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Seasonal variation in thermal energetics of the Australian owlet-nightjar (*Aegotheles cristatus*)

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ABSTRACT

Many birds living in regions with seasonal fluctuations in ambient temperatures (T_a) typically respond to cold by increasing insulation and adjusting metabolic rate. Seasonal variation in thermal physiology has not been studied for the Caprimulgiformes, an order of birds that generally have basal metabolic rates (BMR) lower than predicted for their body mass. We measured the metabolic rate and thermal conductance of Australian owlet-nightjars (*Aegotheles cristatus*) during summer and winter using open-flow respirometry. Within the thermoneutral zone (TNZ; 31.3 to 34.8 °C), there was no seasonal difference in BMR or thermal conductance (C), but body temperature was higher in summer- (38.2 ± 0.3 °C) than winter-acclimatized (37.1 ± 0.5 °C) birds. Below the TNZ, resting metabolic rate (RMR) increased linearly with decreasing T_a , and RMR and C were higher for summer- than winter-acclimatized birds. The mean mass-specific BMR of owlet-nightjars ($1.27 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was close to the allometrically predicted value for a 45 g Caprimulgiformes, but well below that predicted for birds overall. These results suggest that owlet-nightjars increase plumage insulation to cope with low winter T_a , which is reflected in the seasonal difference in RMR and C below the TNZ, rather than adjusting BMR.

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1. Introduction

Thermoregulatory responses of birds to cold can include increasing insulation, behavioural thermoregulation, and augmenting heat production (Calder and King, 1974). Some species have a reduced thermal conductance (C) in winter partially due to increased plumage insulation and, in some cases, subcutaneous fat (Swanson, 1991; Cooper, 2002; Lill et al., 2006). However, birds may be limited in the degree to which they can increase plumage and fat deposits (Scholander et al., 1950), presumably due to the necessity of maintaining a body mass that allows for efficient flight. Thus, increasing insulation in winter may not be adequate to offset the added energetic costs of maintaining a high body temperature (T_b) at low ambient temperatures (T_a). It has been proposed that many species can only achieve a thermal balance during winter by adjusting heat production and basal metabolic rate (BMR; Calder and King, 1974), yet the relationship of BMR to seasonal acclimatization remains unclear. BMR does not change consistently with season in small birds, but may vary with the severity of the thermal climate (Swanson, 1991; Cooper and Swanson, 1994; Liknes et al., 2002) and body or organ masses (Daan et al., 1990; Piersma, 2002).

In Australia, the few studies on seasonal variation of bird thermal physiology have all been restricted to small diurnal passerines

weighing less than 15 g. The outcome of these studies are conflicting, with species inhabiting arid climates increasing their BMR during winter (Collins and Briffa, 1983; Ambrose and Bradshaw, 1988), while those in mesic regions with greater seasonal variation in T_a exhibiting no seasonal variation or a lower winter BMR (Maddocks and Geiser, 2000; Lill et al., 2006). This contrasts with most studies on birds in North America where winter BMR is generally higher than summer BMR (Pohl and West, 1973; Cooper and Swanson, 1994; Liknes et al., 2002). Resting metabolic rate (RMR) and thermal conductance below the thermoneutral zone (TNZ) were lower in winter for the two Australian species in which it was measured (Maddocks and Geiser, 2000; Lill et al., 2006). The body mass (BM) of passerines in these studies did not differ seasonally or was only slightly higher for birds during winter (Maddocks and Geiser, 2000; Lill et al., 2006).

