Daily Torpor in Free-Ranging Whip-Poor-Wills (*Caprimulgus vociferus*)

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ABSTRACT

The use of heterothermy is well documented in the order Caprimulgiformes, but there is conflicting information regarding whether whip-poor-wills are heterothermic. Consequently, we sought to rigorously examine the thermoregulatory abilities of this species. Our study was conducted in southeast South Dakota (42°47′N, 97°0′W), where 35 individuals were captured and outfitted with external, temperature-sensitive radio transmitters. We found evidence that whip-poor-wills used daily torpor during the autumn of 2000 and the spring of 2001 ($n = 12$ torpor bouts, based on 346 bird-nights of observation). The average minimum skin temperature of two torpid whip-poor-wills ($n = 5$ torpor bouts) in spring 2001 was $20.1° \pm 2.6°C$, and bouts of reduced skin temperature lasted an average of 360.0 ± 93.7 min. The distribution of heterothermy within the Caprimulgiform phylogeny suggests that the trait is ancestral in the order. Specific heterothermic parameters, however, differ among the different species. In particular, the frequency of torpor use in whip-poor-wills is lower than for other species. These data suggest that several factors, including weather conditions and gender-specific reproductive ecology, influence the propensity of whip-poor-wills and other Caprimulgiformes to enter torpor.

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Introduction

The maintenance of an elevated body temperature (T_b) during periods of low ambient temperature (T_a) entails a substantial energetic cost to endotherms (birds and mammals; Wang 1989). This cost is exacerbated for insectivorous and nectarivorous species by reduced food abundance during cold and wet weather (Dawson and Hudson 1970; Csada and Brigham 1994; Maddocks and Geiser 1997; Körtner and Geiser 2000). To overcome these energetic challenges, a number of species of mammals and birds use heterothermic endothermy (hereafter, heterothermy). Heterothermy is the facultative reduction of metabolic rate and body temperature to reduce energy expenditure (Wang 1989; Geiser and Ruf 1995). Short-term heterothermy, typically lasting 1.5–22 h (Geiser and Ruf 1995), has been termed "daily torpor" and is characterized by a drop in body temperature to as low as 17.4°C. Long-term heterothermy, with bouts lasting up to 6 wk (Geiser and Ruf 1995), is termed "seasonal hibernation" and is characterized by body temperatures as low as −2.9°C (Barnes 1989).

Although heterothermy seems to be less common in birds than in similarly sized mammals, nine avian orders have been identified as containing heterothermic members (Reinertsen 1996; Downs and Brown 2002; McKechnie and Lovegrove 2002). The phylogenetic distribution of heterothermy has not yet been mapped within the order Caprimulgiformes, but it does appear widespread. Species from North America, Europe, and Australia have been recorded to use daily torpor (Marshall 1955; Peiponen 1965; Dawson and Fisher 1969; Brigham 1992; Brigham et al. 2000; Körtner et al. 2000), and the North American common poorwill (*Phalaenoptilus nuttalli*) is capable of entering long-term heterothermy, reminiscent of mammalian hibernation (Jaeger 1948, 1949; Woods 2002).

Whip-poor-wills (*Caprimulgus vociferus*) are North American nightjars that are ecologically, phylogenetically, and morphologically similar to common poorwills. Both species are active during crepuscular and nocturnal periods and forage for aerial insects by sallying from a perch or the ground (Holyoak 2001). The genus *Phalaenoptilus* is so closely allied with *Caprimulgus* that Holyoak (2001) argues that they hardly warrant separation. Although whip-poor-wills are marginally larger than poorwills (whip-poor-wills, 50–55 g; common poorwills, 40–45 g), the energetic model of Prothero and Jürgens (1986) and the body mass range of species known to use torpor (Geiser and Ruf 1995) both predict that whip-poor-wills are well within the mass range to derive considerable benefit from

using this strategy. Lastly, whip-poor-wills and poorwills occupy similar latitudinal ranges in North America during the summer breeding season, and both species range into southern South Dakota (American Ornithologists' Union 1998; Tallman et al. 2002).

Although the apparent similarities between whip-poor-wills and common poorwills (and other members of the Caprimulgiformes capable of heterothermy) lead to the prediction that whip-poor-wills should be capable of using torpor to conserve energy, a field study conducted in southwest Ontario, Canada, suggested that they do not have this ability (Hickey 1993). The author acknowledged that his conclusions relied on a relatively small data set (38 bird-nights from seven individuals), which may have been inadequate for detecting torpor use if it is not a common occurrence. The purpose of our study, therefore, was to more rigorously examine whether whip-poor-wills use torpor to cope with energetic challenges. Because common poorwills use torpor frequently during the spring and autumn, we hypothesized that whip-poor-wills would use a similar thermoregulatory strategy. However, if an incubating bird allows its body temperature to drop, the concomitant drop in incubation temperature can cause physiological imbalances in the embryo leading to developmental delays and potentially death (Webb 1987; Kissner and Brigham 1993). Due to these potential reproductive costs, we predicted that incubating and brooding individuals would not use torpor.

