

DO FREE-RANGING COMMON NIGHTHAWKS ENTER TORPOR?¹

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Abstract. There is conflicting evidence as to whether Common Nighthawks (*Chordeiles minor*) can enter torpor. The purpose of this study was to determine if torpor is used by free-ranging individuals under natural conditions. Nighthawks were monitored from June until August 1990 near Okanagan Falls, British Columbia, using temperature sensitive radio-transmitters. Record-high precipitation in 1990 apparently stressed the birds energetically by preventing foraging during poor weather and by reducing the abundance of the main prey item, caddisflies (Trichoptera). Energetic stress was manifested in several ways. Compared to previous years, nighthawks foraged diurnally, changed foraging habitats resulting in a broadening of the diet, and increased the duration of foraging periods. Furthermore, two tagged birds died, apparently of starvation. Despite indications that 1990 was a stressful year, the temperature of nighthawks never fell below homeothermic levels. If nighthawks are physiologically capable of entering torpor, an energetically stressful year would be expected to induce it. Our observations support the idea that they are not physiologically adapted to enter torpor as a means of energy conservation.

Key words: *Common Nighthawk; Chordeiles minor; torpor; thermoregulation; energetics; foraging.*

INTRODUCTION

An integral part of an organism's interaction with its environment is determined by its energy budget. When foraging, animals should maximize efficiency in part by minimizing unnecessary energy expenditure. This allows maximum allocation of assimilated energy to maintenance, movement, and reproduction. A large component of the energy budget of endothermic animals is thermoregulatory heat production, particularly at low ambient (T_a) temperatures. Typically, endotherms maintain thermal equilibrium by balancing heat loss with endogenous metabolic heat production. However, low T_a or food shortages can induce some normally endothermic mammals and birds to save energy by reducing metabolic heat production and entering torpor (Wang 1989). The Caprimulgidae are a group of birds of special interest in this respect because several species use torpor (Marshall 1955,

Reinertsen 1983) and possibly even hibernate (Jaeger 1948, 1949), as a means of reducing energy expenditure during periods of inactivity. Recent data show that torpor is used regularly outside of the breeding season by free ranging Common Poorwills (*Phalaenoptilus nuttallii*; Brigham 1992).

The Common Nighthawk (*Chordeiles minor*) is a caprimulgid whose ability to enter torpor is uncertain. The use of torpor by 80 g nighthawks, assuming torpor bouts of 6 hr and T_b (body temperature) of 15°C, should be energetically advantageous (Prothero and Jurgens 1986). Under laboratory conditions however, Lasiewski and Dawson (1964) could only induce nighthawks to enter torpor following the loss of 28–34% of original mass. Further, only one of four experimental birds induced to enter torpor survived a drop in T_b below 25°C. They concluded that nighthawks would be unlikely to use torpor under field conditions. Field data on foraging efficiency and diet (Aldridge and Brigham 1991), suggest that nighthawks must either capture more than one prey item simultaneously, a strategy not known to be used by any aerial insectivore, or use energy far

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more efficiently than predicted by allometric equations (Nagy 1987). If nighthawks use torpor, it could explain Aldridge and Brigham's (1991) calculation that less energy than expected is needed. The purpose of this study was to test the hypothesis that free-ranging nighthawks will enter torpor under natural conditions.

METHODS

The study took place in the vicinity of Okanagan Falls, British Columbia (49°20'N, 119°35'W) from May to August 1990, centered at Okanagan Falls Provincial Park ("the park"), where nighthawks congregate to forage on emerging trichopterans (Brigham 1990, Aldridge and Brigham 1991, Brigham and Fenton 1991). Summers in this semi-arid area are usually very dry, with high daytime temperatures and low temperatures at night. The vegetation is characteristically open, with grassy patches alternating with stands of coniferous trees (see Cannings et al. 1987 for a more detailed description).

