Chapter 16
Heterothermy in Caprimulgid Birds: A Review of Inter- and Intraspecific Variation in Free-Ranging Populations

R. M. Brigham, A. E. McKechnie, L. I. Doucette and F. Geiser

Abstract Caprimulgid birds represent one of the best studied endotherm taxa in terms of the occurrence of heterothermy in free-ranging populations. In this chapter, we review currently available data on heterothermy in this group, and examine potential ecological correlates of these responses. To date, heterothermic responses have been examined in at least one population of each of six species, ranging in body mass (M_b) from 40 to 450 g and occurring in habitats from deserts to mesic woodlands. Patterns of heterothermy vary from infrequent, shallow bouts to periods of uninterrupted torpor lasting several days, during which body temperature may be reduced below 5°C. Overall levels of heterothermy, as quantified using a recently proposed metric, do not show statistically significant relationships with M_b nor with ecological variables such as minimum air temperature or habitat aridity. Nevertheless, it is striking that the two most heterothermic species recorded to date, the Common Poorwill and the Freckled Nightjar, both inhabit arid habitats. Moreover, the former species remains the only bird known to hibernate. Within species, patterns of heterothermy may vary considerably among populations, with lunar cycles, temporal fluctuations in insect abundance and roost site characteristics being among the ecological determinants of heterothermy.

R. M. Brigham
Department of Biology, University of Regina, Regina, SK S4S 0A2, Canada
e-mail: mark.brigham@uregina.ca

A. E. McKechnie (✉)
DST/NRF Centre of Excellence at the Percy FitzPatrick Institute,
Department of Zoology and Entomology, University of Pretoria,
Private Bag X20, Hatfield, 0028, South Africa
e-mail: aemckechnie@zoology.up.ac.za

L. I. Doucette · F. Geiser
Centre for Behavioural and Physiological Ecology, Zoology,
University of New England, Armidale, NSW 2351, Australia

16.1 Introduction

Approximately 65% of extant endotherms are birds, yet heterothermic responses in this taxon have received considerably less attention than in mammals (Geiser and Ruf 1995; McKechnie and Mzilikazi 2011). Nevertheless, the available evidence suggests that heterothermy is widespread among birds, with approximately 100 species representing 11 orders (including the Caprimulgiformes, Coraciiformes, Coliiformes, Apodiformes, Trochiliformes, Columbiformes and Passeriformes) known to facultatively reduce body temperature (T_b) below normothermic levels (i.e. rest-phase T_b observed at thermoneutral environmental temperatures) (McKechnie and Lovegrove 2002). Nearly all these species employ either daily torpor (substantial reductions in T_b accompanied by lethargy and reduced responsiveness), or shallower reductions of rest-phase T_b during which behavioural responses to stimuli are retained (Prinzinger et al. 1991); hibernation has been reported for only one species, the Common Poorwill.

In terms of heterothermy, the order Caprimulgiformes is one of the best studied avian taxa. Traditionally, the Caprimulgiformes consist of the frogmouths, potoos, Oilbird, nightjars, eared-nightjars and owlet-nightjars (Holyoak 2001), although Sibley and Ahlquist (1990) placed these families within the Strigiformes alongside the owls, and recent work has raised the possibility that the owlet-nightjars may in fact be more closely related to swifts than to the other caprimulgid families (Hackett et al. 2008; Mayr 2002). Although there are avian taxa (such as the hummingbirds) for which data on heterothermy are available for more species than is the case for the caprimulgids, what sets the latter group apart in terms of our current knowledge of avian heterothermy is the number of detailed studies involving free-ranging populations (Table 16.1). Thus, data on the caprimulgids present a valuable opportunity to investigate the ecological correlates of avian heterothermy in inter- and intraspecific analyses, and understand the significance of these responses for wild birds in their natural habitats.