Australian owlet-nightjars (*Aegotheles cristatus*; 45 g) are sexually monomorphic birds of the order Caprimulgiformes whose range encompasses all of Australia, including Tasmania. Owlet-nightjars are sedentary nocturnal insectivores that roost singly in cavities year round. Caprimulgiformes is one order of birds containing species which have lower BMRs than expected from BM and allometric equations (Bennett and Harvey, 1987), and are one of the few orders of birds capable of reducing metabolic rate (MR) and T_b during torpor (Brigham et al., 2000; McKechnie and Lovegrove, 2002). Our aim was to determine whether the BMR of one species of owlet-nightjar (*Aegothelidae*) was comparable to other families of Caprimulgiformes and whether its thermal physiology varied with season in a region that experienced a substantial disparity in seasonal T_a . Ours is the first

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study to assess seasonal variation in thermal energetics for a species of Caprimulgiformes and to measure the BMR for a species of the family Aegothelidae.

2. Material and methods

2.1. Experimental procedures

Open-flow respirometry was used to measure the MR of owl-nightjars at T_a s ranging from 0 to 35 °C during summer and winter. The owl-nightjars used in this study were captured at Imbota Nature Reserve (30° 35' S, 151° 45' E, 1000 m elevation), 10 km southeast of Armidale on the Northern Tablelands, New South Wales during summer (December 2005 to February 2006) and winter (June to August 2006). The mean daily minimum and maximum temperatures for Armidale are 13.0 °C and 26.6 °C in summer and 1.0 °C and 13.2 °C in winter (1857–1997, Australian Bureau of Meteorology). Mean monthly rainfall in summer (93.8 mm) is almost double of that in winter (51.5 mm).

Individual owl-nightjars were captured in the evening by broadcasting taped conspecific calls to lure individuals into mist-nets. After capture birds were immediately transported to the laboratory and kept in dark boxes overnight. Metabolic experiments commenced the following morning. Only one bird was measured at a time, except for one occasion when two birds were caught simultaneously and measured together (separate chambers) the following day. As there are no external characteristics which can reliably identify gender of owl-nightjars, the sex of birds was later determined based on DNA extracted from chest feathers (Genetic Science Services, Fitzroy, VIC; Griffiths et al., 1998). The sex of two birds could not be determined, thus these birds were excluded from analysis by gender. Birds were examined for signs of feather moult and details of stage and location of moulting feathers recorded. All summer birds were caught after the completion of the breeding season (February), with the exception of one individual caught in late December whose young were known to have fledged successfully the previous week.

BM was measured for each bird at the start and end of the experiment and a linear rate of mass loss was assumed for calculation of mass-specific MR. Cloacal temperatures for measurement of core T_b were measured at the start and end of each experiment and at each major change in T_a using a pre-calibrated fine thermocouple inserted 1.5 to 2 cm into the cloaca and read with an Omega digital thermometer accurate to within ± 0.1 °C (Model HH-71T, Omega Engineering Inc., Stamford, CT, USA).

Seven adult owl-nightjars were measured in summer and six in winter. Owl-nightjars were placed in the chamber at 8:00 h. Birds were not fed and were post-absorptive, given that at least 10 h had elapsed since their last potential feed (prior to latest capture at 22:00 h). T_a (± 0.1 °C) was measured using a thermocouple inserted 1 cm into the respirometry chamber. The thermocouple signal was amplified and recorded with an Omega multiplex thermocouple thermometer (DP 116, Omega Engineering Inc., Stamford, CT, USA). T_a was increased every ~ 2 h to record MR at 0 °C, 8 °C, 17 °C and 28 °C. During the final 2 h T_a was gradually increased in ~ 2 °C intervals from 28 °C to 36 °C to define the TNZ. Thus, birds were in the metabolic chamber for ~ 10 h. After completion of metabolic measurements, birds were released at night at the point of capture.

2.2. Respirometry

Birds were placed in respirometry chambers (diameter=120 mm, length=205 mm, volume=2.0 L) made from air-tight acrylic containers with rubber seals. Each chamber had two short copper tubes affixed for air inlet and outlet, and a third opening for the thermocouple to measure T_a . The chambers were placed horizontally inside a

temperature-controlled cabinet (± 0.5 °C) and covered with a layer of fabric to dim the lighting and create the effect of a tree cavity. A small piece of oven-dried bark was placed in the bottom of the chamber for the bird to stand on. No perch was provided given that owl-nightjars lie flat in hollows (Doucette, 2007a). Light in the chamber was provided by a shaded 15 W bulb.