Nighthawks were captured in mist nets while they foraged at dusk over the Okanagan River at the park, and sexed by throat and tail plumage patterns respectively (Selander 1954). All birds were at least one-year old based on plumage and the fact that they were caught early in the season before young had fledged. Mass was measured to the nearest 0.1 g using a portable electronic balance. Temperature sensitive radio transmitters (model PD-2T—Holohil Systems Ltd, Woodlawn, Ontario), with an average mass of 2.4 g were affixed to the back of the birds using an elastic harness. The transmitter package weighed only 3.0% of nighthawk body mass, well below the recommended maximum of 5% for this size of volant animal (Aldridge and Brigham 1988). The packages used in 1990 were 3 g lighter than those used in previous studies of nighthawks without obvious ill effects (Brigham 1989, Brigham and Fenton 1991).

Movement and body temperature data were collected using Merlin 12 (Custom Electronics, Urbana, IL) and LA12-DS (AVM Electronics Co., Dublin, CA) telemetry receivers and 5-element Yagi antennas. At five minute intervals, each bird was classified as either moving or stationary (Brigham and Barclay 1992). A minimum of twenty pulses were used to determine movement, indicated by a change in signal strength or direction. Transmitters were affixed so that the harness kept the temperature sensor in contact

with the bird's interscapular region, and thus we monitored skin temperature (T_{sk}). T_{sk} was measured every 20 min between sunset and sunrise by averaging three timings of the interval required for 10 pulses and comparing the interval with calibration curves prepared for each transmitter by the manufacturer. In poorwills, there is a significant correlation between T_{sk} and T_b , measured cloacally, with T_{sk} being on average 1.5°C cooler (Brigham 1992).

Following Hudson (1978), we define "torpor" as a drop in temperature below 30°C, slightly more conservative than the 32°C used by Lasiewski and Dawson (1964) reflecting our use of T_{sk} and the fact that active nighthawks have a relatively broad range (6°C) of "normal" body temperatures (Lasiewski and Dawson 1964).

We concentrated tracking efforts on cooler nights when flying insect abundance is reduced (Williams 1961) and thermoregulatory costs are high, making torpor likely to occur. Weather data (ambient temperature and precipitation) were obtained from a weather station at the Penticton airport (15 km north of the study site). For all statistical analyses, a rejection level of 0.05 is used and data are presented as means \pm one standard error.

RESULTS

Four nighthawks (one male, three females) were captured and outfitted with radio-tags on 6 June. Two of the females died between 13 and 15 June (see below). On 16 June, two more females and one male were radio-tagged and from then until the end of August, two male and three female nighthawks carried active transmitters. T_{sk} and foraging activity was monitored on 20 different nights, representing a total of 39 bird-nights of tracking.

The harnesses used on the first four nighthawks did not hold the transmitter close enough to the skin and as a result gave temperature readings intermediate between true T_{sk} and ambient (T_a). We therefore compared the temperature readings taken throughout the night with readings from the same bird when it was at a known body temperature (e.g., immediately after foraging) when the bird was still warm but not moving. Subsequent inactive temperatures were then compared relative to this "equivalent" active temperature and not taken as absolute values. The second set of transmitters attached to nighthawks enabled us to measure true T_{sk} values.