Several ecological factors are thought to be broadly responsible for the widespread use of heterothermy in caprimulgids. First, most species are nocturnal aerial insectivores, and the availability of prey is thus strongly dependent on variables such as air temperature and rainfall (Ashdown and McKechnie 2008; Jetz et al. 2003; Rydell et al. 1996). Second, caprimulgids are visually orientating predators, and foraging opportunities are severely reduced during periods with low ambient light levels (Ashdown and McKechnie 2008; Jetz et al. 2003). Third, the foraging activity of caprimulgids may be constrained by the risk of predation (Brigham et al. 1999; Woods and Brigham 2008). Since caprimulgids are a cosmopolitan group that occur on all continents except Antarctica, inhabit habitats ranging from tropical rainforest to deserts and vary in body mass (M_b) by more than an order of magnitude (<40–600 g, Holyoak 2001), this taxon offers rich opportunities to test predictions concerning ecological determinants of heterothermy.

The data available in 2002 regarding ecological correlates of caprimulgid heterothermy were qualitatively reviewed by Brigham et al. (2006). However, the

Table 16.1 Summary of attributes of heterothermic responses by seven species of Caprimulgiform birds

Species	Body mass (g)	Use	Period	Min. T_b (°C)	Duration	Timing	Location[a]	References
Common Poorwill (*Phalaenoptilus nuttallii*)	40–45	Common (all year)	Night/day	3–5	h-days	All but summer	AZ, BC, SK N. America	French (1993); Brigham (1992); Woods (2002); Woods and Brigham (2004)
Australian Owlet-nightjar (*Aegotheles cristatus*)	40–50	Common	Day	20	4–8 h	Winter (all year)	NSW, NT Australia	Brigham et al. (2000); Doucette et al. (2011, 2012)
Whippoorwill (*Caprimulgus vociferus*)	50–55	Rare	Day	20	3–8 h	Spring, fall (spring-fall)	ON, SD N. America	Hickey (1993); Lane et al. (2004)
European Nightjar (*Caprimulgus europaeus*)[b]	54–82	Rare	Day	7	9–12 h	Spring, fall (spring-fall)	Finland	Peiponen (1965, 1966)
Freckled Nightjar (*Caprimulgus tristigma*)	73–81	Common	Night/day	10	2–8 h	Winter (winter)	NC, NW South Africa	McKechnie et al. (2007); Smit et al. (2011)
Common Nighthawk (*Chordeiles minor*)	75–85	V. rare	Night/day	25	<8 h	Fall (spring-fall)	BC, SK N. America	Firman et al. (1993); Fletcher et al. (2004)
Tawny Frogmouth (*Podargus strigoides*)	350–550	Common	Night	29	3–11 h	Winter (winter)	NSW Australia	Körtner et al. (2000, 2001)

Use is a qualitative assessment of the frequency of heterothermy based on the number of days it was recorded. *Period* represents the most common time of the 24h cycle for heterothermy. *Min* T_b is the lowest body or skin temperature recorded by any individual during the study(-ies). *Duration* is the length of typical heterothermic bouts. *Timing* is the period of the year when torpor was recorded followed by the period when the study occurred in parentheses. *Location* refers to the province or state and/or country where the study(-ies) took place

[a] *AZ* Arizona, *BC* British Columbia, *SK* Saskatchewan, *NSW* New South Wales, *NT* Northern Territory, *ON* Ontario, *SD* South Dakota, *NC* Northern Cape, *NW* Northwest Province

[b] Data collected under semi-natural conditions

subsequent decade has seen an increase in the number of studies on free-ranging populations, and has also seen new data on intraspecific variation in heterothermy among populations that differ in factors such as habitat aridity. Moreover, a recently proposed comparative metric [Heterothermy index (HI), Boyles et al. 2011] provides a quantitative index of overall levels of heterothermy, allowing for statistical analyses that were previously not available. HI is calculated using an equation similar to that for standard deviation, and increases with increasing depth and/or duration of heterothermic bouts (Boyles et al. 2011). Values range from 0°C when T_b is perfectly stable, to approximately 40°C in a continuously hibernating animal in which T_b is 40°C lower than normothermic T_b. Our aims are to review currently available data on heterothermy in free-ranging caprimulgids, and examine potential ecological correlates of these responses. As the relatively small number of species investigated (and the large gap in M_b between the Tawny Frogmouth and the other species) imposes constraints on the statistical power of these analyses, we intend this to be an exploratory analysis aimed at developing hypotheses that need to be addressed in future.

