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THERMOREGULATION IN FREE-RANGING WHIP-POOR-WILLS¹

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Key words: Whip-poor-wills; *Caprimulgus vociferus*; thermoregulation; torpor; energetics; radiotelemetry; goatsuckers.

Torpor is a strategy that allows animals to reduce their body temperature as a means of saving energy during periods of low ambient temperature or low food availability. Brigham (1992) has shown that free-living Common Poorwills (*Phalaenoptilus nuttallii*) are capable of daily torpor. In contrast, free-living Common Nighthawks (*Chordeiles minor*) do not use torpor (Firman et al. 1993).

Interspecific variation in thermoregulatory patterns among caprimulgids could be the result of different foraging styles (Whip-poor-wills, *Caprimulgus vociferus*, sally from a perch whereas Common Nighthawks are aerial insectivores), body size, or reproductive biology (e.g., number of clutches per breeding season).

The biology of free-ranging caprimulgids is poorly understood and no studies have addressed the ther-

moregulatory behavior of Whip-poor-wills in the field. Brigham and Barclay (1992) predicted that Whip-poor-wills are incapable of torpor, and that this difference may explain different responses to levels of moonlight between Whip-poor-wills and Common Poorwills. Whip-poor-wills synchronize their breeding cycle to the lunar cycle (Mills 1986), whereas Common Poorwills do not.

In the Okanagan Valley, British Columbia, Brigham and Barclay (1992) found that two of five Common Poorwill pairs made second breeding attempts, whereas Mills (1986) found that only one out of eight pairs of Whip-poor-wills laid a second clutch. The ability to enter torpor may allow Common Poorwills to use their available energy reserves more efficiently and lay two clutches during the breeding season (Brigham and Barclay 1992). To successfully lay two clutches, Common Poorwills may have to begin laying their first clutch as early in the spring as possible, precluding them from synchronizing their nesting with the lunar cycle (Brigham and Barclay 1992).

Alternatively, if Whip-poor-wills lay only a single clutch, they may maximize their reproductive success by synchronizing their nesting cycle with the lunar cycle. This would ensure that eggs hatch during a waxing moon so that parents can increase their nightly foraging

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activity when the energetic demands of feeding offsprings are greatest (Mills 1986).

Although Brigham and Barclay (1992) predicted that Whip-poor-wills are not capable of torpor, spring arrival dates suggest otherwise. In Ontario, Whip-poor-wills begin arriving at Point Pelee in late April, whereas Common Nighthawks arrive much later—usually mid to late May (Speirs 1985). At Pinery Provincial Park, Ontario, Whip-poor-wills arrive and establish territories by early May. This is at least two to three weeks before Common Nighthawks arrive. During this time when insect density and air temperatures are low (regularly dropping below 5°C), Whip-poor-wills vocalize for long periods (pers. observ.). Other sympatric nocturnal insectivores (e.g., hoary bats, *Lasiurus cinereus* and red bats, *L. borealis*) reduce their foraging activity at this time (pers. observ.) and hoary bats rely on torpor to survive these periods of cold temperatures and low prey availability (unpubl. data). Energetic costs of Whip-poor-will vocalizations and territory defense are unknown but it seems likely that remaining active during early May, when insect density and ambient temperature are low, is costly.

Daily torpor is one tactic that could allow Whip-poor-wills to reduce energetic costs during early spring when prey availability is low and they must expend energy in territorial defense. Based on their small body size and sit-and-wait foraging strategy, Firman et al. (1993) also predicted that Whip-poor-wills should be capable of torpor. The purpose of this study was to test the hypothesis that free-ranging Whip-poor-wills use torpor to reduce energy demands during periods of low ambient temperature and prey availability.

STUDY SITE AND METHODS

The study was conducted between May and July in 1988, 1989, and 1990, at Pinery Provincial Park, Ontario. This site is on the shore of Lake Huron, about 50 km northeast of Sarnia, Ontario. The park covers about 2,532 ha, about half of which is oak savanna and the rest mainly planted White (*Pinus strobus*) and Red Pine (*P. resinosa*).

I captured Whip-poor-wills by playing tape-recordings of territorial vocalizations under mist nets or by setting mist nets near nests and flushing birds into the net. I used an Ohaus (Model C200M) electronic balance or a Pesola spring balance to weigh each bird to the nearest gram and determined the bird's sex by the color of its outer tail feathers. Temperature-sensitive radio-transmitters (Model RI-2T, Holohil Systems Ltd., Woodlawn, Ontario) were attached to the back of each bird using an elastic harness that fitted around the bird's wing (Mills 1986, Brigham 1992). The total mass of the transmitter and harness was 4.9 g.