To measure oxygen consumption, we used a single channel oxygen analyzer (FOX, Sable Systems International Inc., Las Vegas, NV, USA), placed inside an insulated foam box in a temperature-controlled room at 19 ± 2 °C. A sub-sampling design was used to keep the flow rate through the analyzer constant (125 mL min^{-1}) throughout the measurements. Outside air was pumped through silica gel to remove moisture while rotameters (Aarborg 7908, New York, USA) controlled the rate of airflow to the chambers. After passing through the chamber, excurrent air was dried again using silica gel and the flow rate of air was measured using a mass flow meter (Omega FMA-5606, Stamford, CT, USA). A flow rate of 800 mL min^{-1} was sufficient to maintain the oxygen content in the excurrent air above 20%. The excurrent air from the chamber was sampled every 3 min for three readings, followed by a 6 min sampling of a reference channel of dried outside air. Channel changes were controlled by a solenoid valve connected to a computer. Thus, one measurement for each bird was obtained every 3–9 min (Coburn and Geiser, 1998; Geiser and Brigham, 2000). Measurements of T_a were taken simultaneously to those of MR. Digital data from the oxygen analyzer were transferred to a computer via a serial connection. Millivolt outputs from the flow meter and analogue output of the oxygen analyzer were transferred to a computer via a 14 bit A/D converter. Data acquisition and processing were performed using software written by G. Körtner.

2.3. Data analysis

The rate of oxygen consumption of birds was calculated using Eq. (3a) of Withers (1977). A RQ of 0.85 was assumed for all measurements, which would have resulted in a maximum error of $\pm 3\%$ if the RQ was actually 0.7 or 1.0 (Withers, 1977). RMRs were calculated for each individual as the average of the six consecutive lowest VO_2 values (i.e. over 21 min) in normothermic resting individuals at each T_a . Only data from the final 75 min of testing once the chamber had reached the designated T_a were considered in the analysis. BMRs were determined as the minimum RMR within the range of T_a s measured. The lower critical temperature (T_{lc}) of the thermoneutral zone (TNZ) was determined by calculating the T_a of the RMR/BMR intersect of each individual using the T_a versus RMR regression line below the TNZ. Similarly, the upper critical temperature (T_{uc}) was calculated from the RMR/BMR intercept above the TNZ of pooled data, as there was insufficient data from individual birds above the TNZ. The T_{uc} is technically the point where evaporative water loss (EWL) increases (Withers, 1992), however, as EWL was not measured in our study the above method achieves the best possible estimation. Mass-specific thermal wet conductance was calculated using the equation $\text{Conductance} = \text{MR} / (T_b - T_a)$ (Schleucher and Withers 2001).

RMR regression lines were compared using analysis of covariance (ANCOVA), with T_a as a covariate, and means were compared using Student's *t*-tests. Numerical values are presented as means \pm SE for *n* individuals and *N* observations. An alpha value of 0.05 was employed for all tests.

3. Results

The average BM of owl-nightjars did not differ between summer (45.56 ± 0.89 g, *n*=7) and winter (45.71 ± 2.37 g, *n*=6; $t_{0.05,11} = 0.06$, *P*=0.95), nor between sexes (males: *n*=6, 45.21 ± 1.77 g; females: *n*=4, 47.25 ± 2.68 g; $t_{0.05,8} = 0.67$, *P*=0.52). However, BM decreased significantly during the winter (June: 50.58 ± 1.66 g, *n*=3; August: 40.84 ± 1.25 g, *n*=3; $t_{0.05,4} = 4.68$, *P*<0.01).

