

S22-3 Ecological correlates of torpor use among five caprimulgiform birds

R. Mark BRIGHAM¹, Christopher P. WOODS¹, Jeffrey E. LANE¹, Quinn E. FLETCHER¹, Fritz GEISER²

1. Dept. of Biology, University of Regina, Regina, SK S4S 0A2, CANADA; mark.brigham@uregina.ca;
ChrisWoods@velocity.net; jelane@ualberta.ca; fletcher@utsc.utoronto.ca

2. Dept. of Zoology, BBMS, University of New England, Armidale, NSW 2351, Australia; fgeiser@metz.une.edu.au

Abstract We review recent studies of torpor use by free-ranging caprimulgiform birds in North America and Australia: common poorwill (45 g), whip-poor-will (55 g), common nighthawk (80 g), Australian owlet-nightjar (50 g), and Tawny Frogmouth (500 g). Reproductive activity, ambient temperature, body size, and prey abundance influence the energy status of endotherms and may be correlated with torpor use under natural conditions; our review suggests that no one factor is most important. To date, most studies have been correlational in the wild, and experimental studies at multiple locales are now needed to resolve uncertainties concerning the evolutionary and ecological significance of torpor.

Key words Torpor, Caprimulgiformes, Ecology, Energetics, Temperature, Foraging

1 Introduction

Endothermy is a process of thermoregulation characterized by a high, controlled rate of heat production which helps mammals and birds maintain an elevated body temperature (T_b ; IUPS Thermal Commission, 2001). While a constant elevated T_b provides a thermally stable internal environment for optimizing physiological functions, it requires a metabolic rate (MR) 10–30 times (Nagy et al., 1999) greater than the standard MR of ectothermic reptiles. The cost is especially pronounced in small endotherms, which lose most endogenously produced heat to the environment (Song et al., 1998). To conserve energy or other resources, many mammals and a growing list of birds abandon normal elevated T_b . Such facultative heterothermy or torpor is a physiological state characterized by reduced MR and T_b . To date, the vast majority of studies have focused on the ability of mammals to reduce energy expenditure through daily or seasonal bouts of torpor (hibernation; Geiser and Ruf, 1995). Prolonged torpor of 1–3 weeks by hibernators typically occurs during winter at low ambient temperatures (T_a ; Geiser, 1998). In contrast to hibernation, daily torpor is employed at a variety of T_a s and throughout the year (Geiser, 1998).

Until recently, birds were thought to be less prone to use torpor than mammals (McKechnie and Lovegrove, 2002). Daily torpor has now been recorded from seven orders of birds, most commonly in hummingbirds (Trochilidae; Calder and Booser, 1973; Calder, 1994; Bech et al., 1997) and nightjars (Caprimulgiformes; Bartholomew et al., 1957; Peiponen, 1966; Reinertsen, 1983). In both orders, daily

torpor bouts typically last several hours, T_b dropping by 4–35°C and metabolic rate by 5%–90%. “Hibernation” has been anecdotally reported for only one species, the common poorwill (Jaeger, 1948; 1949). The factors that prompt birds to use torpor or hibernation, however, remain unclear.

Daily torpor and hibernation appear to be outwardly similar among birds and mammals, except for greater reported frequency in mammals (McKechnie and Lovegrove, 2002). Reinertsen (1983) postulated that the apparent rarity of torpor in birds might be related in part to migration, which allows them to avoid adverse weather conditions and prolonged food shortages. Geiser (1998) recently addressed the evolution of torpor and concluded that in birds, unlike mammals, it occurs in modern rather than ancestral orders, suggesting that it is not an ancestral avian condition. However, there are qualitative similarities in ecology, and morphology and physiology between heterothermic birds and mammals. For example, torpor in both groups appears most commonly in small, temperate-zone species that exploit a fluctuating food supply (e.g., nectar and insects; Reinertsen, 1983). This suggests that predictable ecological constraints, resulting in periodic energy shortfalls, represent important selection pressures for both groups.

