

Free-ranging common nighthawks use torpor

Quinn E. Fletcher^{a,*}, Ryan J. Fisher^b, Craig K.R. Willis^c, R. Mark Brigham^c

^aDepartment of Life Sciences, University of Toronto at Scarborough, 1265 Military Trail, Scarborough, ON, Canada M1C 1A4

^bDepartment of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK, Canada S7N 5E2

^cDepartment of Biology, University of Regina, Regina, SK, Canada S4S 0A2

Received 17 July 2003; accepted 21 November 2003

Abstract

Bouts of torpor are characterized by substantial reductions in body temperature and metabolic rate. Many birds in the order Caprimulgiformes use torpor; however, there is conflicting evidence whether or not Common Nighthawks (*Chordeiles minor*) have this ability. The purpose of our study was to examine whether free-ranging nighthawks enter torpor. Three out of eight birds that were monitored entered torpor on a total of four occasions. Our results suggest that torpor is not used as commonly as it is in other species of Caprimulgids providing incentive for further research to explain the ecological determinants of torpor use in Caprimulgids.

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Keywords: *Chordeiles minor*; Caprimulgidae; Caprimulgiformes; Aves; Temperature telemetry; Heterothermy; Thermoregulation; Energetics; Torpor

1. Introduction

Endothermy is associated with high energetic costs during cold weather, particularly in small mammals and birds with large surface area: volume ratios (Song et al., 1995). Some birds allow their body temperature (T_b) to fall below normothermic levels during facultative hypothermic responses; in a hypothermic state their metabolic rate decreases and substantial energetic savings accrue (Prinzinger et al., 1991). Birds may use ambient heat to arouse from facultative hypothermia (Geiser and Drury, 2003) but they also have the ability to spontaneously increase T_b using metabolically generated heat (Hudson, 1978). Facultative hypothermia is often induced by energetically stressful conditions including cold ambient temperatures (T_a) and/or reduced food availability (Brigham et al., 2000).

Two types of daily facultative hypothermic responses have been described for birds. Torpor is defined as a

state of reduced responsiveness to external stimuli associated with body temperatures below normothermia (Geiser and Ruf, 1995; McKechnie and Lovegrove, 2002). Rest-phase hypothermia is a second category that is characterized by normal responsiveness to external stimuli and shallower reductions in T_b below normothermia (McKechnie and Lovegrove, 2002). Distinguishing between rest-phase hypothermia and torpor in free-ranging animals is usually impossible because it is difficult to obtain behavioural observations (but see Pierce and Vogt, 1993). Therefore, we evaluated the ability of birds to facultatively reduce their T_b and use the term torpor to define this state.

The use of torpor is common in the avian Order Caprimulgiformes. Torpor occurs in Common Poorwills (*Phalaenoptilus nuttallii*, Brigham et al., in press), Whip-poor-wills (*Caprimulgus vociferus*, Lane et al., in press), European Nightjars (*Caprimulgus europaeus*, Peiponen and Bosley, 1964), Australian Owlet-nightjars (*Aegotheles cristatus*, Brigham et al., 2000), and Tawny Frogmouths (*Podargus strigoides*, Körtner et al., 2000, 2001). The Common Nighthawk (*Chordeiles minor*) is a member of the Caprimulgiformes for which there is

*Corresponding author. Tel.: +1-4162877442; fax: +1-4162877642.

E-mail address: fletcher@uts.utoronto.ca (Q.E. Fletcher).

conflicting evidence about torpor use. Free-ranging nighthawks in the Okanagan Valley of British Columbia did not use torpor (mean minimum $T_{\text{skin}} = 34.5 \pm 0.5^\circ\text{C}$ [SE], 39 bird-nights) even though local environmental conditions were unusually harsh (above average precipitation) during the study period (Firman et al., 1993). In the laboratory, three of four nighthawks died when forced into torpor by food deprivation with a 28–34% drop in body mass (Lasiewski and Dawson, 1964). Even though one nighthawk entered and aroused from torpor in this study (its T_b fell to 18°C at a T_a of 16°C), the authors suggested that torpor would not be employed in the wild because only one individual survived. Conversely, an energetic model that attempted to predict the foraging time of nighthawks suggested that these birds may use torpor to balance their energy budget (Aldridge and Brigham, 1991). In addition, Brigham et al. (1995) made anecdotal observations of two nighthawks that were cold to the touch; however, these were not confirmed bouts of torpor because the fate of these birds was undetermined.

