

## The Avian Enigma: “Hibernation” by Common Poorwills (*Phalaenoptilus nuttalli*)

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**Abstract.** Common Poorwills, small nocturnal insectivorous birds found across western North America, are seemingly unique because of their alleged ability to remain torpid for extended periods during winter. We used temperature-sensitive radio transmitters to assess patterns of torpor use at sites in the Sonoran desert of southern Arizona. Poorwills used torpor extensively whenever ambient temperature ( $T_a$ ) dropped below 10° C, and there was little evidence for thermoregulation when  $T_a$  was above 5° C. During the winter months (December through February), birds remained entirely inactive on 72% of bird-nights, and continuously inactive periods of 10 days or longer were common. The extent of inactivity is similar behaviorally to that of hibernating small mammals. Roost selection, however, facilitated routine passive solar warming, and inactive birds exhibited a regular pattern of arousal on sunny days, followed by reentry into torpor at sunset. We argue that daily arousals are likely an adaptation to the circumstances that characterize surface dormancy. We hypothesize that the relationship between  $T_a$  and availability of flying insects at night, in combination with unique ecological aspects of arid regions, contributed to the evolution of multiday torpor use by poorwills.

### Introduction

Amongst birds, species in 29 families representing 11 orders have been reported capable of a variety of heterothermic responses (reviewed by McKechnie and Lovegrove 2002). Most birds known to use true torpor are small-bodied specialized foragers, and hummingbirds are the best studied of these (McNab 2002).

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The other group for whom torpor use is well known are nightjars and their allies, most of whom are nocturnal insectivores (Holyoak, 2001). Most nightjars studied use torpor for brief periods, but among this group and indeed all other birds, the Common Poorwill (*Phalaenoptilus nuttallii*; henceforth poorwill) is unique because of its alleged ability to remain torpid for extended periods e.g., hibernate during the winter (French 1993); although McAtee (1947) summarized unconfirmed reports that some swifts (*Chaetura* sp.) and possibly swallows (*Progne* sp.) may hibernate.

Poorwills are small (ca. 50 g) nocturnal insectivores found across western North America in arid or semiarid habitats with limited overhead cover. Indigenous peoples of the American southwest were ostensibly aware of the poorwill's habits; it is known as Hölchoko, 'the sleeping one' to the Hopi, and Rea (1983) argued that the Pima were aware of its ability to enter torpor. Culbertson (1946) provided the first scientific documentation of torpor and Jaeger (1948, 1949) monitored a seemingly hibernating poorwill. Subsequent workers investigated torpor use by poorwills under a variety of laboratory conditions (Austin and Bradley, 1969; Bartholomew et al., 1957, 1962; Brauner, 1952; Howell and Bartholomew, 1959; Ligon, 1970; Withers, 1977). The development of small radio-transmitters permitted an assessment of torpor use by free-ranging birds, which indicated that torpor is used regularly before and after nesting, as well as in winter (Brigham, 1992; Csada and Brigham, 1994; French, 1993). However, the way in which poorwills use torpor remained unclear. Some authors described torpor bouts in winter with daily or cyclical arousals (French, 1993; Ligon, 1970), whereas others suggested that overwintering birds typically remain continuously torpid for many days (Bartholomew et al., 1957; Jaeger, 1949). We present data on torpor use and "hibernation" by free-ranging birds at an overwintering site, and speculate about why poorwills are the only birds currently known to remain inactive for extended periods during winter.