Thus the purpose of our paper is to review hypotheses, drawn from the mammalian literature, concerning ecological, behavioral and morphological determinants that may account for patterns of torpor use by birds. We also review recent data for five species of free-ranging nocturnal caprimulgiforms and specifically address the influence of body size, T_a , prey availability, foraging strategy, and reproductive activity on torpor use (Table 1).

2 Torpor occurrence in five caprimulgiform birds

2.1 Common poorwill (*Phalaenoptilus nuttallii*)

Outside of the breeding season, bouts of daily torpor are routinely used by common poorwills (45 g) throughout their range in western North America (Brigham, 1992; Csada and Brigham, 1994; Woods, 2002). Both sexes typically forage for 30–240 minutes after dusk before entering torpor and remain in torpor throughout the night, foregoing a foraging bout at dawn. Torpor bouts typically last 8–12 h, with arousals triggered by increasing T_a the following morning. In Arizona, most birds use torpor when minimum T_a falls below 10°C; and there is a clear relationship between T_a and the abundance of flying insects (Woods, 2002). On a given night, however, some individuals remain euthermic whereas others fall into torpor (Brigham, 1992; Woods, 2002). Individuals of both sexes rarely enter torpor when incubating and brooding (Brigham, 1992; Kissner and Brigham, 1993; Csada and Brigham, 1994; Woods, 2002).

Jaeger (1948, 1949) reported that some poorwills in the southern California desert remain in the same location for weeks during winter, and was the first to suggest that they hibernate. French (1993) characterized such hibernation as “seasonal dormancy” based on individuals remaining inactive for prolonged periods without foraging. Woods (2002) followed radio-tagged birds near Tucson, Arizona, and found a range of thermoregulatory and behavioral responses to low T_a . Some individuals remained inactive for weeks without interruption. Inactive birds used deep torpor every day but invariably warmed to near euthermic levels on sunny days, principally due to exposure to solar radiation. However, when inactive birds were shaded to prevent solar exposure, birds aroused about every five days using endogenous heat, resembling the periodic arousal pattern of classic mammalian hibernators. This suggests that periodic arousals may be common to both birds and mammals, but that birds rely more on an exogenous heat source to facilitate re-warming and reduce arousal costs.

2.2 Common nighthawk (*Chordeiles minor*)

High mortality in captive birds forced into torpor (3 of 4; Lasiewski and Dawson, 1964), and a lack of evidence for it in free-ranging common nighthawks (80 g) in British Columbia, Canada (Firman et al., 1993), suggests that torpor is not used regularly by this species. Brigham et al. (1995) anecdotally reported torpor in two nighthawks, and

Fletcher et al. (in review) found two free-ranging birds in southwest Saskatchewan, Canada, using shallow torpor at night during late August prior to migration. Taken together, these observations suggest that while nighthawks can enter shallow torpor if stressed, they probably do not normally use heterothermy for conserving energy.

2.3 Whip-poor-will (*Caprimulgus vociferus*)

Whip-poor-wills (55 g) are marginally larger than poorwills and are found throughout deciduous woodlands in eastern North America. A short-term study in Ontario failed to record torpor (Hickey, 1993), but Lane (2002), working in southeast South Dakota, recorded occasional torpor use in spring (May) and fall (September) by both sexes, beginning at dawn. The lowest body temperature recorded was about 18°C. Passive re-warming by the sun appeared to be important but not essential for re-warming.

2.4 Australian owlet-nightjar (*Aegotheles cristatus*)

The Australian owlet-nightjar (50 g) is ubiquitous in Australian woodlands where it roosts in cavities that may offer protection from predators and greater thermal stability than exposed roosts (Brigham et al., 1998). Free-ranging birds regularly use shallow bouts of torpor during winter (May–September) near Armidale NSW (Brigham et al., 2000) but not during the breeding season (October to January). Like whip-poor-wills, owlet-nightjars rarely use torpor during normal activity at night; most (95%) torpor bouts begin at dawn (Geiser et al., this symposium).