Below the TNZ, mass-specific RMR was negatively correlated with T_a during both summer and winter (ANCOVA: $F_{1,49}=200.31$, $P<0.0001$). Winter RMRs were significantly lower than those measured in summer ($F_{1,49}=26.03$, $P<0.0001$; Fig. 1). Below the T_{lc} , RMR increased with decreasing T_a at a rate of $0.08 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ for birds in summer and $0.06 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$ for birds in winter (Fig. 1).

The range of the TNZ was similar between summer (31.7 to $34.8 \text{ }^\circ\text{C}$) and winter (31.3 to $34.0 \text{ }^\circ\text{C}$) and there was no significant difference in the T_{lc} between seasons ($t_{0.05,8}=0.34$, $P=0.74$). Within the TNZ, there was no difference in mass-specific BMR between summer ($1.29 \pm 0.07 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$, $n=7$) and winter ($1.24 \pm 0.08 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$, $n=5$; $t_{0.05,10}=0.41$, $P=0.69$), or in whole animal BMR between seasons (summer: $63.10 \pm 5.53 \text{ mL O}_2 \text{ h}^{-1}$; winter: $51.08 \pm 1.87 \text{ mL O}_2 \text{ h}^{-1}$, $t_{0.05,10}=1.76$, $P=0.11$). Likewise, birds measured in early winter (June: $1.15 \pm 0.11 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) exhibited no difference in BMR compared to those in late August ($1.37 \pm 0.03 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$; $t_{0.05,3}=1.48$, $P=0.24$). Mass-specific BMR did not differ between sexes (male: $1.21 \pm 0.06 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$, $n=6$; female: $1.23 \pm 0.09 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$, $n=4$; $t_{0.05,8}=0.15$, $P=0.88$).

No winter-caught owl-nightjars exhibited any sign of moult and all had dense plumage. Four of the seven birds captured during summer were in active moult of most their body feathers (e.g. breast, flanks and back) and two of these birds were also moulting flight feathers (birds caught in early February). One bird caught in late December showed no moult activity and two birds caught in late February showed only slight moult of body feathers. The mass-specific BMRs of the four actively moulting birds ($1.35 \pm 0.21 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) did not differ significantly from birds not or only slightly moulting ($1.30 \pm 0.18 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$; $t_{0.05,5}=0.32$, $P=0.76$). Even at $0 \text{ }^\circ\text{C}$ the RMR of actively moulting birds ($4.04 \pm 0.22 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was not significantly higher than non-moulting birds in summer ($3.51 \pm 0.05 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$; Tukey post-hoc $q=2.80$, $P=0.17$), although it did differ significantly from the RMR at $T_a 0 \text{ }^\circ\text{C}$ of winter birds ($3.00 \pm 0.16 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$; ANOVA: $F_{2,11}=9.57$, $P<0.01$). The RMR values for the pre-moulting December bird fell within the range of RMR values for the six other summer birds at all measurement T_a s.

Values of T_b ranged from 34.0 to $39.0 \text{ }^\circ\text{C}$. Core T_b was not correlated with T_a below the TNZ (ANCOVA: $F_{1,45}=5.19$, $P=0.14$), but was significantly lower in winter than in summer ($F_{1,45}=5.19$, $P<0.05$;