In light of the conflicting evidence, our objective was to determine if Common Nighthawks enter torpor under relatively harsh natural conditions. We predicted that nighthawks would enter bouts of torpor on cold mornings and nights because their crepuscular foraging bouts would be less successful, and their thermoregulatory costs would be higher, relative to warm mornings and evenings (Körtner and Geiser, 2000).

2. Materials and methods

2.1. Study area

This study was conducted in the West Block of Cypress Hills Provincial Park, Saskatchewan ($49^\circ 34'\text{N}$ and $109^\circ 53'\text{W}$) after the nesting season during the summers of 2000 and 2001. The local vegetation of the Cypress Hills consists of rolling hills of short grass fescue prairie, intermixed with stands of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera*). This area is also characterized by colder temperatures and more precipitation (Csada and Brigham, 1994) than the Okanagan Valley where free-ranging nighthawks were not found to use torpor (Firman et al., 1993). Therefore, we predicted that nighthawks would use torpor at this site.

2.2. Temperature telemetry

All procedures were approved by University of Regina President's Committee on Animal Care (Protocol #97–02). Nighthawks were captured in mist nets after being attracted using playback calls (Csada and

Brigham, 1994) or with a hoop net after they were spotlighted roosting on gravel roads at night (Poulin et al., 1998). Each captured bird was weighed to the nearest 0.1 g using an electronic scale and sexed using distinctive throat and tail plumage patterns (Poulin et al., 1996).

Backpack-style temperature-sensitive radio transmitters (model PD-2T, transmitter mass: 3.9 g; 5% of average body mass; Holohil Systems Ltd, Carp, Ont., Canada) were affixed using elastic harnesses so that the side with the temperature sensor was in contact with the skin in the interscapular region (Brigham, 1992; Firman et al., 1993). Transmitters were calibrated by the manufacturer to measure temperatures between 0 and $40 \pm 0.5^\circ\text{C}$. We observed radio-tagged nighthawks while roosting and in flight and could detect no change in their behaviour compared with non-tagged nighthawks. One bird was determined to have a loose transmitter because we recorded low T_{skin} values just prior to a foraging bout when we knew the bird was normothermic. We omitted the data for this individual but are confident that the other transmitters remained firmly attached because the effect of a loose transmitter was obvious.

We used a hand-held telemetry receiver (R-1000 Communication Specialists, Orange, CA, USA) and five-element Yagi antennae to track nighthawks. T_{skin} data were primarily recorded using a data-logging scanning receiver (SRX 400, Lotek Engineering, Aurora, Ont., Canada) that recorded T_{skin} at 7.5 min intervals. However, in the 2001 field season we determined T_{skin} using a stopwatch to record the interval required for a transmitter to emit 10 pulses. We then compared the average duration of three 10-pulse intervals to calibration curves for each transmitter provided by the manufacturer. Our sampling effort was concentrated during the morning (sunrise to 11:00 CST) and at night (sunset to sunrise), when other caprimulgids typically use torpor (Brigham, 1992; Brigham et al., 2000).

We recorded T_a ($\pm 0.5^\circ\text{C}$) every 15 min at a location central to the day and night roosts of nighthawks (except on 18 August 2000 when temperature data were collected every 30 min) using a temperature data-logger (iButton, Dallas Semiconductor, Dallas, TX, USA) suspended 1.5 m above the ground from a tree branch. Overhanging foliage shaded the data-logger, and its reflective metal casing prevented excess heating due to solar radiation.

Previous studies of free-ranging birds suggest that T_a affects T_{skin} because the transmitter is fastened externally (Brigham et al., 2000). We excluded any data collected on rainy nights because rain has a cooling effect on transmitters causing T_{skin} readings to be greatly underestimated (J.E. Lane pers. comm.). Flight may also reduce recorded T_{skin} because of convective cooling of

transmitters and disrupted contact between the temperature sensor and the skin. These measurements were easily identified based on rapid changes in the intensity of transmitter signals and were excluded.