Material and Methods

Our study was conducted on state and privately owned land near the town of Vermillion, South Dakota (42°47′N, 97°0′W). All study sites except one (Union County State Park) were in riparian woodlands along the Missouri River (Union County State Park was an upland wooded area with a small stream running along its northern edge). The Missouri River study sites were characterized by an overstory of cottonwood (*Populus deltoides*) and an understory dominated by prickly ash (*Zanthoxylum americanum*), rough-leaved dogwood (*Cornus drummondii*), elm (*Ulmus* spp.), and eastern red cedar (*Juniperus virginiana*). The herbaceous ground cover consisted of poison ivy (*Toxicodendron radicans*) and Virginia creeper (*Parthenocissus quinquefolia*). Union County State Park was dominated by green ash (*Fraxinus pennsylvanica*), box elder (*Acer negundo*), and bur oak (*Quercus macrocarpa*).

Whip-poor-wills began returning to the study area on April 21, 2001 (the study commenced after spring arrival in 2000) and left the area between October 1 and 3, 2000, and September 30 and October 2, 2001. We lured the birds into an array of three to six mist-nets using playbacks of taped calls. Captured birds were outfitted with 3-g external radio transmitters, calibrated by the manufacturer to measure temperatures from 0° to 40°C (± 0.5°C; model PD-2T, Holohil Systems, Carp, Ont.). This type of transmitter effectively records the skin temperature

(T_{sk}) of free-ranging endotherms (e.g., Brigham 1992; Barclay et al. 1996; Brigham et al. 2000), and T_{sk} is tightly correlated to the core body temperature (T_b) of the animals (Brigham 1992; Brigham et al. 2000; Willis and Brigham, in press).

We measured body mass and wingspan and calculated an index of body condition by dividing body mass by wingspan. Birds were sexed and aged based on plumage characteristics (Bent 1940). Reproductive condition was assessed for females by gently palpating the abdomen to determine the presence or absence of eggs and by tracking the females after release to determine whether they were incubating eggs or brooding chicks. Reproductive condition was more difficult to assess in males because only one adult male (of 22 tracked) was ever found brooding chicks.

Captured birds received a numbered aluminium U.S. Department of the Interior leg band before release (Master Permit 22199). We did not recapture the birds to remove the radio transmitters but allowed the elastic thread, used to attach the transmitter, to naturally weather and break. The scientific collecting permit numbers were SD-11 and SCCL-758442, and the University of Regina President's Committee on Animal Care approved all procedures.

Skin temperatures were measured both manually and automatically. Merlin 12 (Custom Electronics, Urbana, Ill.) and R1000 (Communication Specialists, Orange, Calif.) telemetry receivers attached to either a five-element Yagi antenna or an omni-directional, vehicle-roof mounted antenna were used for manual measurements. Temperature readings were taken in this manner from dusk (2030–2130 hours) until dawn the next morning (0600–0730 hours). Temperature recordings for each bird were collected every 30 min and opportunistically during the day. From August 31 to September 27, 2000, temperature data were only collected opportunistically during the night and early morning. Concurrent measurements of T_a were made using a thermistor thermometer (accurate to 0.1°C, model 8402-00, Cole Parmer, Vernon Hills, Ill.) placed 1 m above the ground within 1 km of the focal bird(s). Automated telemetry receivers (model SRX_400, Lotek Engineering, Aurora, Ont., running version 3.61 W21 software) measured T_{sk} every 15 min for 24 h, and temperature data were uploaded to a notebook computer every 7–14 d. During the periods when we used the automated receivers, T_a's were recorded with portable temperature data loggers (model DS1921 Thermochron iButton, Dallas Semiconductor, Dallas), which were placed beside the receiver. There was no difference between temperatures taken manually and temperatures taken automatically, so the data were pooled.