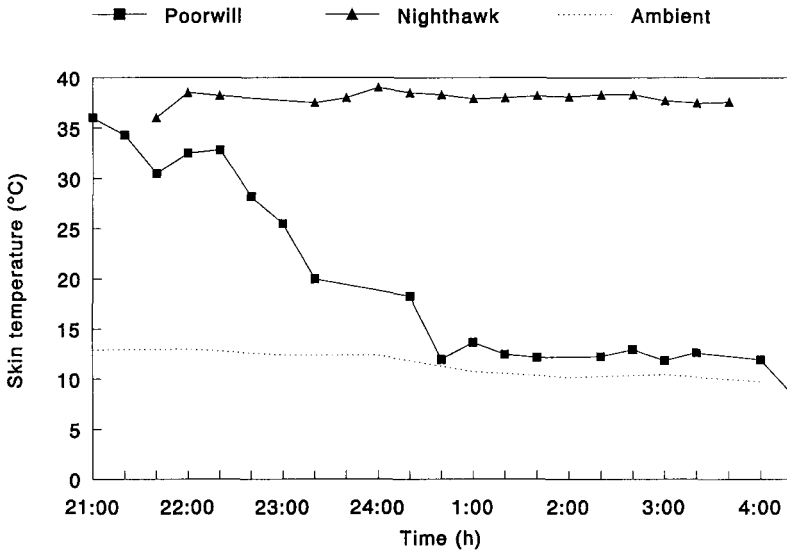


FIGURE 1. Skin temperature of a homeothermic nighthawk on 8 June and a poorwill who entered torpor on 3 June in relation to ambient temperature. The ambient temperatures on the two nights were within 2° of each other between 21:00 and 04:00.

We recorded no instances of a depressed T_{sk} indicative of torpor for any birds carrying transmitters. For nighthawks with snug harnesses, the mean minimum T_{sk} during each night's resting period was $34.5 \pm 0.5^{\circ}\text{C}$, significantly higher than the lower homeothermic temperature (32°C) suggested by Lasiewski and Dawson (1964; $t = 5.09$, $df = 11$, $P < 0.001$). The mean fluctuation of T_{sk} for nighthawks with loose harnesses during the night was $3.74 \pm 0.42^{\circ}\text{C}$. This is significantly smaller than the normal range of 6°C (Lasiewski and Dawson 1964; $t = 5.38$, $df = 12$, $P < 0.001$), indicating that fluctuations in body temperature were no greater than that experienced by a homeothermic bird.

Typical T_{sk} profiles for a torpid poorwill and a homeothermic nighthawk are shown in Figure 1. On 3 June, T_a dropped by 4.6°C through the night, while the poorwill's T_{sk} quickly fell 15°C and then continued to drop following T_a (Fig. 1). On 8 June, the T_{sk} of a homeothermic nighthawk remained relatively stable all night. The inactive nighthawk's temperature did not drop significantly below its active temperature until flight occurred.

After nighthawks arrived in this study area (30 May), but before any were radio-tagged, two tagged poorwills entered torpor on one night (3–4 June). On that night, we observed male night-

hawks actively flying and calling during both the typical dusk and dawn activity periods. We do not know whether female nighthawks were also active.

Several lines of evidence indicated that 1990 was a stressful year for nighthawks in the Okanagan.

WEATHER

Weather data from 1990 was compared to that from 1989 when poorwills were monitored (Brigham 1992) and from 1985–1987 when nighthawk foraging was observed (Brigham and Fenton 1991). The summer of 1990, like the other study years, was generally warmer than the long-term average (Table 1), although differences in mean monthly temperatures were usually less than 2°C .

The entire field season of 1990 was wetter than normal. Although other years also had months with significantly higher than average precipitation (Table 2), May and June 1990, which coincides with the period when nighthawks arrived in the study area, set precipitation records (both approximately three times greater than the 40 year mean) for the area. As a consequence, the Okanagan River, which flows through Okanagan Falls Park, had unusually high levels and flow rates.

TABLE 1. Monthly mean temperatures for 1985–1990 (May–August) compared to 40-year average for Penticton, B.C. Arrows indicate months with significant differences ($P < 0.05$, 2-tailed t -test; † = significantly warmer, ‡ = significantly cooler.)

Temperature °C	May	June	July	August
40-year mean	13.4	17.2	20.3	19.3
1990	13.1	16.9	†21.7	‡21.3
1989	13.7	†19.0	†20.7	19.3
1987	†14.7	†19.6	†20.7	19.4
1986	13.5	†19.1	‡18.3	‡21.5
1985	13.7	†19.0	†20.7	19.3

TABLE 2. Monthly precipitation (mm) for 1985–1990 (May–August) compared to 40-year average for Penticton, B.C. Arrows indicate months with significant differences ($P < 0.05$, 2-tailed t -test; † = significantly more, ‡ = significantly less). Asterisks indicate months with record precipitation.