Data were collected between 1996 and 1999 at two sites in the Sonoran desert ecosystem in southern Arizona (Woods 2002). Both sites were within 100 km of Tucson: the Audubon Society Appleton-Whittell Research Ranch (31° 36' N, 110° 30' W) and foothills of the Tortolita Mountains (32° 32' N, 111° 00' W). Most poorwills were caught at night either using mist nets and taped playbacks of territorial calls or a spotlight and long-handled net (Jackson, 1984; Swenson and Swenson, 1977). Captured birds were outfitted with a temperature-sensitive radio transmitter (Holohil Systems Inc., Carp, ON), affixed to an elastic harness slipped over the wings (Brigham, 1992; Hill et al.,

1999). Transmitters were positioned against the intrascapular skin, where overlying feathers insulated them, and we inferred body temperature ( $T_b$ ) based on the measured skin temperature ( $T_{sk}$ ; Brigham, 1992). Tagged birds were monitored remotely with a Lotek SRX 400 data-logging receiver (Lotek Engineering, Inc., Newmarket, ON). Transmitter pulse rate varied with temperature, and in conjunction with transmitter-specific calibration curves, we were thus able to continuously monitor  $T_{sk}$ .

### Torpor Use by Poorwills and its Correlates

We conservatively defined torpor bouts based on  $T_{sk} < 25^\circ\text{C}$ , since one bird was active at  $27.3^\circ\text{C}$  and several were active with  $T_{sk}$  at or just below  $30^\circ\text{C}$ . During torpor bouts, however,  $T_{sk}$  dropped rapidly to near  $T_a$ , and there was little evidence for thermoregulation unless  $T_a$  dropped below about  $5.5^\circ\text{C}$ , below which they apparently defended  $T_b$ , since  $T_{sk}$  did not fall appreciably below  $5.5^\circ\text{C}$  regardless of the extent to which  $T_a$  did (Woods 2002).

Torpor was used extensively by poorwills whenever  $T_a$  approached or dropped below ca.  $10^\circ\text{C}$ , and the likelihood that birds used torpor was highly correlated with  $T_a$  at sunset ( $F_{1,442} = 629.0$ ,  $R^2 = 0.59$ ,  $p < 0.001$ ,  $\beta = -0.77$ ). Bouts of torpor were recorded as late as 15 June and commenced as early as 5 October (Fig. 1). Entry into torpor by active (versus inactive, see “Inactivity During Winter” below) birds was invariably preceded by foraging. For bouts in October, November, March, and April, torpor bouts commenced 216 min after sunset on average. Bouts by these birds averaged 12.9 h in duration, and the minimum  $T_{sk}$  of torpid birds averaged  $9.6^\circ\text{C}$ .

We evaluated the influence of prey availability on torpor using artificial lighting to attract and illuminate insects for foraging poorwills during autumn. In each of three open areas used for foraging by a radio-tagged poorwill, we erected a “supplemental” light, which consisted of an 18-watt fluorescent bulb mounted 2 m above the ground. Each light came on at twilight, remained on for four to eight hours, and illuminated an area ca. 20 m in radius. Field observations confirmed that the birds often foraged in the circle of light provided (in fact, at dusk on many evenings birds flew directly to the lights from their day roosts). Torpor was used on fewer nights by birds that had supplemental illumination (34.4% of bird-nights) compared to those that did not (72.3% of bird-nights;  $\chi^2_1 = 15.6$ ,  $P < 0.001$ ). Moreover, other data collected in the context of this study demonstrated that the density of flying insects was tightly and positively correlated with  $T_a$  such that when  $T_a$  dropped below ca.  $10^\circ\text{C}$  few or no flying insects were