Temperature measurements were made from May 8 to September 27, 2000, and from April 23 to October 1, 2001. We monitored the natural thermoregulatory behavior of 35 birds, including 27 males (22 adults and five juveniles) and eight females (seven adults and one juvenile) over the two summers (12 birds in 2000 and 23 birds in 2001). In total, we collected
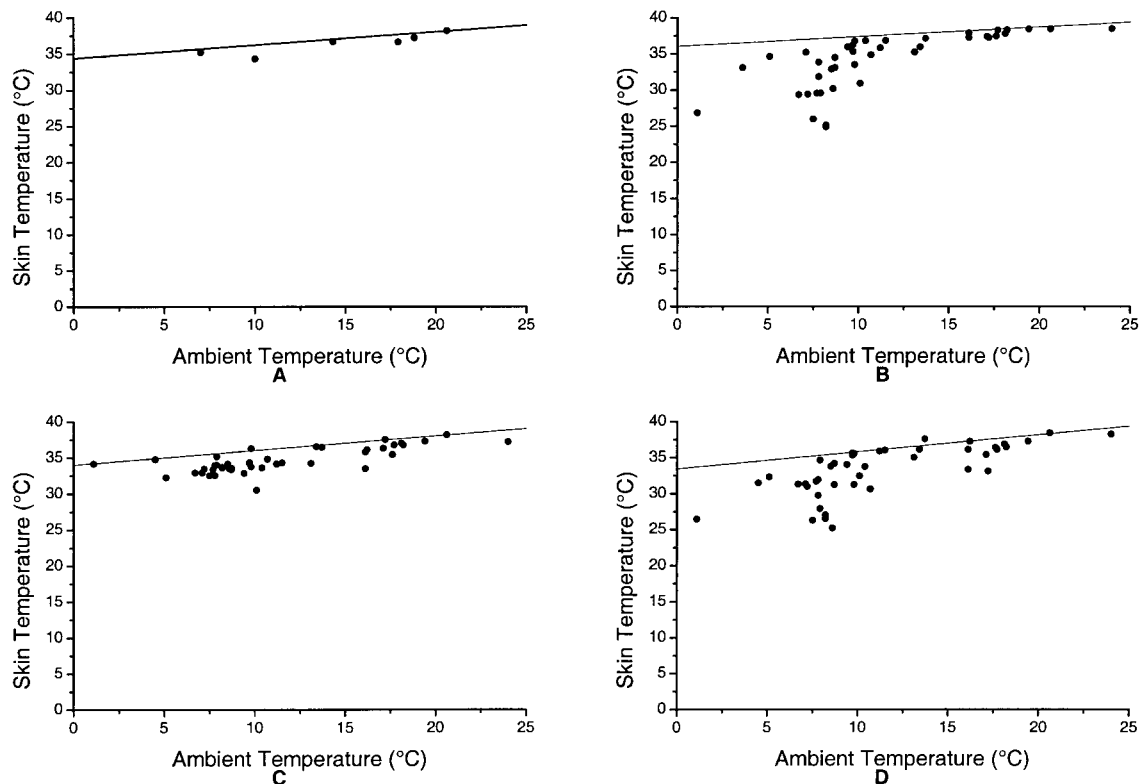
Figure 1. Skin temperatures of four whip-poor-wills monitored from late August to late September 2000. The regression lines, which indicate the significant effect of ambient temperature on skin temperatures using the entire summer data set for each of the four transmitters, are included on the plots.

346 bird-nights (where one bird-night represents one individual being followed for one night) of temperature data (120 bird-nights in 2000, and 226 in 2001). All birds monitored during 2001 were different individuals from those monitored during 2000.

We defined birds to be in torpor when T_{sk} fell below 30°C, following Brigham (1992), and validated this definition during 2001 by locating birds experiencing depressed T_{sk} readings and recording their behavior (i.e., lethargic and unable to respond to stimuli, or active and able to flush when approached). On one occasion, when measurements by the Lotek indicated the lowest T_{sk} of all tagged birds, the core body temperature of this lethargic bird was measured by capturing the bird by hand and inserting the copper constantan lead of a thermocouple thermometer (model 8500-40, Cole Parmer, Vernon Hills, Ill.) approximately 1 cm into the cloaca.

The low number of torpor bouts (see "Results") precluded conducting a correlation analysis of the relationship between T_{sk} and T_b. However, to examine the validity of T_{sk} data as a means to assess heterothermy, we evaluated the effect of T_a on T_{sk} for 11 of the birds monitored. This analysis was conducted to determine whether the effect of T_a is substantial enough to obscure true heterothermic responses. This analysis used only euthermic temperature data from birds for which we had at least 10 bird-nights of measurements to ensure a representative sample.

We used the cladogram of Sibley and Ahlquist (1990) to map what is currently known regarding the phylogenetic distribution of thermoregulatory strategies within the Caprimulgiformes. We classified species as heterothermic, not-heterothermic, or unknown (i.e., have not yet been investigated) based on the primary literature.

Morphological variables were compared using Student's t-tests (Zar 1999). To test for the presence of multiple physiological states in the discontinuous T_{sk} data set (autumn 2000), the data were split between T_a's of 0°–12°C and 12°–24°C, and the variance was compared using a Brown-Forsythe test for homogeneity of variances (Zar 1999). A Kolmogorov-Smirnov test was used to compare the distribution of T_a's when torpor was used to the distribution when torpor was not used (Zar 1999). We used least squares linear regression to assess the effect of T_a on T_{sk} and an ANCOVA to determine whether the slopes of these regression lines were different (Zar 1999). All statistical analyses were conducted using Systat software (ver. 9; SPSS).
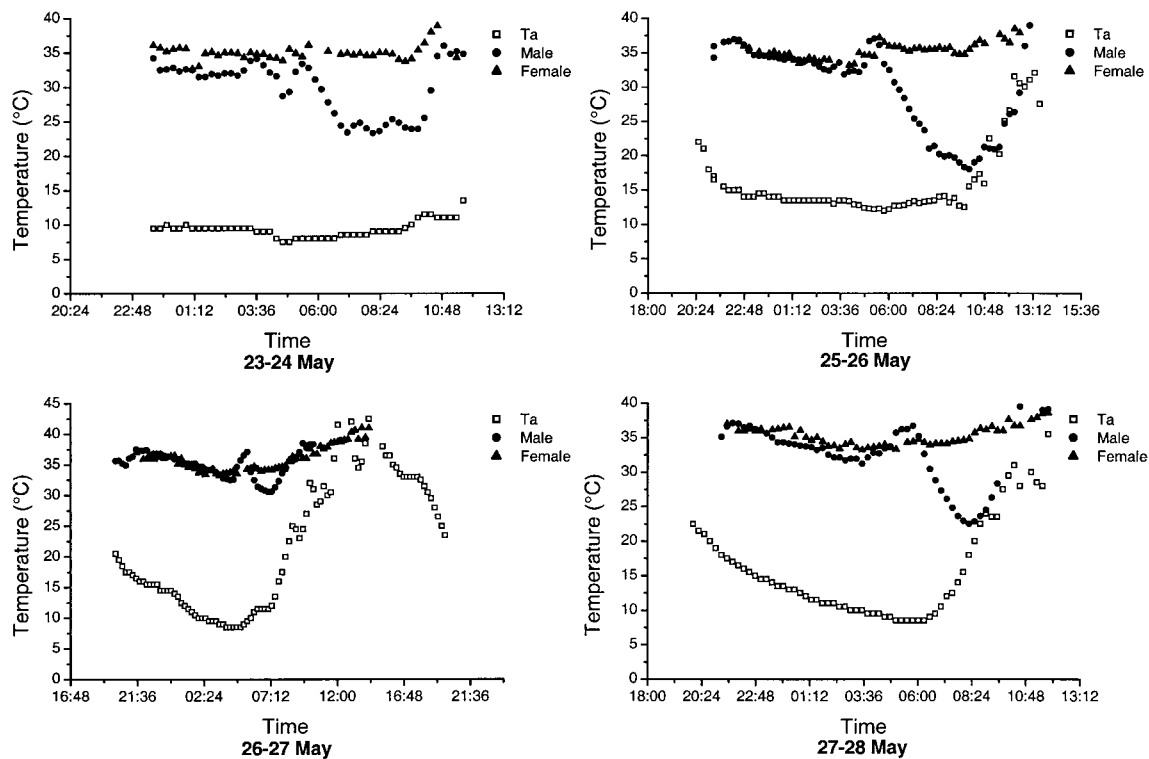
Figure 2. Skin temperatures for a reproductive female and a nonreproductive male recorded during a week of low ambient temperatures (T_a) in 2001. The use of torpor by the male was recorded on May 23–24, May 25–26, and May 27–28. The early increase in T_a on May 26–27 potentially allowed the bird to remain euthermic.