	May	June	July	August
40-year average	29.1	27.6	21.1	26.5
1990	*†86.4	*†87.8	†25.4	‡36.8
1989	†39.2	†45.3	†28.8	†47.6
1987	‡20.0	†57.2	†58.7	30.8
1986	‡17.6	‡13.8	†36.0	‡17.6
1985	32.6	†38.0	‡2.8	22.4

UNUSUAL FORAGING BEHAVIOR

During the first break from stormy weather after nighthawks had returned, diurnal foraging was regularly observed for 11 consecutive days (June 14–25). Up to a dozen birds were observed at a time and foraging occurred during all parts of the day. Nighthawks were seen to forage diurnally over orchards, vineyards and open woodlands but not over the Okanagan River, the usual site for crepuscular foraging in previous years. Diurnal foraging had not been observed during any of the previous four field seasons.

DEATHS

During the poor weather and just prior to the onset of the unusual diurnal foraging behavior, two radio-tagged nighthawks died (sometime between 13 and 15 June). The birds apparently died of starvation since there was no evidence of predation, or injury due to the transmitter harness. There was no evidence of starvation in over 30 nighthawks carrying the heavier transmitters between 1985 and 1987. Poorwills (approximately half the body mass of nighthawks) in 1990, had no difficulties carrying identical 2.4 g transmitters (Brigham 1992; Brigham and Barclay 1992). A decreased body mass at death would support the starvation hypothesis, but post mortem drying of the nighthawk carcasses prevented our collecting these data.

RADIO-TRACKING

Nighthawks foraged at the park (either dawn or dusk foraging period) on only 39 out of 52 (75%) occasions, significantly less often than in 1985–1987 ($n = 362$, $\chi^2 = 85.4$, $P < 0.001$; Brigham 1988). Trichoptera and nighthawk densities were lower in 1990 during dusk foraging periods, than in previous years (Brigham, unpubl. data). The

mean duration of dusk foraging bouts, which make up the majority of foraging time ($\approx 64\%$; Brigham and Fenton 1991), was significantly longer in 1990 than in 1985–1987 (2-tailed t -test, $df = 380$, $t = 9.81$, $P < 0.001$; $\bar{x} = 82.2 \pm 5.5$ min [1990]).

DIET

The diet of nighthawks in 1986–1987 as determined by fecal analysis on pellets collected from captured birds (Brigham 1990; Brigham and Fenton 1991; Fig. 1), was composed mainly of trichoptera and some hymenoptera. Analysis of 1990 fecal samples in the same manner, indicates an obvious increase in the percentage of homoptera and coleoptera and a corresponding decrease in trichoptera and hymenoptera (Fig. 2).

BATS

In the same study area, the proportion of adult female insectivorous bats making breeding attempts was significantly reduced, and those who did reproduce were significantly delayed in 1990 relative to other years (Grindal et al., 1992). These observations were attributed to the effects of the unusually wet conditions on foraging activity.

DISCUSSION

It is essential to portray 1990 as being harsh on nighthawks, since if torpor is an option, it would most likely occur during energetically stressful conditions. The skin temperature of nighthawks never dropped below 30°C prompting us to suggest that these birds are physiologically unable to enter torpor. Our data indicate that for nighthawks, May and June 1990 was an energetically stressful period. If torpor is an energy conser-

