of torpor was not evenly distributed throughout the summer (table 1). No individual male or female used torpor while incubating eggs or brooding chicks or during periods not spent on the nest. The latest date in the spring that an individual entered torpor was June 3, 1990, and the earliest date in the fall was September 1, 1989. The body mass of nine males and six females captured during April, May, and September, the period when torpor was used, varied between 36.9 and 54.5 g, with males weighing 44.7 and females 48.3 g, on average.

Table 1

Distribution of torpor bouts during the summers of 1989 and 1990

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<th>April–May</th>
<th>June</th>
<th>July–August</th>
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<td>55</td>
<td>44</td>
<td>58</td>
<td>7</td>
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<td>Torpor</td>
<td>24</td>
<td>2</td>
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Usually (28 of 29 torpor bouts), individuals were active at dusk and entered torpor at the end of nautical twilight (fig. 2). This suggests that the birds use cues available during the dusk foraging period to determine whether or not to enter torpor. With one exception, torpor bouts lasted less than 12 h. On May 22–23, 1990, a male bird remained torpid for at least 36 h and did not forage during the dusk period of May 23.

The use of torpor on a given night varied among individuals. On five of the nine nights when I monitored the $T_b$ of more than one bird simultaneously (two birds on eight nights and three birds on one night) one individual remained homeothermic while one entered torpor. On the night when three birds were tracked, two remained homeothermic and one entered torpor.

The lowest $T_{sk}$ I recorded was 2.8°C for a male bird at 0650 hours on May 13, 1989, when $T_{min}$ reached −1°C. From the regression equation this corresponds to a predicted $T_c$ of 4.3°C. Not surprisingly, I never recorded minimum predicted $T_c$ below $T_{min}$ (fig. 3); however, there was no significant correlation between $T_{min}$ and predicted $T_c$ ($r^2 = 0.38$, $n = 16$, $P > 0.10$). On nine occasions I measured the cooling rates of poorwills entering torpor. The values ranged from a minimum of 4.2°C per hour to a maximum of 13.2°C per hour.

**Fig. 2.** Mean $T_{sk}$ (°C) for three male poorwills during the period from April 30–May 20, 1989. Abscissa values show the time of the night. The $T_{sk}$ was measured for at least one bird all night on 15 dates during this period, with a total sample of 20 bird-nights (11 active and nine torpid). Error bars represent ±1 SE. The arrow indicates the end of nautical twilight.
In an attempt to identify the cues birds might use in determining whether or not to enter torpor, I compared the distributions of $T_{\text{min}}$, $T_{\text{twi}}$, total insect abundance, and the abundance of large insects for nights when birds did and did not enter torpor using two-sample Kolmogorov-Smirnov tests (figs. 4, 5). These distributions represent 29 bird-nights when torpor was used and 40 nights when it was not for the same 10 individual birds (six males and four females). For those nights when some individuals entered torpor and some did not, I included data for the relevant individuals in both distributions. As poorwills never became torpid during the nesting or brooding period (between June 4 and August 31), this period was not included in the analysis.

There were no significant differences between the torpid and nontorpid distributions with respect to the $T_{\text{min}}$, total insect, or large insect variables (Kolmogorov-Smirnov $D$'s of 0.20, 0.10, and 0.20, respectively; $P > 0.05$ in all cases). There was, however, a significant difference in the distributions of $T_{\text{twi}}$ measured at the Penticton airport for nights when birds did and nights when they did not enter torpor ($D = 0.43$; $P < 0.01$). The nonoverlapping portion of the distributions suggests that, when $T_{\text{twi}}$ at the airport was below 8°C, poorwills entered torpor, while, above 12°C, birds generally remained homeothermic.

Homeothermic poorwills are more active on nights with moonlight than on “dark” nights (Brigham and Barclay, in press). Therefore, I compared the distribution of %MFI for just the nights when birds entered torpor with
Fig. 4. a, Distribution of $T_{\text{min}}$ ($^\circ$C) for nights when birds did (n = 29) and nights when they did not (n = 40) enter torpor. Data for June 4–August 31 are not included, since this was a period when birds did not enter torpor. b, Distribution of $T_{\text{w}}$ ($^\circ$C) for nights when birds did (n = 29) and nights when they did not (n = 40) enter torpor. A Kolmogorov-Smirnov test shows that the distributions are significantly different (see text).
Fig. 5. a, Distribution of the total number of insects sampled by sticky traps on nights when birds did (n = 12) and nights when they did not (n = 17) enter torpor. Data for June 4–August 31 are not included, since this was a period when birds did not enter torpor. b, Distribution of the number of large insects sampled by sticky traps on nights when birds did (n = 12) and nights when they did not (n = 17) enter torpor.
the distribution of %MFI on all nights that I tracked on (excluding the period from June 4 to August 31, when torpor was never recorded). I found no significant relationship between the lunar condition and the use of torpor ($\chi^2 = 0.66, P > 0.10$; table 2).

### Discussion

Adult free-ranging poorwills of both sexes enter torpor regularly except during the breeding season. Body temperature of torpid birds regularly dropped below 10°C, and in one case a bird remained torpid for at least 36 h. I found limited evidence that $T_{rew}$, but not the abundance of insects, can be used to predict whether poorwills will remain active or enter torpor on any given night.

On 97% of the nights when individuals ultimately entered torpor, foraging activity occurred at dusk. Foraging occurred at dusk on every night when birds did not enter torpor. Activity levels at dusk were lower for individuals that ultimately became torpid, but the birds appeared to compensate for this lower activity by initiating foraging activity significantly earlier (R. M. Brigham, unpublished data). This difference in behavior may be a result of poorer foraging conditions on those nights when torpor is subsequently used. Activity at dusk and the almost complete cessation of activity at the beginning of true night by birds using torpor suggests that environmental conditions near the end of the dusk foraging bout influence the likelihood of entering torpor.