Means are presented $\pm$ 1 SD, and significance was accepted at the $\alpha = 0.05$ level (Zar 1999).

Results

The mean mass and wingspan of adults ($n = 30$) was 53.8 ± 4.4 g and 41.4 ± 3.3 cm, respectively. Adult males ($n = 24$) and females ($n = 6$) did not differ significantly in mass ($t_{28} = -0.7$; $P = 0.462$) or wingspan ($t_{25} = -0.4$; $P = 0.706$). Adults were significantly heavier than juveniles ($n = 7$; juvenile mass, 48.1 ± 3.4 cm; $t_{35} = 3.1$; $P = 0.004$), but the wingspans of the two age classes were not significantly different ($t_{29} = -0.9$; $P = 0.326$).

We found evidence that two individual whip-poor-wills during the autumn of 2000 (September 24–26) and two different individuals during the spring of 2001 (May 23–28) used torpor. In total, we recorded 12 (seven in 2000 and five in 2001) torpor bouts used by these four individuals. Although our T_{sk} data from the autumn of 2000 were discontinuous records (Fig. 1), three of the five bouts during the spring of 2001 were complete records showing entry into, and arousal from, torpor (Fig. 2).

When the T_{sk} data set from heterothermic birds in the autumn of 2000 was split between T_a's of 0°–12°C and 12°–24°C, the variance was equal in both data sets for birds not using

torpor ($F_{1,4} = 0.1$, $P = 0.826$; $F_{1,41} = 0.2$, $P = 0.646$; Fig. 1B, 1D). However, the variance was significantly higher for the 0°–12°C data set than the 12°–24°C data set for birds using torpor ($F_{1,39} = 13.7$, $P < 0.001$; $F_{1,41} = 6.4$, $P = 0.016$; Fig. 1A, 1C).