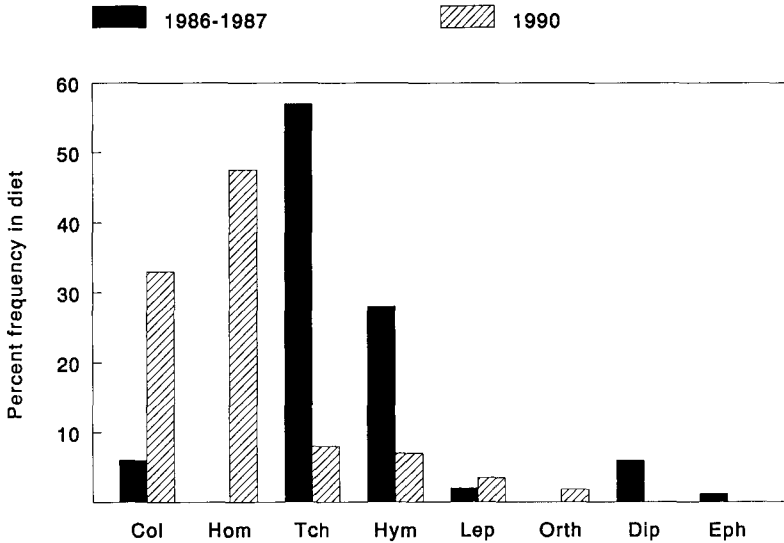


FIGURE 2. Percent distribution of the major insect taxa in the diet of nighthawks in 1990, and 1986-1987. Abbreviations for insect groups are as follows: Col—coleopterans, Hom—Homopterans, Tch—Trichopterans, Hym—Hymenopterans, Lep—Lepidopterans, Orth—Orthopterans, Dip—Dipterans, Eph—Ephemeropterans.

vation option open to nighthawks, it should have been used during this period. Foraging success seemed to be reduced by the wet conditions, since two radio-tagged birds apparently starved during the poor weather, and others fed during the day once good weather returned, as if attempting to make up for the earlier unsuccessful foraging. Neither starvation nor diurnal foraging were observed in previous years. The broadening of the diet was also likely induced by foraging stress (e.g., Thompson and Colgan 1990). The decreased foraging activity at the park is consistent with the increased number of non-aquatic insects in the diet. A reduced abundance of trichopterans (the main prey type in previous years; Brigham 1990) likely resulted from the high flow rate in the Okanagan River (Perry et al. 1986). In contrast, poorwills who forage largely on beetles and moths did not broaden their diet in 1990 (Csada et al., 1992), indicating that the wet conditions had less of an impact on these birds. When nighthawks did feed at the park, they increased the duration of foraging bouts suggesting that the lower prey abundance increased the time required to obtain sufficient energy.

Unfortunately we do not have telemetry data for a night when poorwills entered torpor and nighthawks did not. However, between the time nighthawks arrived in the area and the attach-

ment of radio-tags, at least two poorwills entered torpor on a night when male nighthawks were heard calling while flying at dawn. Since only male nighthawks call, at least some individuals of that sex did not use torpor during a night when the poorwills did.

The fact that we do not have direct evidence of torpor by poorwills and homeothermy by nighthawks on the same night is not particularly surprising however, as we would predict that poorwills should be less affected by poor weather and potential energy stress than nighthawks. Poorwills use a sit and wait foraging strategy which is energetically less expensive than the continuous flight strategy employed by nighthawks. Furthermore, poorwills are able to forage throughout the night, albeit depending on the lunar condition (Brigham and Barclay 1992), compared to nighthawks who normally forage only at dusk and dawn (Brigham and Fenton 1991). Therefore, 80 g nighthawks likely require considerably more energy than 40 g poorwills and have a shorter foraging time (crepuscular period) in which to acquire it. Based on size differences alone, poorwills will deplete their energy reserves faster (per unit mass) than nighthawks and have a greater conductance leading to a greater heat loss. Smaller body size would make it relatively cheaper for poorwills to rewarm if

T_b drops. Our data leads to the conclusion that it is unlikely that Common Nighthawks are capable of entering torpor under normal conditions in the field.

The question of the generality in the use of torpor by caprimulgids remains, with body mass and foraging strategy implicated as being two potentially important factors. If small size and a sit and wait foraging strategy are important, we predict that Whip-poor-wills (*Caprimulgus vociferus*) should readily enter torpor under natural and laboratory conditions. To our knowledge, this species has never been so challenged.

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