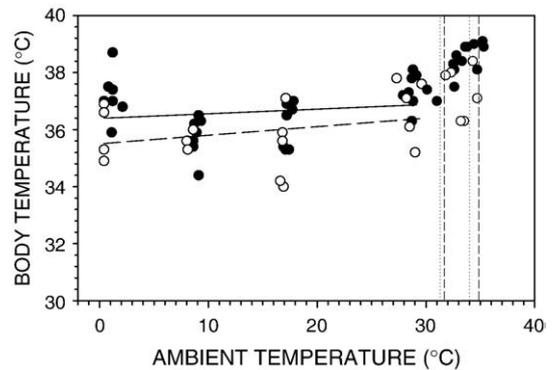


Fig. 2. Body temperature (T_b) of owl-nightjars during summer (● solid line; $n=7$) and winter (○ dashed line; $n=6$). T_b was measured using a pre-calibrated fine thermocouple inserted 1.5 to 2 cm into the cloaca. Each point represents the value for a single individual. Vertical lines represent the upper (T_{uc}) and lower (T_{lc}) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). Below the TNZ, T_b did not vary significantly with ambient temperature (T_a), but T_b was significantly higher in summer than in winter (T_a : $F_{1,45}=2.27$, $P=0.14$; season: $F_{1,45}=5.19$, $P<0.05$; model $R^2=0.15$); linear regressions for summer: $T_b=36.39+0.02(T_a)$, $F_{1,27}=0.78$, $P=0.38$; winter: $T_b=35.50+0.03(T_a)$, $F_{1,17}=1.57$, $P=0.23$.

model $R^2=0.15$; Fig. 2). Within the TNZ, summer T_b ($38.2 \pm 0.3 \text{ }^\circ\text{C}$) did not differ from winter T_b ($37.1 \pm 0.5 \text{ }^\circ\text{C}$; $t_9=2.08$, $P=0.07$).

Thermal conductance (C) below the TNZ was positively correlated with T_a in both summer and winter (ANCOVA: $F_{1,49}=112.09$, $P<0.0001$) and was higher in summer than in winter ($F_{1,49}=7.93$, $P<0.01$; model $R^2=0.72$; Fig. 3). Mean minimum C values at $T_a 0 \text{ }^\circ\text{C}$ were significantly greater in summer ($0.106 \pm 0.005 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) versus winter ($0.085 \pm 0.004 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$; $t_{0.05,10}=3.12$, $P<0.01$), but did not differ between seasons within the TNZ (summer: $0.228 \pm 0.025 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$; winter: $0.282 \pm 0.039 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$, $t_{0.05,9}=1.21$, $P=0.26$).

4. Discussion

Our study shows that owl-nightjars seasonally adjust thermal conductance and metabolism below the TNZ. RMR and C values were

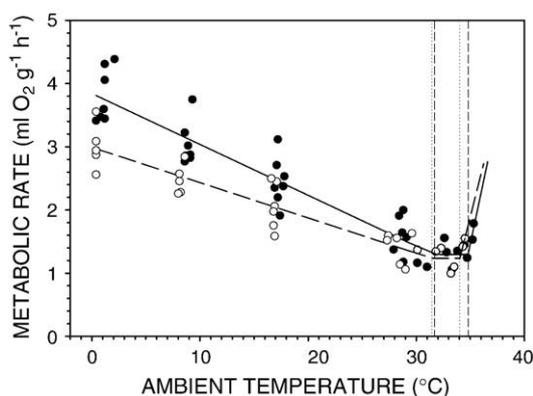


Fig. 1. Mass-specific metabolic rate of resting owl-nightjars over a range of ambient temperatures (T_a) during summer (● solid line; $n=7$) and winter (○ dashed line; $n=6$). Each point represents a measurement for one individual. The vertical lines represent the upper (T_{uc}) and lower (T_{lc}) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). Below the TNZ, RMR increased with T_a and differed significantly with season (T_a : $F_{1,49}=200.31$, $P<0.0001$; season: $F_{1,49}=26.03$, $P<0.0001$; T_a *season: $F_{1,49}=6.78$, $P<0.05$; model $R^2=0.84$); linear regression for summer: $\text{RMR}=3.84-0.08(T_a)$, $F_{1,27}=134.62$, $P<0.0001$; winter: $\text{RMR}=2.99-0.06(T_a)$, $F_{1,21}=84.49$, $P<0.0001$. Within the TNZ (31.7 – $34.8 \text{ }^\circ\text{C}$ summer; 31.3 – $34.0 \text{ }^\circ\text{C}$ winter) BMR was $1.29 \pm 0.19 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in summer-acclimatized birds and $1.24 \pm 0.18 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$ in winter-acclimatized birds.