Eight different definitions have been used to differentiate torpor from normothermia in thirteen studies of free-ranging animals, based on behaviour or an arbitrary T_b (Barclay et al., 2001). Torpor is difficult to define in free-ranging animals because obtaining field measurements of oxygen consumption, a much more reliable measure of metabolic rate and therefore, torpor, is impractical (but see Schmid, 1996). Thus, at present for free-ranging animals it is not possible to pinpoint a threshold T_b between torpor and normothermia based on a direct measurement of energy expenditure.

Internally implanted transmitters and data-loggers can provide a direct measurement of T_b that correlates well with metabolic rate. We attempted to surgically implant one nighthawk with a temperature data-logger (iButton: 17 mm diameter \times 6 mm height) to obtain a continuous record of T_b but this proved impractical for two reasons. First, after foraging, the bird's crop was fully engorged so there was insufficient space in the peritoneal cavity to implant the data-logger. This is likely to be a consistent problem in this species because nighthawks are most easily captured during and immediately following their dusk foraging bouts. Second, recapturing nighthawks is very difficult, so the probability of recovering implanted data-loggers and retrieving data is remote. Even if we had been able to implant transmitters, the limited pulse detection range of implanted tags (<50 m) was too short to allow us to record transmitter signals without disturbing birds at their exposed roost-sites.

T_{skin} readings have been used effectively in other studies of torpor in free-ranging birds and mammals (Brigham, 1992; Csada and Brigham, 1994; Brigham et al., 2000; Körtner et al., 2000, 2001; Turbill et al., 2003). Most relevant to our study, Brigham et al. (2000) validated the use of external transmitters for Australian Owllet-Nighthawks (Caprimulgiformes: *Aeogothales cristatus*, ~50 g) by simultaneously measuring T_{skin} with backpack-style transmitters and T_b using surgically implanted transmitters. Although T_a did have an effect on T_{skin} (average $T_b - T_{skin} = 3.0 \pm 0.8^\circ\text{C}$), T_b and T_{skin} were significantly related ($r^2 = 0.85$, $P < 0.01$, $n = 11,014$ observations), therefore T_{skin} is a reliable indicator of T_b (Brigham et al., 2000).

In the majority of studies on Caprimulgids, torpor has been arbitrarily defined as a drop in T_{skin} below 30°C (Brigham, 1992; Firman et al., 1993; Brigham et al., 2000). However, Barclay et al. (2001) suggest that if external transmitters that measure T_{skin} have to be used, torpor should be defined as a drop with respect to the "active" (T_{act}) or normothermic temperature of each individual. The primary reason for defining torpor in

this manner is that it accounts for natural variability in normothermic T_b , as well as inter-individual differences in transmitter attachment and plumage density (Kurta, 1986; Lovegrove and Raman, 1998; Barclay et al., 2001). Following the suggestion of Barclay et al. (2001), we defined a normothermic active skin temperature (T_{act}) for each tagged bird, as the lowest T_{skin} recorded within 15 min of departure for the dusk foraging bout over all the days it carried a transmitter. The average T_b of nighthawks is 37°C ($34\text{--}40^\circ\text{C}$ over T_a s ranging from 2°C to 35°C ; Lasiewski and Dawson, 1964) and T_{skin} underestimates T_b by $\sim 3^\circ\text{C}$, thus, we predicted that the T_{act} of nighthawks would be $\sim 34^\circ\text{C}$. Given that a T_{skin} threshold of 30°C has been used as a threshold to define torpor in Caprimulgids in the past (Brigham, 1992; Firman et al., 1993; Brigham et al., 2000) and we wanted to have an individually specific definition of torpor based on T_{act} , we defined torpor as a drop of 4°C below T_{act} (i.e. $34 - 4^\circ\text{C} = 30^\circ\text{C}$). We did not use $T_{skin} < 30^\circ\text{C}$ as our threshold for torpor because we wanted to have an individually specific definition of torpor based on T_{act} . We submit that clear problems exist with the use of T_{act} for making estimates regarding energy expenditure in free-ranging animals (Willis and Brigham, 2003). However, defining torpor with respect to T_{act} may still be useful as a means of simply identifying the presence of torpor in free-ranging animals.