During the spring of 2001, entry into torpor was always initiated early in the morning (between 0516 and 0546 hours) and lasted an average of 360.0 ± 93.7 min (range 285–465 min). Cooling rates ranged from 4.0° to 5.7°C/h. The maintenance phase of torpor (i.e., defense of a lower T_b set point) was only evident in one of the five bouts (May 23–24; Fig. 2). On this night, the bird maintained an average torpid T_{sk} of 24.2°C and remained in the maintenance phase of the torpor bout for 165 min. The average minimum torpid T_{sk} for all bouts was $20.1° \pm 2.6$°C (range 18.8°–24.0°C). The cloacal temperature (T_{cl}) of the single torpid bird for which it was measured was 18.5°C (corresponding $T_{sk} = 18.8$°C). In the bouts that did not feature a clearly demarcated maintenance phase, arousal began in concert with the morning increase in T_a (May 25–26 and 27–28; Fig. 2). Arousal occurred between 0816 and 1001 hours, and arousal rewarming rates ranged from 7.0° to 12.0°C/h. The highest rate of arousal occurred without a noticeable increase in T_a (May 23–24; Fig. 2). Birds returned to euthermic T_{sk} between 1031 and 1301 hours. Individuals that used torpor
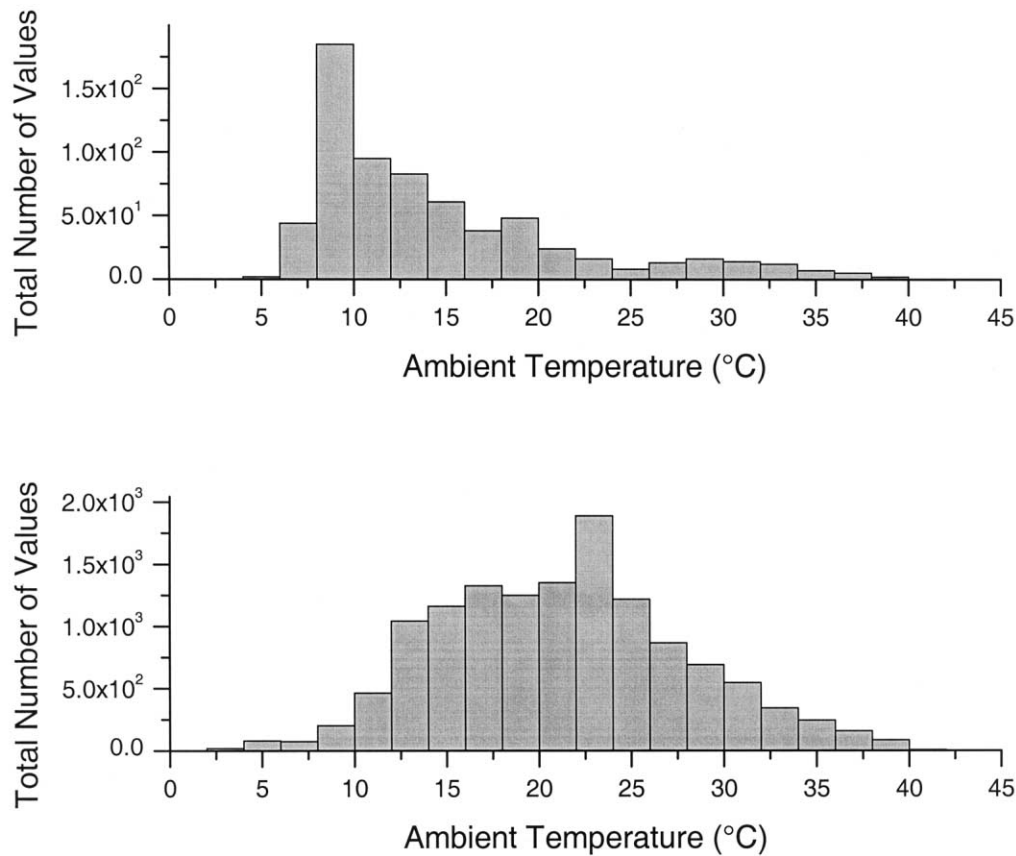
Figure 3. Distribution of ambient temperatures (recorded every 15 min for 24 h) during the period when whip-poor-wills were recorded to use torpor (*top panel*) compared with when torpor was not used (*bottom panel*).

always did so after a dusk foraging bout. All birds defended a euthermic T_{sk} until just before sunrise, and then entered torpor. As such, birds forewent a dawn foraging bout in favor of using torpor. We found no evidence of multiday torpor. All torpor bouts lasted less than 8 h, and the minimum T_{cl} (18.5°C) is typical of daily torpor rather than hibernation (Geiser and Ruf 1995). All of the birds with T_{sk} values below the threshold definition for torpor in spring 2001 were lethargic and did not flush when approached.

The distribution of T_a's recorded during the period when torpor was used in 2001 was significantly lower than the period when torpor was not used ($D = 0.5$; $P < 0.001$; Fig. 3). During this period, four birds (two males and two females) carried functional radio transmitters. Although torpor was recorded for both males, neither female exhibited any evidence of torpor use. While both females were incubating eggs at the time, neither male was ever observed incubating eggs or brooding chicks. The use of torpor by one male in the spring of 2001 occurred in the week immediately following capture. The mass and wingspan of this bird at capture were 46.4 g and 42.8 cm, respectively. This yields the lowest body condition score (1.11 g/cm)

of all the adults we measured (mean = 1.31 ± 0.17 g/cm; range, 1.11–1.75 g/cm; $n = 28$).

There was a significant positive correlation between T_a and T_{sk} for data from 11 birds (R^2 between 0.15 and 0.46, $P < 0.001$ for all comparisons; Fig. 4), and the slopes of these lines were significantly different ($F_{10, 11,216} = 151.7$; $P < 0.001$).

Discussion

Similar to most other nightjars that have been studied, whip-poor-wills were found to use torpor (e.g., Marshall 1955; Peiponen 1965; Dawson and Fisher 1969; Brigham 1992; Brigham et al. 2000; Körtner et al. 2000). During mornings in autumn and spring, with low T_a's, whip-poor-wills allowed T_{sk} to drop to as low as 18.8°C. The state of lethargy of the torpid birds and the T_{cl} of the measured torpid bird (18.5°C) provide strong evidence for the ability of this species to use daily torpor.