No T_a threshold delineates days on which owlet-nightjars do or do not enter daytime torpor. The individual monitored over the winter of 1998 used torpor every morning for 64 consecutive days from June–August, despite variable minimum T_a s from –7 to 11°C (Brigham et al., 2001). The regularity of torpor implies that it is used for more than energetic emergencies (*sensu* Carpenter and Hixon, 1988). Night torpor was uncommon and then only on very cold nights ($T_a < 5^\circ\text{C}$). This, when combined with data on activity, suggests that foraging is profitable on most nights (Brigham et al., 1999).

2.5 Tawny frogmouth (*Podargus strigoides*)

Despite avoiding torpor in the laboratory (Bech and Nicol, 1999), free-ranging tawny frogmouths (500 g) regularly use shallow torpor in bouts about 7 hours after foraging at dusk (Körtner et al., 2000, 2001). At dawn, frogmouths re-warmed and resumed foraging or moved to new roosts and re-entered torpor (Körtner and Geiser, 1999). The mini-

Table 1 Summary of data on life history and thermoregulatory parameters for five free-ranging caprimulgiform birds

	Mass (g)	Roost	Foraging	Torpor use	Depth	Duration	Timing
Common poorwill	45	Ground	Sally	Common	Deep	> One day	Night
Whip-poor-will	55	Ground	Sally	Rare	Shallow	Hours	Morning
Common nighthawk	80	Ground/branch	Hawk	Very rare	Very shallow	Hours	Night
Aust. owlet-nightjar	50	Cavity	Sally/walk	Common	Shallow	Hours	Morning
Tawny frogmouth	500	Branch	Sally/pounce	Common	Shallow	Hours	Night

imum T_b of frogmouths was about 29°C. Its timing was markedly different from that in owlet-nightjars, although the studies were done at the same time of year at the same site.

3 Ecological determinants

3.1 Body size

It is generally thought that small animals are more likely to use deep torpor than large ones because of their large surface area to volume ratio (Geiser, 1998). This assumption is not supported by the data for tawny frogmouths (Körtner et al., 2000, 2001). Recent work on geese and pigeons corroborates the finding that large birds do use torpor (Butler and Woakes, 2001; Schleucher, 2001). These discoveries demonstrate that body size does not account for patterns of torpor in birds alone. Future studies of other large caprimulgidiform birds are imperative. Clearly, the energetic savings of torpor need to be treated as an integrative function because depth, duration and frequency of bouts all influence the energy savings. Thus, while deep torpor appears restricted to small endotherms, shallow bouts appear important for the energy budgets of larger species.

3.2 Breeding

The five caprimulgidiforms studied in the field to date rarely use torpor when nesting. It is not clear whether this reflects active avoidance of torpor by reproducing birds, or a consequential result of usually greater abundance of prey and more favorable weather during the nesting period. High concentrations of particular hormones (e.g., testosterone) were thought to be incompatible with the regular use of seasonal or daily torpor in mammals (Lee et al., 1990), although this does not appear true for bats, ecologically perhaps most similar to caprimulgids (Willis, 2006). In birds, prolonged bouts of torpor may compromise the development of embryos and chicks (Webb, 1987; Csada and Brigham, 1994), in connection with which the non-incubating member of a breeding pair will occasionally use torpor during the nesting period (Woods, 2002). Laboratory and field studies addressing torpor use by animals living in relatively non-seasonal climates will help to separate the effect of reproduction from T_a as proximate determinants of torpor use.

3.3 Foraging strategy

Of the five caprimulgidiforms so far known to use torpor naturally, four are strictly nocturnal; nighthawks are mostly crepuscular. Whip-poor-wills, poorwills and owlet-nightjars sally after prey, owlet-nightjars also searching for it while walking on the ground. Frogmouths commonly pounce on terrestrial arthropods while nighthawks catch flying insects on the wing. Apart from an insectivorous lifestyle, there is no obvious connection between torpor use and foraging strategy in these birds. Furthermore, foraging style does not explain the differences in timing of torpor bouts (Table 1). In this context, studies that address the importance of T_a and roost selection to facilitate passive re-warming are needed.