Transmitter signals were received with Merlin 12 (Custom Electronics, Urbana, Illinois) or AVM (AVM Instrument Co., Dublin, California) receivers with a five-element Yagi antenna. The transmitter signals were detectable from 500–1,000 m away, depending on the local terrain.

The transmitters allowed me to locate the Whip-poor-wills and monitor changes in their body temperatures. The interpulse intervals of the radiotransmitters varied with temperature, allowing me to remotely monitor the temperature adjacent to the birds' skin. I

refer to these temperatures as transmitter temperatures (T_t), since they are not true skin temperatures. For each transmitter temperature measurement (T_t), I used a stop watch to record the total duration of 10 interpulse intervals. This procedure was repeated and an average of the two measurements used to calculate the interpulse interval. The interpulse interval was converted to an estimate of transmitter temperature (T_t) using calibration curves supplied by the manufacturer for each transmitter.

In most cases I measured ambient air temperature (T_a) with a mercury bulb thermometer within 30 minutes of recording the Whip-poor-wills' transmitter temperatures. These temperatures were measured in the shade, at approximately 1 m from the ground, and usually within 1 km of the bird's location when its transmitter temperature was taken. When I did not obtain ambient temperatures this way, I used hourly temperatures from the Environment Canada Atmospheric Environment Service weather office at Sarnia. These instances represented only 26 of 388 (<7%) temperature measurements.

RESULTS

I monitored the temperatures adjacent to the skin (T_t) of seven Whip-poor-wills (six males and one female) for a total of 38 bird-days (i.e., one bird monitored on one day) (Table 1). On 12 bird-days, I recorded the temperature (T_t) of Whip-poor-wills approximately hourly for a 24-hr period beginning at dusk on one night until dusk the following night. I refer to these 24-hr samples as complete days. I was not always able to record the skin temperatures of each Whip-poor-will during each hourly sampling period. I considered a sample a complete day if I recorded a bird's temperature (T_t) at least 15 times during a 24-hr period, including the coldest part of the day (usually early morning). In addition to these complete days I measured the birds' temperatures (T_t) for an additional 26 partial days when I focused my sampling effort during the coldest part of a 24-hr period or during the day when Whip-poor-wills are least active. The number of complete days, the total number of days and the total number of temperature (T_t) measurements for each Whip-poor-will are shown in Table 1. In total, I made 388 measurements of Whip-poor-will temperatures (T_t) at ambient temperatures ranging from 2–34°C (Table 1). The lowest transmitter temperature I recorded for the seven Whip-poor-wills ranged from 29–38°C (Table 1).

There was a significant positive correlation between ambient air temperature and transmitter temperature for six of the Whip-poor-wills ($r > 0.38$, $P < 0.001$ in all cases; Fig. 1). The sample size for the other (Band #86011) was too small to permit statistical analysis.

DISCUSSION

Over a range of ambient temperatures (2–34°C), Whip-poor-wills always maintained high body temperatures (i.e., $T_t \geq 29^\circ\text{C}$). Different studies have used a variety of criteria for distinguishing between active and torpid animals. Lasiewski and Dawson (1964) considered Common Nighthawks torpid if their temperature fell below 32°C, whereas Brigham (1992) and Firman et al. (1993) used a more conservative threshold of 30°C.

The accuracy with which transmitters reflect a bird's

TABLE 1. Date of capture, sex (M = male, F = female), mass, number of complete days, total number of days, total number of temperature readings (total n), range of ambient temperature in °C, and lowest transmitter temperature (T_1) in °C for each whip-poor-will (see text for complete explanation).

Band number	Date of capture	Sex	Mass (g)	Complete days	Total days	Total n	Range of T_a	Min T_1
86002	20 June 1988	M	53.5	3	6	86	5–24	31
86003	22 June 1988	M	51.8	4	6	85	8–34	37
86004	24 June 1988	F	50.4	3	5	77	5–34	36
86006	23 May 1989	M	60.3	0	12	64	3–25	33
86009	20 May 1990	M	64.0	1	4	48	2–23	29
86010	21 May 1990	M	61.0	1	4	26	2–23	32
86011	31 May 1990	M	58.0	0	1	2	3–4	38
Totals				12	38	388	2–34	29

body temperature depends partly on how closely the harness holds the transmitter to the skin (Firman et al. 1993). This may explain the differences in minimum transmitter temperatures among Whip-poor-wills (Table 1).