Although caution must be exercised when drawing conclusions based on the discontinuous records from autumn 2000, we are confident that the depressed T_{sk}'s from that period do, in fact, represent torpor bouts and not ambient effects. The
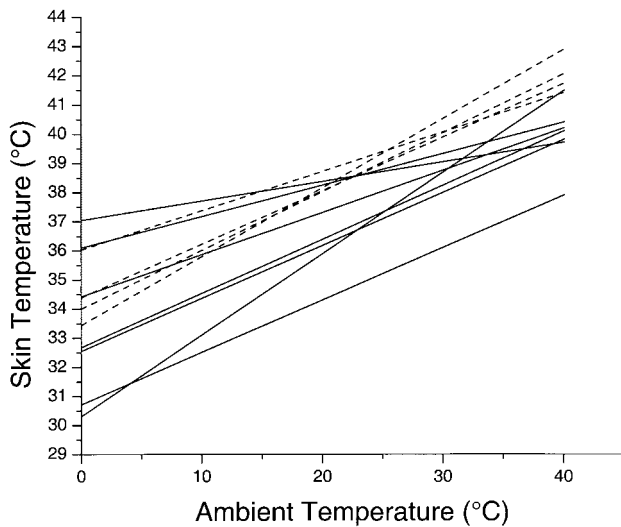
Figure 4. Regression lines corresponding to the significant effect of ambient temperature on skin temperature readings for 11 different whip-poor-wills monitored during the summers of 2000 and 2001. Dashed lines define the four whip-poor-wills monitored in the autumn of 2000 and shown in Figure 1.

temperatures we classify as representing heterothermy were far below the regression line of T_{sk} versus T_a (Fig. 1B, 1D). Further, we conclude that the significantly higher variance in T_{sk} values (0°–12°C vs. 12°–24°C) for birds we classify as heterothermic can be attributed to the occurrence of various thermoregulatory states (euthermia, torpor, entry, arousal) yielding a range of T_{sk} values below 12°C. The fact that two of the four birds monitored during this period showed no evidence of depressed T_{sk} (Fig. 1A, 1C) further supports our contention that the depressed temperatures represent torpor bouts.

In contrast to the low frequency of heterothermy bouts that we recorded for whip-poor-wills, common poorwills studied in British Columbia and Saskatchewan, Canada (Brigham 1992; Csada and Brigham 1994) use heterothermy often during spring and autumn. Additionally, poorwills use deep torpor (to T_{sk} of 3°C) and multiday torpor bouts have been observed (36 h) on the summer breeding grounds (Brigham 1992). This difference is somewhat surprising given the similarities between the two species. However, the more northern locations of both British Columbia (Okanagan Valley) and Saskatchewan (Cypress Hills) may be more energetically demanding than those in southeast South Dakota. Furthermore, the energetic benefits of heterothermy should be greater for poorwills because of lower T_b's and metabolic rates than those of whip-poor-wills while torpid (Withers 1977; Lane 2002). The discrepancies in torpid metabolic rates and T_{sk}'s between the two species may result from the ability of poorwills to use seasonal heterothermy (hibernation; Jaeger 1948; Geiser and Ruf 1995; Woods 2002). In fact, we argue that although previous investigators have attributed

the heterothermic patterns of poorwills during the summer to daily torpor (Brigham 1992; Kissner and Brigham 1993; Csada and Brigham 1994), it may actually be short-term hibernation. Recent work suggests that daily torpor and seasonal hibernation are physiologically distinct processes reflected in heterothermic metabolic rates that differ, on average, by an order of magnitude (Geiser and Ruf 1995). Common poorwills are known to remain inactive for long periods during the winter (Jaeger 1948; Woods 2002), and the T_b defended during the summer (3°C) is typical of hibernation. The use of multiday torpor bouts during the summer (Brigham 1992) further supports the contention that these birds use short-term hibernation.

Our most complete torpor records came from the male with the lowest body condition index of all birds in this study. When coupled with the low frequency of torpor, even during cold
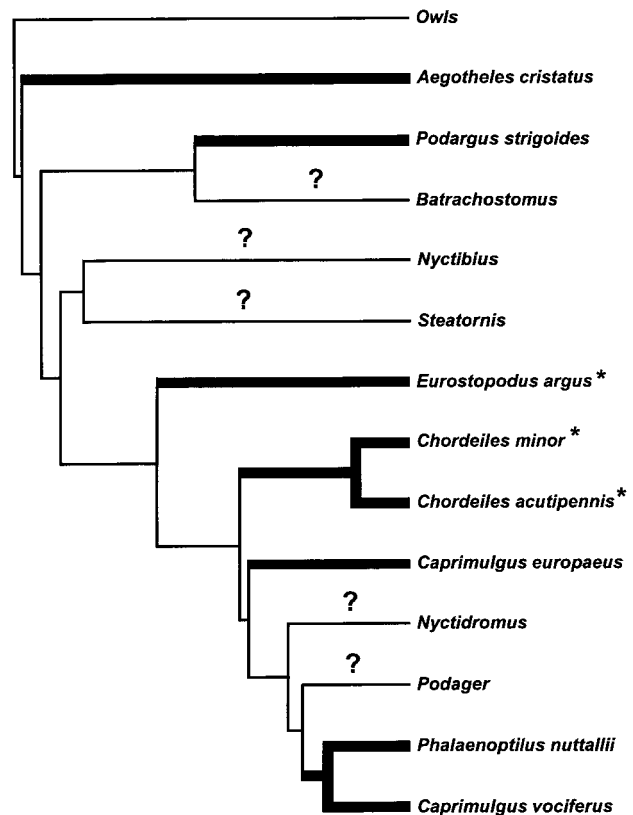