3.4 Ambient temperature and prey abundance

Among endotherms generally and in caprimulgidiforms specifically, torpor is assumed to represent an energy saving strategy to cope with low T_a . However, most studies have been conducted in temperate areas where it is difficult to separate T_a and prey abundance as proximate factors. Furthermore, most studies make no attempt to measure prey abundance. In a tantalizing experiment, Woods (2002) erected lights to create prey concentrations within the territories of poorwills. Despite a small sample size, he found that poorwills occupying territories with prey concentrations entered torpor less often than controls. Experimental studies like this, especially at sites that remain warm year-round, hold promise for teasing apart the ecological basis for torpor use.

In conclusion, this review suggests that no single ecological, behavioral or morphological factor single-handedly explains patterns of torpor observed in free-ranging birds. Rather, it seems that the interactive effects of a number of environmental and evolutionary constraints combine to shape avian heterothermy. We suggest that three approaches will be useful for future studies. First, experimental manipulations such as hormone treatment and shading of roosts, secondly, comparative studies of sympatric species to address the importance of phylogeny, and thirdly, data from tropical species and wide-ranging conspecifics.

Acknowledgements We gratefully acknowledge the financial support of the Natural Sciences and Engineering Research Council, Canada, and the Australian Research Council. G. Körtner, D. Gummer and C. Willis provided constructive comments on drafts of the paper.

References

- Bartholomew GA, Howell TR, Cade TJ, 1957. Torpidity in the white-throated swift, Anna hummingbird, and poor-will. *Condor* 59: 145–155.
- Bech C, Abe AS, Steffensen JF, Berger M, Bicudo JEPW, 1997. Torpor in three species of Brazilian hummingbirds under semi-natural conditions. *Condor* 99: 780–788.
- Bech C, Nicol SC, 1999. Thermoregulation and ventilation in the tawny frogmouth, *Podargus strigoides*: a low-metabolic avian species. *Aust. J. Zool.* 47: 143–153.
- Brigham RM, 1992. Daily torpor in a free-ranging goatsucker, the common poorwill (*Phalaenoptilus nuttallii*). *Physiol. Zool.* 65: 457–472.
- Brigham RM, Morgan KH, James PC, 1995. Evidence that free-ranging common nighthawks may enter torpor. *Northw. Nat.* 76: 149–150.
- Brigham RM, Debus SJS, Geiser F, 1998. Cavity selection for roosting and nesting, and roosting ecology of forest-dwelling Australian owlet-nightjars (*Aegotheles cristatus*). *Aust. J. Ecol.* 23: 424–429.
- Brigham RM, Gutsell RCA, Wiacek RS, Geiser F, 1999. Foraging behaviour in relation to the lunar cycle by Australian owlet-nightjars *Aegotheles cristatus*. *Emu* 99: 253–261.
- Brigham RM, Körtner G, Maddocks TA, Geiser F, 2000. Seasonal use of torpor by free-ranging Australian owlet-nightjars (*Aegotheles cristatus*). *Physiol. Biochem. Zool.* 73: 613–620.
- Butler PJ, Woakes AJ, 2001. Seasonal hypothermia in a large migrating bird: saving energy or fat deposition. *J. Exper. Biol.* 204: 1361–1367.
- Calder WA, Booser J, 1973. Hypothermia of broad-tailed hummingbirds during incubation in nature with ecological correlates. *Science* 180: 751–753.