3. Results

The mean mass of the fifteen male and four female nighthawks captured was 82.7 ± 1.5 g. T_{skin} data from seven males and one female were collected during 28 bird-mornings and 31 bird-nights (range of 4–13 bird-mornings and nights per individual). The average T_{act} was $33.6 \pm 0.6^\circ\text{C}$. Similar to Brigham et al. (2000), T_{skin} appears to underestimate T_b by about 3°C since the average T_{act} was $\sim 3^\circ\text{C}$ below the normothermic temperature recorded under laboratory conditions ($T_b = 34\text{--}40^\circ\text{C}$ over T_a s ranging from 2°C to 35°C ; Lasiewski and Dawson, 1964).

Three of the eight birds entered torpor on four occasions at night or in the morning. Nighthawk 01 entered torpor on the morning of 18 August 2000 (Fig. 1). The T_{skin} of this bird dropped 4.8°C below T_{act} ($T_{skin} = 29.1^\circ\text{C}$) then warmed up at about the same rate as T_a . The initial drop in T_{skin} could not have been the result of ambient effects because T_a was increasing at the time (Fig. 1). Nighthawk 01 also entered torpor on the night of 22–23 August 2000 (Fig. 2). The first T_{skin} recorded on this night was 8.4°C below T_{act} ($T_{skin} = 25.5^\circ\text{C}$). This bout cannot be attributed to ambient effects either because T_{skin} increased throughout the night even though T_a remained constant. Nighthawk 06 entered torpor on the morning of 22

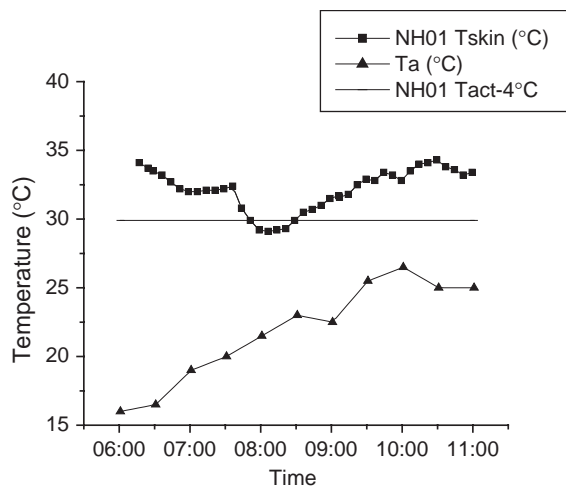


Fig. 1. T_{skin} of Nighthawk 01 (NH01) and ambient temperature (T_{a}) on the morning of 18 August 2000.

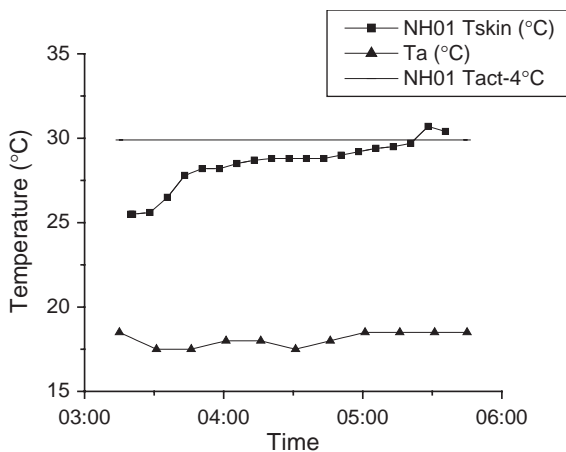


Fig. 2. T_{skin} of Nighthawk 01 (NH01) and ambient temperature (T_{a}) on the night of 22–23 August 2000.

August 2001; its minimum T_{skin} was 5.2°C below T_{act} ($T_{\text{skin}} = 28.1^{\circ}\text{C}$). Nighthawk 07 entered torpor on the night of 13–14 August 2001; its minimum T_{skin} was 7.2°C below T_{act} ($T_{\text{skin}} = 25.3^{\circ}\text{C}$). For all individuals that entered torpor we recorded normothermic T_{skin} s when the T_{a} was considerably colder than at the time that torpor was employed (e.g. for Nighthawk 01: Fig. 3). This eliminated the possibility that these bouts can be attributed to ambient cooling effects.