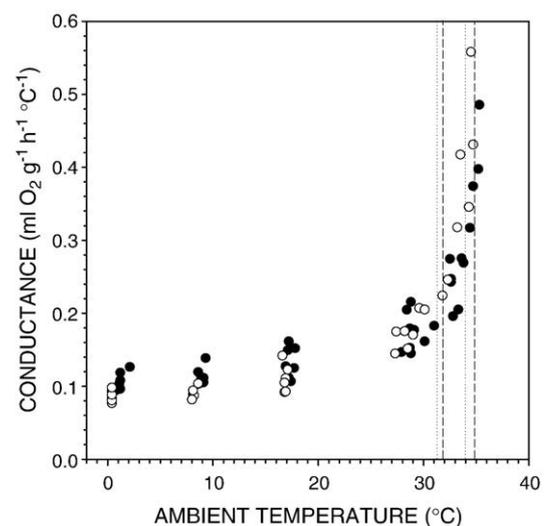


Fig. 3. Thermal conductance ($\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$) of owl-nightjars as a function of ambient temperature (T_a) during summer (● $n=7$) and winter (○ $n=6$). The vertical lines represent the upper (T_{uc}) and lower (T_{lc}) critical temperatures of the thermoneutral zone (TNZ) for summer (dashed line) and winter (dotted line). Below the TNZ, conductance values increased with ambient temperature (T_a) and differed significantly with season (T_a : $F_{1,49}=112.09$, $P<0.0001$; season: $F_{1,49}=7.93$, $P<0.01$; model $R^2=0.72$).

higher in summer-acclimatized than winter-acclimatized birds. Irrespective of season, RMR increased with decreasing T_a , as the regulation of a high T_b became energetically more expensive with an increasing difference between T_b and T_a (Withers, 1992). In contrast, no seasonal changes in mean BMR by owlet-nightjars were apparent, despite the cold T_a s experienced at the high altitude of Armidale during winter. Although birds had higher BM at the beginning of winter, presumably due to an increase in fat deposits, these were spent by mid-winter, and there was also no difference between early and late winter BMR. Thus, the lower RMR and C during winter are most likely attributable to better insulating plumage, which would reduce C and enable birds to maintain T_b at low T_a with lower energetic costs.

4.1. Seasonal energetics

Species and populations that experience a greater seasonal range of T_a s, such as those at high latitudes, high altitudes and non-migratory species, are predicted to show greater seasonal thermal acclimatization in the form of increased insulation and changes to MRs (Weathers, 1979). Large changes in seasonal T_a are generally compensated for by increases in tissue (fat deposits) and the amount of plumage or fur insulation in birds and mammals (Calder and King, 1974). Animals with adequate insulation should be able to maintain a constant T_b without increasing their BMR over a wider range of T_a s (Scholander et al., 1950). However, species differ in their capacity to increase fat stores and insulation during winter, an effect which appears to be correlated with the climate the species inhabits (Dawson and Marsh, 1989; Swanson, 1991; Liknes et al., 2002). There are also small-body-size constraints associated with carrying extra mass (Scholander et al., 1950), and constraints imposed by requirements for flight. Thus, physiological adjustments to BMR may be required to cope with low T_a s for some species, especially those with small BM.

The BMR of small birds (<100 g) may be up to 50% higher in winter than in summer (Weathers and Caccamise, 1978), and be accompanied by an increase in body mass. Liknes et al. (2002) suggested that the increased fat stores in Nearctic birds during winter provides them with a larger energy reservoir to draw upon during cold exposure, which could in turn accommodate a higher winter BMR. However, Lovegrove et al. (1991) proposed that a reduction in body mass in winter that did not sacrifice an animal's ability to maintain thermal balance should be advantageous as it would decrease the absolute energy requirements of the animal.