- Calder WA, 1994. When do hummingbirds use torpor in nature? *Physiol. Zool.* 67: 1 051–1 076.
- Carpenter FL, Hixon MA, 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 90: 373–378.
- Csada RD, Brigham RM, 1994. Reproduction constrains the use of daily torpor by free ranging common poorwills (*Phalaenoptilus nuttallii*). *J. Zool. Lond.* 234: 209–216.
- Firman MC, Brigham RM, Barclay RMR, 1993. Do free-ranging common nighthawks enter torpor? *Condor* 95: 157–162.
- French AR, 1993. Hibernation in birds: comparisons with mammals. In: Carey C, Florant GL, Wunder BA, Horwitz B ed. *Life in the Cold: Ecological, Physiological and Molecular Mechanisms*. Boulder, Colorado: Westview Press, 43–53.
- Geiser F, 1996. Torpor in reproductive endotherms. In: Geiser F, Hulbert AJ, Nicol SC ed. *Adaptations to the Cold: Tenth International Hibernation Symposium*. Armidale, NSW: University of New England Press, 81–86.
- Geiser F, 1998. Evolution of daily torpor and hibernation in birds and mammals: importance of body size. *Clin. Expt. Pharm. Physiol.* 25: 736–740.
- Geiser F, Ruf T, 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol. Zool.* 68: 935–966.
- Geiser F, Körtner G, Maddocks TA, Brigham RM, 2006. Torpor in Australian Birds. In: Schodde R ed. *Proc. 23rd International Ornithological Congress, Beijing*. *Acta Zool. Sinica* 52(Suppl.): 405–408.
- Hickey MBC, 1993. Thermoregulation in free-ranging whip-poor-wills. *Condor* 95: 744–747.
- IUPS Commission on Thermal Physiology, 2001. *Glossary of terms for thermal physiology*, 3 edn. Japan. *J. Physiol.* 51: 245–280.
- Jaeger EC, 1948. Does the poorwill “hibernate”? *Condor* 50: 45–46.
- Jaeger EC, 1949. Further observations on the hibernation of the poorwill. *Condor* 51: 105–109.
- Kissner KJ, Brigham RM, 1993. Evidence for the use of torpor by incubating and brooding Common Poorwills *Phalaenoptilus nuttallii*. *Ornis Scan.* 24: 333–334.
- Körtner G, Geiser F, 1999. Roosting behaviour of the tawny frogmouth (*Podargus strigoides*). *J. Zool. Lond.* 248: 501–507.
- Körtner G, Brigham RM, Geiser F, 2000. Winter torpor in a large bird. *Nature* 407: 318.
- Körtner G, Brigham RM, Geiser F, 2001. Torpor in free-ranging tawny frogmouths (*Podargus strigoides*). *Physiol. Biochem. Zool.* 74: 789–797.
- Lane JE, 2002. Thermoregulation of Whip-poor-wills (*Caprimulgus vociferus*) under Natural and Laboratory Conditions. M.Sc. Thesis. Regina, SK: University of Regina.
- Lasiewski RC, Dawson WR, 1964. Physiological responses to temperature in the common nighthawk. *Condor* 66: 477–490.
- Lee TM, Pelz K, Licht P, Zucker I, 1990. Testosterone influences hibernation in golden-mantled ground squirrels. *Amer. J. Physiol.* 259: R760–R767.
- McKechnie AE, Lovegrove BG, 2002. Avian facultative hypothermic responses: A review. *Condor* 104:705–724.
- Nagy KA, Girard IA, Brown TK, 1999. Energetics of free-ranging mammals, reptiles and birds. *Ann. Rev. Nutr.* 19: 247–277.
- Peiponen VA, 1966. The diurnal heterothermy of the nightjar (*Caprimulgus europaeus*). *Ann. Acad. Sci. Fenn. Ser. A4 Biol.* 101: 1–35.
- Reinertsen RE, 1983. Nocturnal hypothermia and its energetic significance for small birds living in the arctic and subarctic regions. A review. *Polar Res.* 1: 269–84.
- Schleucher E, 2001. Heterothermia in pigeons and doves reduces energetic costs. *J. Therm. Biol.* 26: 287–293.
- Song X, Körtner G, Geiser F, 1998. Temperature selection and use of torpor by the marsupial *Sminthopsis macroura*. *Physiol. Behav.* 64: 675–682.
- Webb DR, 1987. Thermal tolerance of avian embryos: a review. *Condor* 89: 874–898.
- Willis CKR, 2006. Daily heterothermy by temperate bats in natural roosts. In: Kunz TH, Akbar Z, McCracken GF ed. *Functional and Evolutionary Ecology of Bats*. Proceedings of the 12th International Bat Research Conference, Univ. Kebangsaan Malaysia, Malaysia. Oxford: Oxford Univ. Press.
- Woods CP, 2002. Ecological Aspects of Torpor Use and Inactivity during Winter by Common Poorwills. Ph.D. Thesis. Regina, SK: University of Regina.