Figure 5. The phylogeny of the Caprimulgiformes, adapted from Sibley and Ahlquist (1990), showing known thermoregulatory patterns. Groups for which evidence of heterothermy has been recorded are shown in bold. Question marks define groups that have not been investigated. An asterisk indicates anecdotal accounts of heterothermy use. Original reports for each species are *Aegotheles cristatus* (Brigham et al. 2000), *Podargus strigoides* (Körtner et al. 2000), *Eurostpodus argus* (Dawson and Hudson 1970), *Chordeiles minor* (Firman et al. 1993; Brigham et al. 1995), *Chordeiles acutipennis* (Marshall 1955), *Caprimulgus europaeus* (Peiponen 1965), *Phalaenoptilus nuttalli* (Jaeger 1948), *Caprimulgus vociferus* (this article).

periods, it appears that individuals of this species are reluctant to become heterothermic. Torpor in whip-poor-wills may be reserved for energetic emergencies (sensu Hainsworth and Wolf 1970; Hainsworth et al. 1977). The reluctance of whip-poor-wills to use heterothermy potentially helps explain why torpor was not observed in Hickey's (1993) study. The probability of not detecting torpor for any given night in our study was 0.9659, based on the Poisson probability (Zar 1999). To compute the probability of not detecting torpor (given this level of occurrence) in Hickey's (1993) study, we raised 0.9659 to the 38th power (for the 38 bird-nights in Hickey's study). This yields a probability of not detecting any torpor bouts in 38 bird-nights as 26.8%. This analysis assumes that the probability of observing torpor is the same on any given night and is the same between the two study sites and times. Thus, if the previous study was conducted during a year of high insect abundance or warmer temperatures, the probability of individuals using torpor would decrease accordingly.

As predicted, heterothermy in whip-poor-wills during the breeding season was restricted to non-incubating males. Although our sample size is small, this apparent reluctance of females to use torpor is compelling. In most previous studies, the effects of reproduction were difficult to distinguish from the effects of warm temperatures because reproduction occurred during the warm parts of the year (Calder and Booser 1973; Brigham 1992; Brigham et al. 2000; Körtner et al. 2000). However, we recorded that whip-poor-wills using heterothermy occurred during cold periods in the breeding season, thereby separating the two proximate effects on heterothermy.

While the agreement between T_{sk} and T_{cl} of the single torpid bird, for which we measured T_{cl}, corroborates evidence from previous studies on small heterothermic endotherms that T_{sk} is a reliable estimate of T_b (Brigham 1992; Audet and Thomas 1996; Barclay et al. 1996; Brigham et al. 2000; Körtner et al. 2000), the significant effect of T_a on T_{sk} highlights the need for caution when using T_{sk} readings alone. Furthermore, the relationship between T_a and T_{sk} was not the same for all individuals, indicating that a simple correction factor cannot be applied for all transmitters. Our use of 30°C as the threshold for torpor appears reasonable on the basis of the y-intercept of all regression lines lying above this value. In other words, T_{sk}'s below 30°C cannot be attributed solely to T_a effects of the transmitter or nonheterothermic physiological responses (i.e., peripheral vasoconstriction), at least over the range of T_a's to which birds were exposed in this study. However, the steepest regression line had a difference of more than 11.5°C between 0°C and 40°C, and the maximum difference between two points on different lines, at the same T_a (0°C), was more than 6°C (Fig. 4). Thus, we suggest that although T_{sk} readings are adequate for a relatively coarse-grained assessment of thermoregulation (i.e., whether or not a species is capable of using torpor), direct measurements of T_b (i.e., with implanted radio trans-

mitters) or metabolic rate are required to detect more subtle effects.

To elucidate the evolutionary history of heterothermy within Caprimulgiformes, we mapped what is currently known regarding the distribution of thermoregulatory strategies on the phylogeny for the order (Sibley and Ahlquist 1990). To date, there is no evidence for heterothermy in any species of owl, the taxon most closely related to the Caprimulgiformes (Sibley and Ahlquist 1990; Fig. 5). The occurrence of heterothermy in owlet-nightjars, which split relatively early in the Caprimulgiform lineage, and its widespread occurrence in Caprimulgiform species from different continents and taxonomic affiliations (Fig. 5), suggests that this trait evolved early in the Caprimulgiform lineage. The general ability to use heterothermy is common among Caprimulgiformes; however, the specific parameters of its use vary in individual species. This diversity of torpor patterns reported for various nightjars has important implications for future studies addressing the thermoregulatory behavior of members from this order. We suggest that, rather than simply determining whether different Caprimulgiform species have the ability to use heterothermy, comparative studies need to be undertaken examining the effects of ecological factors, such as foraging mode, resource abundance, and breeding status, on patterns of heterothermy.

Literature Cited

American Ornithologists' Union. 1998. Checklist of North American Birds. 7th ed. Allen Press, Lawrence, Kans.

Audet D. and D.W. Thomas. 1996. Evaluation of the accuracy of body temperature measurement using external transmitters. Can J Zool 74:1778–1781.

Barclay R.M.R., M.C. Kalcounis, L.H. Crampton, C. Stefan, M.J. Vonhof, L. Wilkinson, and R.M. Brigham. 1996. Can external radio-transmitters be used to assess body temperature and torpor in bats? J Mammal 77:1102–1106.