16.2 Materials and Methods

16.2.1 Heterothermy Data

We surveyed the literature for studies on thermoregulation in free-ranging caprimulgids, and obtained data on variables such as M_b, minimum T_b and study location (Table 16.1). For context we also include information about European nightjars which have been the focus of some field work, albeit in semi-natural conditions with birds deprived of food (Peiponen 1965, 1966). Data from this species were not included in the HI analysis. For each study population, we calculated an average HI value (Boyles et al. 2011) from T_b or skin temperature (T_{skin}) traces, with a mean daily HI value calculated for each individual for which data were available, and an overall mean then calculated for each study population (Table 16.2). For each species, HI was calculated for the daily period during which heterothermic bouts typically occurred, rather than the full 24 h (Table 16.2). We opted to use this approach for two reasons. First, in many studies, data collection was biased towards periods of heterothermy and far fewer data were available from normothermic birds (one reason being that normothermic birds were active and away from roost sites). Second, the HI integrates T_b or T_{skin} both below and above the modal value, and we wanted to minimise the likelihood of HI values being inflated by artificially high normothermic T_{skin} values resulting from solar irradiance on backpack-mounted transmitters during the day. In the case of the Common Poorwill, an average HI value for hibernating birds was calculated by extracting and digitising data from Fig. 8.6 in Woods (2002), and modal normothermic T_b was taken as the average maximum T_b achieved during spontaneous arousal by shaded individuals (33.4°C; Woods 2002).

Table 16.2 Heterothermy index (HI), body mass and environmental variables [aridity index (Q, Emberger 1955) and mean daily minimum air temperature during the coldest month of the year (data from www.worldclimate.com)] for eight caprimulgid taxa

Species/population	Body mass (g)	Aridity index (Q)	Minimum T_a (°C)	HI (n)	Source
Common Poorwill	42.5	212	3.6	20.29[a]	Woods (2002)
Australian Owlet-Nightjar (Alice Springs)	42.3	212	4	4.87 (5)	Doucette et al. (2011, 2012)
Australian Owlet-Nightjar (Armidale)	50.1	1071	0.4	5.40 (6)	Doucette et al. (2011), Brigham et al. (2000)
Whippoorwill[b]	52.5	636	3.2	4.04 (8)	Lane et al. (2004)
Freckled Nightjar (western)	73	224	6.8	7.73 (6)	Smit et al. (2011)
Freckled Nightjar (eastern)	81	677	2.9	4.86 (5)	McKechnie et al. (2007)
Common Nighthawk[b]	83	417	0.5	2.50 (3)	Fletcher et al. (2004)
Tawny Frogmouth	453	1071	0.4	3.42 (8)	Körtner et al. (2001)

[a] Calculated from average trace
[b] Not included in analyses of relationships between HI and environmental variables

16.2.2 Climate Variables

For each population studied, the following historical climate data were obtained from the nearest weather station (www.worldclimate.com): mean annual precipitation (MAP, mm), mean maximum air temperature of the hottest month (T_{max}, °C) and mean minimum air temperature of the coldest month (T_{min}, °C). These data were used to calculate the aridity index $Q = MAP/((T_{max} + T_{min})(T_{max} - T_{min})) \times 1000$ (Emberger 1955), following Tieleman et al. (2003).

16.2.3 Statistical Analyses

The small number of taxa involved here makes it impossible to reliably test for a phylogenetic signal within our data set (Blomberg et al. 2003). Because all the species in this analysis are within the same order, and because of the exploratory nature of this analysis, we analysed the data using conventional (i.e. non-phylogenetically independent) statistics only.