BMR is usually higher in winter-acclimatized passerines in North America (Pohl and West, 1973; Dawson and Carey, 1976; Swanson, 1991; Cooper and Swanson, 1994; Cooper, 2002; Liknes et al., 2002), however, the degree of BMR seasonal variation in small Australian birds is inconsistent, suggesting that different species are using different strategies for seasonal physiology (Collins and Briffa, 1983; Ambrose and Bradshaw, 1988; Maddocks and Geiser, 2000; Lill et al., 2006). Some of this variation may be explained by the severity of winter temperatures. While increased insulation may provide adequate protection from cold exposure in the moderate winter climates of Australia (mean daily winter minimum T_a =1 °C in Armidale), this may not be sufficient in the colder temperate climates of North America (e.g. winter mean=-8.2 °C; Liknes et al., 2002). Thus, birds found in temperate regions may need to increase energy reserves and BMR more during winter to survive colder conditions.

The lack of overall seasonal variation of BM and BMR for owlet-nightjars could be the result of the larger BM of owlet-nightjars (45 g) relative to most other small species studied (<15 g), or due to their nocturnal habits. While food availability decreases in winter for almost all non-predatory birds, diurnal species are further disadvantaged by shorter day length which limits the time available for foraging and imposes long periods of nocturnal fasting (Dawson and Marsh, 1989). In contrast, nocturnal birds have the advantage of

foraging during longer periods of darkness to maintain energy stores. Winter energy expenditure of nocturnal species may be further reduced by selecting roosts exposed to solar radiation during the diurnal rest phase (Doucette, 2007b).

The T_b of owlet-nightjars ranged from 34 to 38 °C at T_a s below the TNZ (Fig. 2). This is not unusual as birds are known to maintain a heterothermic T_b within a range of several degrees (34 to 40 °C) during rest (McKechnie and Lovegrove, 2002). T_b was higher in summer-acclimatized compared to winter-acclimatized owlet-nightjars. Small birds which are heterothermic at low T_a s have been known to have lower T_b during winter than in summer (Chaplin, 1974). The slightly higher T_b s observed at T_a 0 °C in our study may be due to the relatively short exposure time at low T_a (150 to 180 min) when this measurement was taken. Birds may have initially maintained a higher T_b at the lowest T_a s with increases in MR, then slightly relaxed both MR and T_b as T_a increased.

Mean minimum C values for owlet-nightjars were significantly lower in winter compared to summer birds. This is presumably due to an increase in winter plumage. The mean minimum C values for owlet-nightjars at 0 °C during summer (0.106 mL O₂ g⁻¹ h⁻¹ °C⁻¹) and winter (0.085 mL O₂ g⁻¹ h⁻¹ °C⁻¹) were 26% and 41% lower, respectively, than the minimum C values predicted for a 45 g bird at rest (0.143 mL O₂ g⁻¹ h⁻¹ °C⁻¹; $\log_{10}C = -0.0028 - 0.5094 \log_{10}BM$) (Schleucher and Withers, 2001; Fig. 3). This indicates that owlet-nightjars gained extensive thermal benefits from their insulative plumage, which at least in part explains why seasonal adjustments to BMR were apparently not required. For allometric reasons, an increase in feather insulation tends to incur a greater increase in cold resistance for larger birds than for smaller birds (Dawson and Marsh, 1989), thus owlet-nightjars appear to fall in the category of large birds in this respect.

Feather moult has two possible influences on avian metabolic rate. First, feather loss is expected to decrease thermal insulation and increase evaporative heat transfer resulting in greater conductance at temperatures below the TNZ (Murphy, 1996). Second, the production of new feathers increases energetic demands and should be exhibited

Table 1

Published body mass and basal metabolic rate (BMR) values for Caprimulgiformes as plotted in Fig. 4