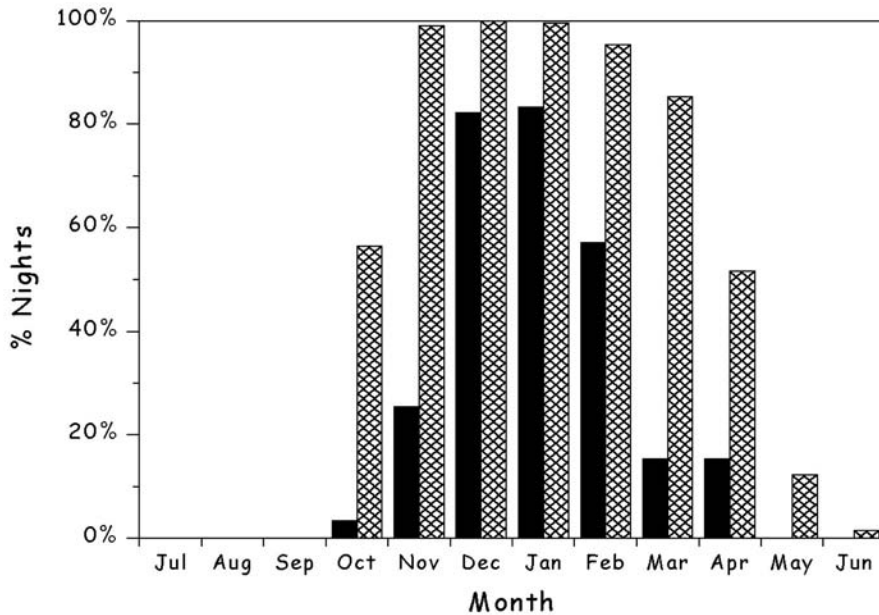


Fig. 1. Percentage of bird-nights by month during which Common Poorwills used torpor (hatched bars) and remained entirely inactive (solid bars) in southern Arizona (see text for distinction between torpor use and inactivity). Sample sizes range from 106 to 270 bird-nights for 8 to 14 individuals per month, and 2,183 bird-nights overall.

available (Woods 2002). Poorwills thus used torpor at times when low  $T_a$  increased metabolic costs while foraging became increasingly inefficient owing to a reduction in prey abundance.

### Inactivity During Winter, or Do Poorwills Hibernate?

We defined a bird as inactive if it remained in torpor or entered torpor without exhibiting physical movement of any kind at or after sunset on any given evening. The earliest date in autumn that an individual remained inactive was 16 October and the latest in spring was 16 April, but most inactivity occurred during December, January, and February. During those three months, nine individuals were inactive on 469 of 654 bird-nights (72%). Of the nine birds, seven were monitored during the unseasonably warm winter of 1998–9 when daily maximum  $T_a$  was ca. 5° C above normal. During the “normal” winter of 1997–8, two birds were inactive on 121 of 132 bird-nights (92%). Overall, individual

nightly inactivity varied between 39.5 and 93.8%. Logistic limitations precluded us from collecting continuous records throughout the winter months for most birds, but nevertheless we recorded continuously inactive periods of  $\geq 10$  days by seven individuals on 13 occasions, and four periods of inactivity of  $\geq 20$  days by three birds (maximum 25 days). This provides strong evidence that under natural conditions poorwills remain inactive for considerable periods of time during winter.

So, do poorwills hibernate? Hibernation is defined as the state of winter lethargy with a reduction in  $T_b$  and metabolic rate by animals that are homeothermic temperature regulators when active (IUPS Thermal Commission 2001). In a typical mammalian hibernator, individuals spend extended periods (days or weeks) torpid interspersed with short bouts of normothermia during which activity may occur (Geiser and Ruf, 1995). We found the extent to which poorwills remained inactive to be behaviorally similar to hibernating small mammals. The birds we monitored routinely remained inactive for periods of  $\geq 10$  days, and when not warmed by the sun (see below) they periodically aroused at roughly five-day intervals (Woods, 2002). Moreover, because poorwills remained entirely inactive for long periods, during which time arousals occurred spontaneously (Woods, 2002), we argue that they may make a useful alternative model to test hypotheses about the utility of periodic arousal.