16.3 Results and Discussion

16.3.1 Interspecific Variation

The caprimulgid species for which thermoregulation has been investigated in free-ranging populations have all been found to exhibit reductions in T_b below normothermic levels. However, the extent of heterothermy varies widely among
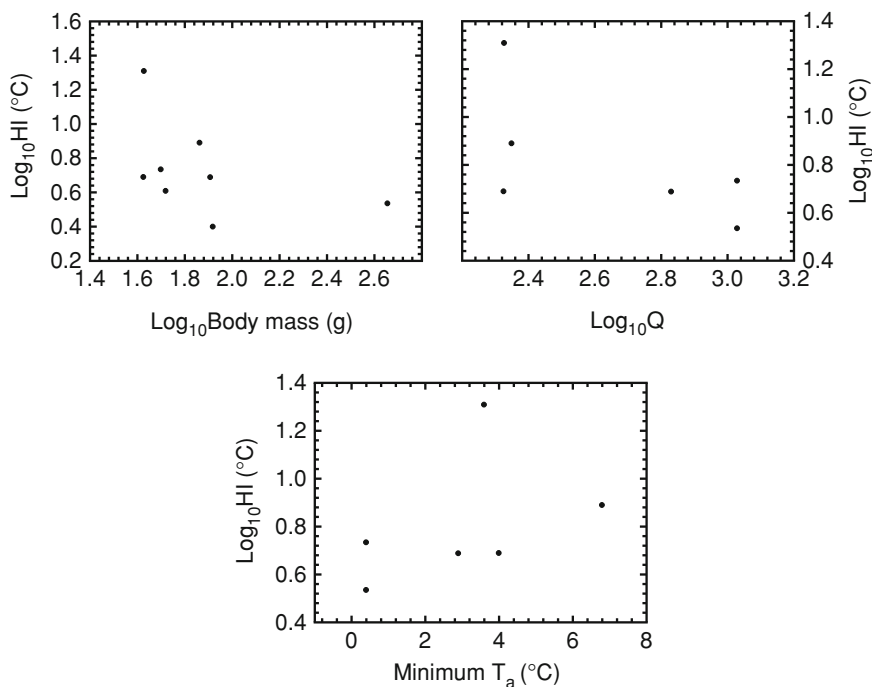
Fig. 16.1 Heterothermy index values for caprimulgids were not significantly related to M_b, aridity index (Q) nor the mean daily minimum air temperature (T_a) for the coldest month of the year. The latter two analyses included only winter studies on non-migratory populations

species, with HI values ranging from 2.5°C in Common Nighthawks to 20.3°C in Common Poorwills (Table 16.2). This variation reflects large differences in the frequency, depth and duration of heterothermic bouts; the former species employed heterothermy infrequently and reduced T_b by only 5–15°C (Fletcher et al. 2004), whereas the latter species exhibited deep, continuous hibernation during winter and reduced T_b to as low as 3°C (Woods 2002, Woods and Brigham 2004). European Nightjars also employ deep torpor, but we have not included this species in our quantitative analysis as the only data available originate from captive birds held under semi-natural conditions (Peiponen 1965, 1966).

The caprimulgid species investigated to date vary approximately tenfold in M_b from 40–450 g (Tables 16.1, 16.2). There does not appear to be any consistent relationship between M_b and HI; neither a linear nor logarithmic regression model fitted to $\log_{10}M_b$ and $\log_{10}$HI data yielded a significant fit (linear: $F_{1,6} = 1.450$, $P = 0.274$, logarithmic: $F_{1,6} = 1.723$, $P = 0.235$; Fig. 16.1). Thus, we compared HI values directly (as opposed to using residuals) with climatic variables for further analyses.

In addition to M_b, the species/populations for which data are available vary widely in the latitude and the climatic characteristics of their habitat (Table 16.2). For the six non-migratory taxa for which heterothermy has been examined during winter (i.e. excluding Common Nighthawks and Whippoorwills), $\log_{10}$HI did not show a significant relationship with either average daily minimum temperature during the coldest month of the year ($F_{1,4} = 0.905$, $P = 0.395$; Fig. 16.1) nor with aridity ($\log_{10}Q$, $F_{1,4} = 2.661$, $P = 0.178$; Fig. 16.1). Despite the latter non-significant result, we would argue that habitat aridity may in fact be the variable to pursue further as a climatic correlate of interspecific variation in heterothermy in caprimulgid birds. It is noteworthy, for instance, that the two taxa with the highest HI values in our data set (Common Poorwills, HI = 20.3°C and western Freckled Nightjars, HI = 7.7°C) both occur in desert habitats. Possible correlations between heterothermy and factors such as gender and foraging mode were reviewed by Brigham et al. (2006), with no clear patterns evident.