Barnes B.M. 1989. Freeze avoidance in a mammal: body temperatures below 0°C in an arctic hibernator. Science 244: 1593–1595.

Bent A.C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. US Natl Mus Bull 176:1–506.

Brigham R.M. 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). Physiol Zool 65:457–472.

Brigham R.M., G. Körtner, T.A. Maddocks, and F. Geiser. 2000. Seasonal use of torpor by free ranging Australian owlet-nightjars (*Aegotheles cristatus*). Physiol Zool 73:613–620.

Brigham R.M., K.H. Morgan, and P.C. James. 1995. Evidence that free-ranging common nighthawks may enter torpor. Northwest Nat 76:149–150.

Calder W.A. and J. Booser. 1973. Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlations. Science 180:751–753.

Csada R.D. and R.M. Brigham. 1994. Reproduction constrains the use of daily torpor by free-ranging common poorwills (*Phalaenoptilus nuttallii*) (Aves: Caprimulgidae). J Zool (Lond) 234:209–216.

Dawson W.R. and C.D. Fisher. 1969. Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). Condor 71: 49–53.

Dawson W.R. and J.W. Hudson. 1970. Birds. Pp. 223–310 in G.C. Whittow, ed. Comparative Physiology and Thermoregulation. Academic Press, New York.

Downs C.T., and M. Brown. 2002. Nocturnal heterothermy and torpor in the malachite sunbird (*Nectarinia famosa*). Auk 119:251–260.

Firman M.C., R.M. Brigham, and R.M.R. Barclay. 1993. Do free-ranging common nighthawks enter torpor? Condor 95: 157–162.

Geiser F. and T. Ruf. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiol Zool 68:935–966.

Hainsworth F.R., B.C. Collins, and L.L. Wolf. 1977. The function of torpor in hummingbirds. Physiol Zool 50:215–222.

Hainsworth F.R. and L.L. Wolf. 1970. Regulation of oxygen consumption and body temperature during torpor in a hummingbird, *Eulampis jugularis*. Science 168:368–369.

Hickey M.B.C. 1993. Thermoregulation in free-ranging whip-poor-wills. Condor 95:744–747.

Holyoak D.T. 2001. Nightjars and Their Allies. Oxford University Press, New York.

Jaeger E.C. 1948. Does the poorwill hibernate? Condor 50:45–46.

———. 1949. Further observations on the hibernation of the poorwill. Condor 51:105–109.

Kissner K.J. and R.M. Brigham. 1993. Evidence for the use of torpor by incubating and brooding common poorwills *Phalaenoptilus nuttalli*. Ornis Scand 24:333–334.

Körtner G., R.M. Brigham, and F. Geiser. 2000. Winter torpor in a large bird. Nature 407:318.

Körtner G. and F. Geiser. 2000. Weather patterns and daily torpor in free-ranging animals. Pp. 103–110 in G. Heldmaier and M. Klingenspor, eds. Life in the Cold. 11th International Hibernation Symposium. Springer, Berlin.

Lane J.E. 2002. Thermoregulation of Whip-Poor-Wills under Natural and Laboratory Conditions. MSc thesis. University of Regina, Saskatchewan.

Maddocks T.A. and F. Geiser. 1997. Energetics, thermoregulation, and nocturnal hypothermia in Australian silvereyes. Condor 99:104–112.

Marshall, J.T., Jr. 1955. Hibernation in captive goatsuckers. Condor 57:129–134.

McKechnie A.E. and B.G. Lovegrove. 2002. Avian facultative hypothermic responses: a review. Condor 104:705–724.

Peiponen V.A. 1965. On hypothermia and torpidity in the nightjar (*Caprimulgus europaeus*). Ann Acad Sci Fenn 87:2–15.

Prothero J. and K.D. Jürgens. 1986. An energetic model of daily torpor in endotherms. J Theor Biol 121:403–415.

Reinertsen R.E. 1996. Physiological and ecological aspects of hibernation. Pp. 125–157 in C. Carey, ed. Avian Energetics and Nutritional Ecology. Chapman & Hall, New York.

Sibley C.G. and J.E. Ahlquist. 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven, Conn.

Tallman D.T., D.L. Swanson, and J.S. Palmer. 2002. Birds of South Dakota. 3d ed. South Dakota Ornithologists' Union, Aberdeen.

Wang L.C.H. 1989. Ecological, physiological, and biochemical aspects of torpor in mammals and birds. Pp. 361–401 in L.C.H. Wang, ed. Animal Adaptation to Cold. Springer, Berlin.

Webb D.R. 1987. Thermal tolerance of avian embryos: a review. Condor 89:874–898.

Willis C.K.R. and R.M. Brigham. 2003. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. J Comp Physiol B 173:379–389.

Withers P.C. 1977. Respiration, metabolism, and heat exchange of euthermic and torpid poorwills and hummingbirds. Physiol Zool 50:43–52.

Woods C.P. 2002. Ecological Aspects of Torpor Use and Winter Inactivity in Common Poorwills. PhD thesis. University of Regina, Saskatchewan.

Zar J.H. 1999. Biostatistical Analysis. Prentice Hall, Englewood Cliffs, N.J.