Unlike mammalian hibernators, however, poorwills always roosted in exposed sites that were open to the south or southwest (typically under prickly pear cactus or alongside exposed rocks). Earlier descriptions of poorwill winter roosts also refer to southerly exposure (Jaeger, 1949; Stebbins, 1957; Thorburg, 1953). Winter days were frequently sunny in our study, and because the sun shone directly on the birds, these roosts facilitated routine passive solar warming. Consequently inactive poorwills exhibited a regular pattern of arousal on sunny days, apparently owing to solar warming, followed by re-entry into torpor at sunset (Fig. 2). For inactive birds,  $T_{sk}$  rose above  $25^\circ\text{C}$  on 84% of bird-days in 1998–9. Torpor bouts by inactive birds averaged 22.7 hours and minimum  $T_{sk}$  averaged  $6.4^\circ\text{C}$ . It is noteworthy that torpor use, regardless of activity, was ubiquitous through the winter months; poorwills entered torpor on 98.4% of bird-nights between 1 December and 28 February.

Apart from poorwills, no animal of which we are aware remains mostly inactive in exposed situations through the winter, whether shaded or in the sun, although torpid fat-tailed antechinus (*Pseudantechinus macdonnellensis*) regularly bask in the morning and use the sun as an energy source for rewarming (Geiser

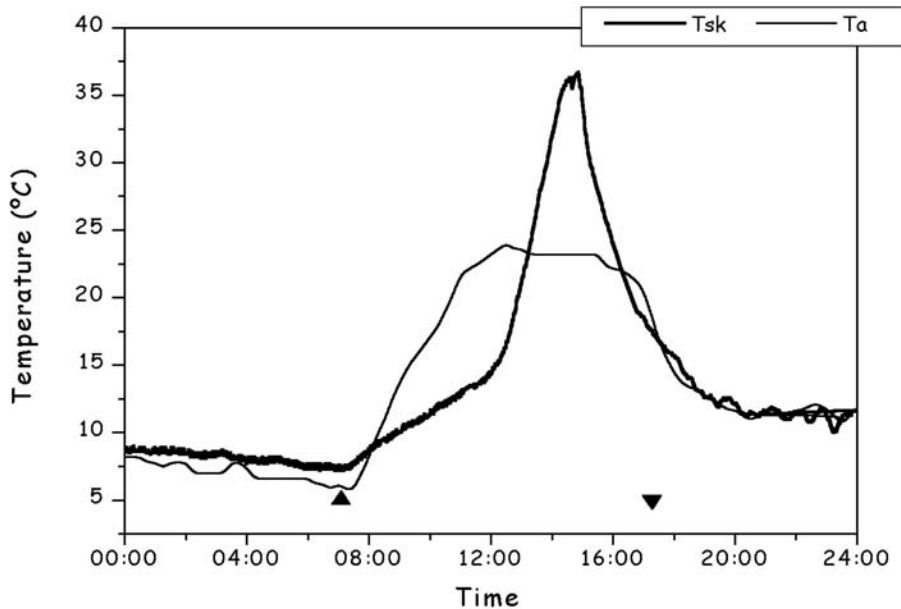


Fig. 2.  $T_{sk}$  (thick) and  $T_a$  (thin) on 1 Dec 1998 for a Common Poorwill in southern Arizona that remained entirely inactive at sunset. Triangles indicate sunrise and sunset time.

et al., 2002). Without exception, mammalian hibernacula are in sheltered locations. Passive daily arousal in poorwills then is likely an adaptation to the circumstances that characterize surface dormancy. Environmental conditions, microclimate, and sundry other factors are clearly more variable for an exposed animal than one in the protective confines of a burrow or cave. Consequently, poorwills that are passively warmed on a daily basis maintain the ability to become active quickly or to forage at dusk in response to changing circumstances with minimal energetic cost.

### The Evolution of Torpor and Inactivity by Poorwills

Factors that limit the range of bats and birds are intriguing because flight allows for the use of spatially discrete habitats. Migration permits breeding and non-breeding requirements to be satisfied in different, often widely separated environments. Perhaps owing to presumed simplicity, factors limiting the range of birds outside the breeding season have been relatively poorly studied. In winter,

torpor reduces the limitations that food availability imposes on where animals can survive, and it is apparently more common in birds than previously thought (McKechnie and Lovegrove, 2002). Why then have no birds other than poor-wills birds evolved deep or multiday bouts of torpor? We hypothesize that this physiological capability is an adaptation to a specialized diet of flying insects in an arid environment with limited productivity and was further selected for by interspecific competition with other similarly sized insectivores for prey in winter.