The Common Poorwill remains the only species known to employ both daily and seasonal bouts of heterothermy (i.e. short bouts of torpor as well as hibernation (Brigham 1992; Woods 2002; Woods and Brigham 2004), and $T_b < 5$°C has been reported in this species, the lowest for any bird. Jaeger's (1948, 1949) early contention that this species is the only bird capable of hibernation has thus been supported by subsequent work (French 1993; Woods and Brigham 2004).

In addition to variation in the depth, duration and frequency of heterothermy, the timing of bouts also varies considerably among species. For example, Australian owlet-nightjars in New South Wales, Australia use torpor mostly during the morning (rest phase), whereas Tawny Frogmouths at the same site most commonly enter torpor at night (active phase) after an evening foraging bout (Brigham et al. 2000; Körtner et al. 2000, 2001). There is evidence that some species employ passive re-warming near midday, and may re-enter torpor in the afternoon prior to activity (Doucette et al. 2012; Körtner et al. 2001; McKechnie et al. 2007; Woods 2002).

Heterothermy appears to be used by both sexes in most species, although the data available to directly evaluate sex differences are extremely limited. Data for Common Poorwills, Whippoorwills and Australian owlet-nightjars during the reproductive season suggest that heterothermic responses, while uncommon, do nevertheless occasionally occur (Kissner and Brigham 1993; Csada and Brigham 1994; Brigham et al. 2000; Woods 2002; Lane et al. 2004). However, the reproductive period typically encompasses the warmest parts of the year when insect prey tends to be most common, and furthermore most studies have been conducted during periods outside the reproductive season. It is commonly argued that the decrease in T_b that accompanies reduced metabolic rates is incompatible with incubation and brooding, but this has not been evaluated directly.

A priori, T_a would seem a likely candidate variable to predict the occurrence of heterothermy, since the availability of aerial insects is strongly temperature-dependent (Ashdown and McKechnie 2008; Rydell et al. 1996). Whereas some published studies have suggested there is an association between T_a and the occurrence of heterothermy in caprimulgids (Brigham 1992; Csada and Brigham 1994;

Körtner et al. 2001), other studies suggest the opposite. For instance, heterothermy in Freckled Nightjars at an arid winter-rainfall site in western South Africa was much more strongly correlated with lunar cycles (i.e. light availability) than T_a, although the latter was nevertheless a significant predictor of heterothermy in a colder, drier year (Smit et al. 2011). On the other hand, several studies have revealed considerable variation among individuals at any given time at a particular site, with some individuals entering deep torpor while others remain normothermic. Thus, all that can reliably be concluded from the data currently available is that the ecological determinants of heterothermy vary across taxa.

16.3.2 Intraspecific Variation

All the caprimulgid species discussed above, with the exceptions of the European Nightjar and Tawny Frogmouth, have been investigated at more than one location (Table 16.3), and variation in the environmental correlates and patterns of heterothermy within species has the potential to shed considerable light on the proximate and ultimate determinants of these responses.

In Common Nighthawks and Whippoorwills, some populations exhibited heterothermy whereas others did not (Table 16.3). In the remaining species, however, populations differed in the type and/or environmental correlates of heterothermy. In South Africa, Freckled Nightjars at a winter-rainfall site exhibited patterns of winter heterothermy that were strongly correlated with lunar phase. As the lunar cycle progressed towards full moon, heterothermy became less pronounced, and then increased in frequency and depth as nights became progressively darker around new moon (Smit et al. 2011). Moreover, entry into and re-warming from torpor was tightly linked to moonset and moonrise respectively (Smit et al. 2011). In contrast, conspecifics at a cooler, summer-rainfall site (Rustenburg) did not show any obvious relationship between winter heterothermy and lunar phase, and moreover heterothermy was exhibited by some individuals but not others (McKechnie et al. 2007). In spite of substantial evidence that owlet-nightjars, poorwills and Whippoorwills are able to increase activity (and presumably foraging) during periods of the lunar cycle with more light (Brigham and Barclay 1992; Brigham et al. 1999, Mills 1986; Woods and Brigham 2008), there is no clear evidence that any of these three species adjust heterothermic responses in response to lunar conditions.