In all four bouts of torpor, T_{skin} dropped below the 30°C threshold that has been set in other studies of Caprimulgid torpor (Brigham, 1992; Firman et al., 1993; Brigham et al., 2000). Had we used the 30°C T_{skin} threshold to delineate torpor as in previous studies, we

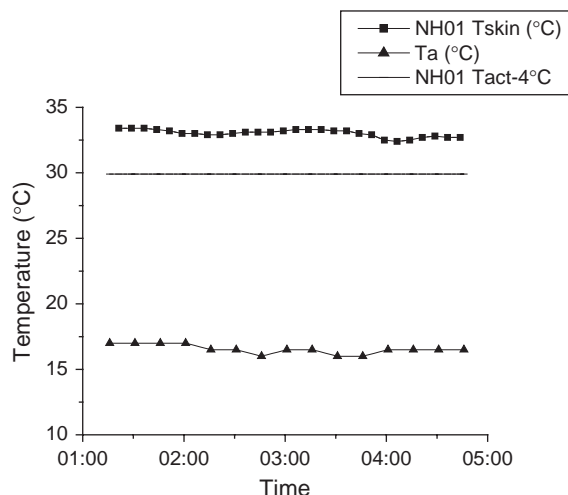


Fig. 3. T_{skin} of Nighthawk 01 (NH01) and ambient temperature (T_{a}) on the night of 8–9 August 2000.

would have recorded three additional bouts of torpor, including a bout each for two additional individuals.

4. Discussion

Our results show that free-ranging nighthawks have the ability to enter torpor. Studying torpor under laboratory conditions allows researchers to quantify metabolic attributes of torpor bouts, but studies of free-ranging animals, like the present one, are essential because some animals that enter torpor under natural conditions are reluctant to do so in the lab (Geiser et al., 2000).

Nighthawks in the Cypress Hills did not appear to use torpor in response to cool T_{a} s. Our finding that only four out of the eight birds entered torpor; and that torpor was not used predictably based on weather conditions; is not surprising. Previous research on Caprimulgids suggests that harsh conditions do not necessarily influence the use of torpor (Brigham, 1992; Brigham et al., 2000). For example, weather conditions could not be used to predict the use of torpor by all individual poorwills examined by Brigham (1992). Further research should focus on what factors determine the “decision” by animals to use torpor.

The use of torpor by nighthawks was not recorded in the Okanagan Valley (Firman et al., 1993). It is possible that torpor is so rare in nighthawks that it was not observed in that study. However, they argued against this suggestion because nighthawks did not enter torpor even though the weather during their study was unusually harsh. In fact, conditions were so poor that some nighthawks died from starvation and others

changed their foraging patterns. The claim that night-hawks faced energetic shortfalls is corroborated by data suggesting that the breeding attempts of female insectivorous bats living in the study area, whose diet is similar to that of nighthawks (Brigham and Fenton, 1991), were disrupted due to poor foraging conditions (Grindal et al., 1992). Given that we recorded torpor in the Cypress Hills, we feel that further research should focus on the possibility of variation in the ability and tendency of animals to use torpor in different locations.

Compared to other Caprimulgids, torpor is not a common strategy for nighthawks. Further research is needed to determine the ultimate reason for this rarity. This will help elucidate the ecological determinants of torpor use in Caprimulgids and will offer insight into the evolution of heterothermy in endotherms.

Acknowledgements

We are grateful to C.M. Voss, S. Martinez, J. Adams, R.G. Poulin and D.J.H. Sleep, for field assistance and to members of the “bird and bat lab” for their support, encouragement and guidance. The work was funded by a Natural Sciences and Engineering Research Council (NSERC) operating grant to RMB, and an NSERC Undergraduate Student Research Award to QEF. We thank F. Geiser, A.E. McKechnie, J.E. Lane and K.A. Edwards for helpful comments that greatly improved the article.

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