Despite this variation, six of seven Whip-poor-wills maintained their transmitter temperature above 30°C. The other bird's transmitter temperature dropped below 30°C on only two of 48 measurements. Even at ambient temperatures below 10°C, all of the Whip-

poor-wills maintained transmitter temperatures well above ambient temperature. In contrast, the skin (and transmitter) temperatures of heterotherms typically fall to within 2–3°C of ambient temperature when they enter torpor (e.g., Big Brown Bats [*Eptesicus fuscus*]: Audet and Fenton 1988; Common Poorwills: Brigham 1992).

My data allow me to reject the hypothesis that Whip-poor-wills use torpor to survive periods of low ambient temperature and prey availability during the spring and

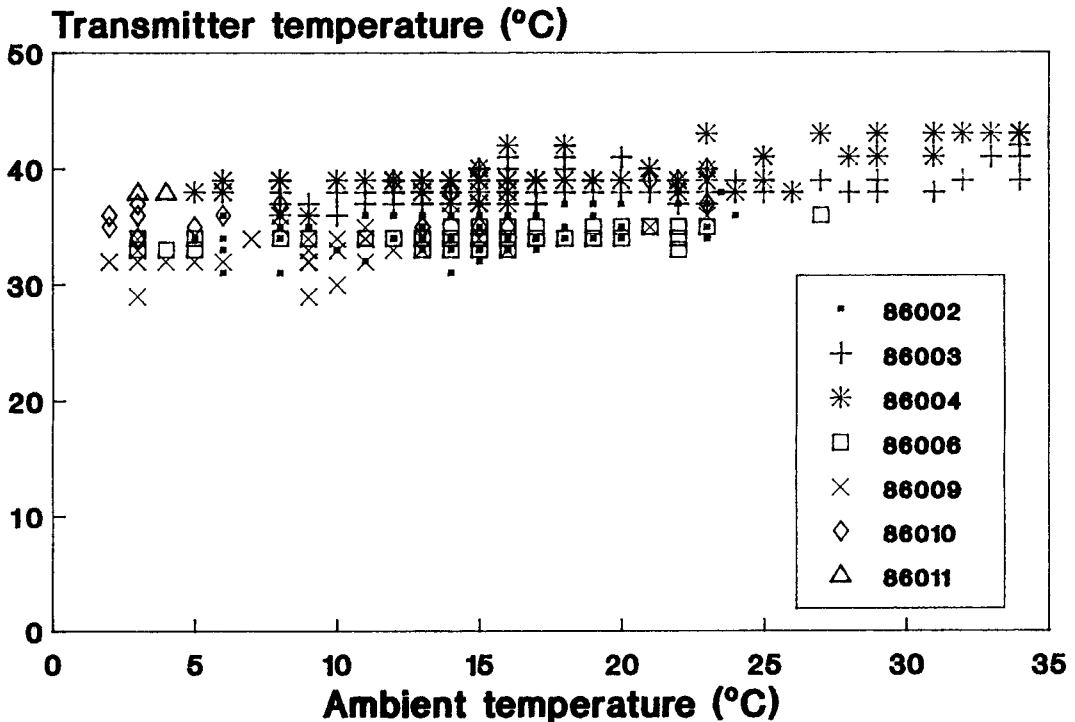


FIGURE 1. Temperature adjacent the skin (T_1) as a function of ambient temperature for seven Whip-poor-wills. Data from each Whip-poor-will are plotted with a different symbol. The numbers in the key refer to the band numbers in Table 1.

summer. My data support Brigham and Barclay's (1992) prediction that Whip-poor-wills are incapable of entering torpor. Whip-poor-wills use a foraging strategy that is energetically inexpensive (i.e., sit-and-wait) and this may allow them to survive periods of low prey availability. The ability of Common Poorwills to enter torpor may allow them to lower their energy demands and use available energy more efficiently, enabling them to lay two clutches in a season. In contrast, Whip-poor-wills do not use torpor and may be unable to lay two clutches in a season. Synchronizing their single clutches with the lunar cycle may ensure that chicks hatch when a full moon permits adults to extend the duration of their foraging period to meet the increased energy demand associated with feeding nestlings (Mills 1986).

Foraging strategy and the ability to enter torpor both influence the energetics and behavior of caprimulgids. Data on individual variation in thermoregulatory strategies in Common Poorwills, and how this variation influences clutch size, number of clutches and reproductive success would increase our understanding of the factors influencing the evolution of foraging behavior in goatsuckers.

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