Common Poorwills investigated at four sites exhibited broadly similar patterns of heterothermy (Table 16.3). Data collected from spring through autumn for a considerable number of individuals suggest that heterothermic responses are commonly employed by both sexes after foraging bouts at dusk (except during the breeding season), and with no obvious effect of T_a, insect availability or the lunar cycle (Brigham 1992; Csada and Brigham 1994; Woods 2002; Woods and Brigham 2004). Prolonged, multi-day torpor has been recorded during winter only at a site north of Tucson. The latter population is the only non-migratory

Table 16.3 Summary of intraspecific variation in heterothermy in caprimulgid birds

Species	Sites	Migrant?	Variation in heterothermy
Common Nighthawk	Okanagan Valley	Migrant	No evidence of heterothermy, despite poor conditions and some individuals starving to death[a]
	Cypress Hills	Migrant	Short, shallow torpor bouts[b]
Whippoorwill	Ontario	Migrant	No evidence of heterothermy[c]
	South Dakota	Migrant	Occasional torpor bouts[d]
Freckled Nightjar	Rustenburg	Non-migrant	Frequent torpor by some individuals but not others during winter; no obvious relationship to lunar cycles[e]
	Namaqualand	Non-migrant	Frequent torpor by all individuals during winter; strongly related to lunar cycles[f]
Common Poorwill	Okanagan Valley	Migrant	Frequent deep torpor (typically <8 h duration) during summer[g]
	Cypress Hills	Migrant	Frequent deep torpor (typically <8 h duration) during summer[h]
	30 km N of Tucson	Non-migrant	Frequent deep torpor (typically <8 h duration) during summer, hibernation during winter[i,j]
	100 km SE of Tucson	Migrant	Frequent deep torpor (typically <8 h duration) during summer[i,j]
Australian Owlet-Nightjar	Armidale	Non-migrant	Frequent torpor during winter[k,l]
	Ormiston Gorge	Non-migrant	Frequent torpor during winter; torpor is significantly more frequent in individuals roosting in tree hollows compared to rock crevices[l,m]
	Alice Springs (irrigated site)	Non-migrant	Frequent torpor during winter; torpor is significantly more frequent in individuals roosting in tree hollows compared to rock crevices[l,m]

[a] Firman et al. (1993), [b] Fletcher et al. (2004), [c] Hickey (1993), [d] Lane et al. (2004), [e] McKechnie et al. (2007), [f] Smit et al. (2011), [g] Brigham (1992), [h] Csada and Brigham (1994), [i] Woods (2002), [j] Woods and Brigham (2004), [k] Brigham et al. (2000), [l] Doucette et al. (2012), [m] Doucette et al. (2011)

population so far investigated, raising the question of whether migratory tendency is a factor in the expression of heterothermy. The fact that heterothermic patterns during spring, summer and autumn are similar in migratory populations in Canada and Arizona suggests little influence, but it remains unknown whether, like the non-migratory Arizona population, these birds use multi-day torpor on their wintering grounds.

Perhaps the most instructive data set for a species studied at multiple locations is for the Australian owlet-nightjar, which has been the focus of projects conducted near Armidale in northern New South Wales (Brigham et al. 2000) and at two sites 150 km apart near Alice Springs in the Northern Territory (NT, Doucette et al. 2011; Doucette et al. 2012). One NT site is natural (Ormiston Gorge, MacDonnell Ranges), whereas the other (Alice Springs Desert Park) has been irrigated to promote re-establishment of native vegetation. At all three sites, data are available from more than 1 year for a number of individuals. Individuals from all three populations are sedentary. Ecologically, there are differences between the populations. In NSW, owlet-nightjars roost and nest in the cavities of intact trees and stumps in a small remnant of relatively moist forest. In contrast, at both NT sites, birds use both tree cavities and rock crevices (Doucette et al. 2011). Different individuals seem to have preferences for the type of roost they use with some using only one type and some both (Doucette et al. 2011). Torpor occurs during winter (May–September) at all study sites and the depth, duration and frequency are similar in an overall sense. However, roost site choice by birds in the NT is a highly important predictor of torpor use. Birds roosting in rock crevices are buffered from fluctuations in T_a and use torpor much less (about half as often) than birds roosting in tree cavities which were less buffered from daily variation in T_a. Perhaps most interesting, birds roosted in tree cavities on about 2/3rds of tracking days, which may imply a benefit of tree roosts where torpor is used more. Doucette et al. (2011) suggested that a reduced risk of predation and lower costs of arousal because of the ability to passively re-warm by birds roosting in trees may be among the reasons. Doucette et al. (2012) noted that the three habitats of their study differed in annual T_a, rainfall and arthropod abundance. They found that torpor frequency, depth and duration were greatest during years and at sites with lower arthropod abundance, although there was a strong correlation between arthropod abundance and environmental variables. These data provide evidence that direct measures of food availability can be used to predict heterothermic responses.