Poorwills have unique physiological adaptations that suggest a long association with hot, arid environments, including a wide thermoneutral zone, an efficient ratio of evaporative water loss to heat production, and white, unmarked eggs (unlike other caprimulgids) with a high solar reflectance (Bartholomew et al., 1962; Lasiewski, 1969; Ingels et al., 1984; Woods, 2002). What makes deserts important for torpor expression? Diapause, torpor, hibernation, migration, and other physiological or behavioral strategies moderate the effects of variation in habitat quality. Moreover, they occur partly in response to increasing variability in components of environmental quality most meaningful to animals living there. Consequently, selection for these strategies should be strongest in habitats where the extremes of variation, as well as their regularity or predictability, occur with the greatest frequency and severity. For example, few animals breeding in tropical regions migrate or hibernate, whereas few breeding in the arctic do not (cf. Newton and Dale, 1996). Arid places with low productivity are characterized by extremes of both temperature and the availability of food and water. These factors often vary daily and/or seasonally in a predictable manner and, consequently, these environments are full of animals that employ hibernation- or estivation-like strategies, which allow residence where conditions may otherwise be unsuitable for survival. Moreover, given the exposed roosts of inactive poorwills and the pattern of torpor bouts, frequent sunny winter days also appear important for overwintering poorwills. Regular solar radiation provides an energy source for passive rewarming not available to heterotherms in regions with long dark winters. Taken together, we propose that the relationship between  $T_a$  and the availability of flying insects at night, the variation in these factors both nightly and seasonally in arid regions, the low productivity of these regions, and the frequency of sunny days all selected for the evolution of multiday torpor bouts by poorwills.

Currently, our knowledge about torpor use by other desert-dwelling caprimulgids is limited. Caprimulgids are insectivores whose prey are uncommon during cold weather. Thus all temperate caprimulgids are migratory to



some extent. In North America, migratory poorwills presumably winter within the year-round range of resident birds in the southern United States and Mexico, and also overlap in southern portions of that range with other caprimulgids. Migrants must therefore compete with resident birds for limited food resources in northern portions of their winter range, and with other resident and migratory caprimulgids for those same resources farther south. Further competition may occur with migratory and resident insectivorous owls and bats, and owing to the geography of North and Central America, these animals are concentrated in a region during winter that is geographically much smaller than the region over which they breed.

Perhaps owing to similar foraging strategies, evidence for competitive displacement has been observed within North American caprimulgids and between them and bats (Bjorklund and Bjorklund, 1983/1984; Boyce, 1980; Brigham and Fenton, 1991; Caccamise, 1974; Shields and Bildstein, 1979; Stevenson et al., 1983). Poorwills are the smallest North American caprimulgid, and timid birds as well, and we occasionally observed poorwills leave foraging areas when bats arrived. It is thus plausible that they would be displaced in interactions with larger or more aggressive species, and poorwills probably moderate this competition by wintering north of the winter range of those species, where torpor use is necessary to balance long-term energy budgets. Consequently, historical overwinter survival was probably greater for northern birds that used torpor to lower energy requirements, and extended periods of inactivity likely developed as an extension of daily torpor bouts, as is evidenced by the daily arousal of inactive birds. A similar combination of factors may occur for other caprimulgids overwintering in arid regions, and other “hibernating” species may yet be documented. We propose that Spotted Nightjars in Australia (*Eurostopodus argus*), Band-winged Nightjars (*Caprimulgus longirostris*) in South America, and Freckled Nightjars (*Caprimulgus tristigma*) in southern Africa are candidates worthy of investigation.

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