Temperature and insect abundance are the two most obvious potential cues birds might use to “decide” whether to enter torpor. However, my measures of prey abundance, especially of large insects, which make up the vast majority of the diet (R. D. Csada, unpublished data) and therefore

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<td>4</td>
<td>4</td>
<td>8</td>
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<td>Torpor . . . . . .</td>
<td>9</td>
<td>2</td>
<td>3</td>
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should be related to the rate of energy intake and $T_{\text{min}}$, could not be used to reliably predict the nights when birds entered torpor. Although there was a significant difference between the distributions of $T_{\text{min}}$ for nights when poorwills did and nights when they did not enter torpor, there was no obvious threshold temperature that would allow the prediction of whether an individual would enter torpor on any given night. This is not surprising, given that moths, which are commonly consumed by poorwills (Bent 1940; R. D. Csada, unpublished data), emerge at different times of the year (see, e.g., Yack 1988) and are influenced by $T_a$ differently (Heinrich and Mommsen 1985). Similarly, there is no precise threshold temperature that can be used to predict activity or the entry into torpor by insectivorous bats (Audet and Fenton 1988). Variation in the use of torpor between individuals is also important, illustrated by the fact that, on the same night, some individuals used torpor whereas others did not. Unfortunately, my small sample size of nights when torpor was used precludes rigorous analysis for the effects of gender, time of year, and foraging success on the previous night on the use of torpor by individual birds. However, it is worth noting that Audet and Fenton (1988) found variation between individual bats in the use of torpor on the same night, which they ascribed to differences in reproductive condition.

Poorwills did not enter torpor in energy emergencies only, as some laboratory studies suggested they would (e.g., Marshall 1955). Except during the nesting period, all tagged individuals ($n = 10$), with a range of body masses, used torpor at one time or another. Thus, the data for poorwills support the conclusions of Carpenter and Hixon (1988), who rejected the hypothesis that under natural conditions torpor is used by hummingbirds only in energy emergencies.

To my knowledge, a $T_{\text{sk}}$ of 2.8°C, which corresponds to a $T_c$ of 4.3°C, is the lowest naturally recorded temperature for any species of bird. Withers (1977) found that captive poorwills could not spontaneously arouse themselves from torpor when $T_b$ was below 5°C. My field data suggest that, under natural conditions, $T_b$ can fall below 5°C and individuals can still spontaneously rewarm. This inconsistency in results could be due to the difference in body mass between individuals in Wither’s study (35 g) and the free-living birds in my study (46 g on average). Heavier birds should have larger energy reserves and may be able to generate the heat required to rewarm from low temperatures. Therefore, these birds should be at less risk when lowering $T_b$ below 5°C. Another possible explanation is that Wither’s birds were captured in southern California and thus could have been less cold tolerant than birds from the Okanagan.
My measurements of cooling rates for poorwills entering torpor are similar to those measurements made in the laboratory. Cooling rates measured under laboratory conditions range from 1.8°C to 17.1°C per hour (Howell and Bartholomew 1959; Lasiewski and Lasiewski 1967; Austin and Bradley 1969; Ligon 1970) and are highly dependent on $T_a$. This suggests that the mechanism by which captive birds enter torpor is similar to the process used under natural conditions.

I found no evidence to support the hypothesis that poorwills use torpor less often on nights with moonlight than dark nights. The use of torpor was not related to the relative illumination provided by the moon, even though this significantly influences the foraging activity of these birds (Brauner 1952; Brigham and Barclay, in press) and other goatsuckers (Wynne-Edwards 1930; Mills 1986). It appears that lunar condition has no effect on the use of torpor by poorwills.

Although the southern Okanagan Valley of British Columbia is close to the limit of the northern range of the poorwill, the climate is moderate for its latitude (Cannings et al. 1987). Still, I expected that individual birds not attending eggs or chicks would enter torpor to conserve energy on nights with low $T_a$ and low insect abundance. Tracking data confirm that both male and female members of the pair participate in incubation and brooding (Aldrich 1935; Orr 1948). There was no obvious gender-related pattern in the way nesting activity was shared. In some pairs, the duties were unequally divided (R. M. Brigham, unpublished data). I predict that the probability of finding torpid birds during the nesting period will increase in areas with more continental climates than the Okanagan. However, if this is not the case, it suggests that the regular occurrence of conditions requiring the use of torpor during the nesting cycle may be an ultimate constraint determining the northern extent of the breeding range of this species.

In conclusion, this paper is the first to provide field data about the use of torpor by the poorwill, a bird whose physiological capabilities have long attracted interest. The study demonstrates the critical need for field data to confirm or reject the conclusions from laboratory studies of thermoregulation (e.g., Carpenter and Hixon 1988). In the case of poorwills, the large body of laboratory data does not completely account for the manner in which poorwills use torpor under natural conditions. The apparently unique attributes of poorwills studied under laboratory conditions prompted Heller (1989) to suggest that conclusions regarding the mechanisms of avian torpor should consider the poorwill as a special case. Whether torpor in these birds really does represent a special case among birds or, for that matter, vertebrates should be addressed by comparing *Phalaenoptilus nuttalii* with other caprimulgids and insectivorous bats. The depth and duration of bouts of
torpor by poorwills appears to be similar to those used by bats (Audet and Fenton 1988), an ecologically similar group of animals. It remains to be determined whether the apparent hibernation by poorwills also resembles that of bats. Heller (1989) and Wang (1989) both conclude that there is strong evidence for physiological homology between all forms of avian and mammalian torpor. Only with further work in the field will it be determined whether this conclusion holds true.

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**Literature Cited**