16.4 Emerging Questions and Future Directions

The steadily increasing body of data on caprimulgid heterothermy has provided key insights into the ecological significance of this phenomenon, both within this taxon and in endotherms in general. These data, however, also raise numerous questions regarding the ecological determinants of these responses. Why, for instance, do many caprimulgids exhibit only shallow heterothermy and short

bout lengths? Some species, such as Australian Owlet-Nightjars and Tawny Frogmouths, exhibit "W"-shaped patterns of T_b consisting of two short bouts interrupted by a re-warming phase, a pattern that is presumably less energetically efficient than a single, longer bout. Similarly, variation between and within species in patterns of heterothermy remains poorly understood—why do some individuals at a particular site enter deep torpor while others remain normothermic?

We would argue that one of the most productive future lines of research on caprimulgid heterothermy would involve experimental manipulations of energy balance. Caprimulgids are not generally suitable subjects for laboratory studies, and the focus would need to be on free-ranging individuals. Energy supply can be experimentally increased using artificial light; Woods and Brigham (2004) showed that patches of high insect density created by erecting lights in the territories of poorwills led to changes in patterns of heterothermy. This approach could readily be used for many species to explore the role of prey availability on patterns of heterothermy. Artificially increasing energy demand is more challenging, but could be achieved by increasing heat loss rates via removal of patches of feathers, or by increasing costs of locomotion via the clipping of flight feathers (e.g. Tieleman et al. 2008) or the attachment of additional mass (e.g. Hughes and Rayner 1991). Such studies could greatly increase our understanding of the factors responsible for variation in heterothermy among individuals within a species.

A key gap in our current understanding of heterothermy in caprimulgids concerns the energetic consequences of heterothermy; while there is little question that heterothermy reduces energy and water demands, the savings associated with these responses under natural conditions have yet to be quantified. Caprimulgids may prove relatively tractable subjects for measurements of energy expenditure using doubly labeled water—they are generally territorial, respond readily to play-back and can be caught using a variety of methods, factors that make it easier to re-capture birds after 24 or 48 h (Speakman 1997). Alternatively, heart rate telemetry may also prove a feasible approach for quantifying energy savings associated with heterothermy, although this method requires careful laboratory calibrations of heart rate—oxygen consumption relationships (Butler et al. 2004). Measurements of metabolic rate and water turnover will provide vital information for understanding when and why individuals use heterothermy.

While descriptive studies may not appear to be particularly imaginative, investigations of the occurrence of heterothermy in more caprimulgid species, particularly in tropical regions (such as South America and southeast Asia) have the potential to significantly improve our understanding of ecological determinants of heterothermy in this group, particularly if they involve species that are carefully selected on the basis of their habitat characteristics. Furthermore, such studies will be vital for answering the interesting question of whether the Common Poorwill is indeed the only avian hibernator. More work is also required during reproductive periods, as well as establishing when heterothermic responses first appear in young birds, particularly since foraging efficiency is often lower in juvenile birds compared with adults (Weathers and Sullivan 1989) and juvenile caprimulgids might a priori be expected to experience more severe energy stress.

Finally, a key set of questions that need to be answered before we can gain a better understanding of caprimulgid heterothermy concerns the costs of these responses. Although increased vulnerability to predation is widely accepted as being one of the key ecological costs of heterothermy, at least for animals occupying exposed roost sites, virtually no data other than anecdotes are available. Studies comparing heterothermy among caprimulgid populations that vary in predation risk and/or experimental manipulations of perceived predation risk could provide key insights into ecological determinants of these responses.

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