Species	Abbreviation	Mass (g)	BMR (mL O ₂ g ⁻¹ h ⁻¹)	Reference
Caprimulgidae				
Common poorwill (<i>Phalaenoptilus nuttallii</i>)	PW	40	0.80	Bartholomew et al. (1962)
Whip-poor-will (<i>Caprimulgus vociferous</i>)	WPW	50	1.25	Lane et al. (2004)
Common nighthawk (<i>Chordeiles minor</i>)	CN	80	1.10	Lasiewski and Dawson (1964)
Spotted nightjar (<i>Eurostopodus argus</i>)	SN	90	0.83	Dawson and Fisher (1969)
White-throated nightjar (<i>Eurostopodus mysticalis</i>)	WN	162	0.53	McNab and Bonaccorso (1995)
Large-tailed nightjar (<i>Caprimulgus macrurus</i>)	LN	70	0.81	McNab and Bonaccorso (1995)
Pauraque (<i>Nyctidromus albigollis</i>)	P	45	1.9	Scholander et al. (1950)
Podargidae				
Tawny frogmouth (<i>Podargus strigoides</i>)	TF	500	0.59	Bech and Nicol (1999)
Marbled frogmouth (<i>Podargus ocellatus</i>)	MF	145	0.70	Lasiewski et al. (1970)
Papuan frogmouth (<i>Podargus papuensis</i>)	PF	315	0.61	McNab and Bonaccorso (1995)
Aegothelidae				
Australian owlet-nightjar (<i>Aegotheles cristatus</i>)	ONJ	45	1.27	This study

as an increase in BMR within the TNZ (Robin et al., 1988; Buttemer et al., 2003). Decreased insulation during moult may explain the 20% higher C and increased RMR below the TNZ in summer versus winter owlet-nightjars. However, the BMR of moulting and non-moulting summer owlet-nightjars did not differ. The cost of feather production varies greatly among species, but has been found to be negatively correlated with BM and positively correlated with BMR (Lindstrom et al., 1993).

4.2. Low BMR of Caprimulgiformes

The mean BMR of owlet-nightjars ($1.27 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was 37% and 41% lower than predicted for birds by Reynolds and Lee (1996) and Rezende et al. (2002) respectively, but were similar to published values for other species of Caprimulgiformes (Table 1; Fig. 4). However, owlet-nightjar BMR was only 12% lower than predicted ($1.45 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) based on the equation of McKechnie et al. (2006), which takes into account migratory tendency, habitat aridity, phylogenetic relatedness, and whether birds were captive-raised or wild caught (McKechnie et al., 2006). While this equation indicates that Caprimulgiformes have BMRs much closer to those found for other birds, all species except for the pauraque (*Nyctidromus albicollis*) still have BMRs below that predicted.

Nocturnal birds, including frogmouths (Podargidae), nightjars (Caprimulgidae), kiwis (Apterygidae), and owls (Strigidae) have significantly lower relative BMRs than diurnal birds (Bennett and Harvey, 1987; Hohtola et al., 1994). The tendency for nocturnal birds to have lower BMRs extends to nocturnal species within taxonomic groups which contain mostly diurnal members (Duriez et al., 2004). Bennett and Harvey (1987) suggested that low relative BMR in nocturnal birds is an adaptive response to the higher T_a s encountered during the day when the birds are resting. Nocturnal birds may choose a site with a favorable microclimate and sun exposure during the rest phase and

hence reduce thermoregulatory costs by basking to raise or maintain T_a , as seen for some species of small mammals (Geiser and Drury, 2003). Diurnal birds typically do not have this opportunity to maintain T_b through solar heating while at rest during the night. This hypothesis is supported by data for tropical diurnal species that forage in the sun, which have BMRs averaging 25% lower than similar species foraging in shaded areas (Weathers, 1979). Heat production by nocturnal birds during activity may also substitute for the increased thermoregulatory expenditure at night when T_a s are lower (Webster and Weathers, 1990; also see Cooper and Sonsthagen, 2007).

Our data represent the first BMR measurement reported for Aegotheidae. The value falls within 3% of the allometric curve for Caprimulgiformes (Fig. 4). Owlet-nightjar BMR is almost identical to that found for whip-poor-wills (*Caprimulgus vociferous*; 50 g), a migratory North American species. It appears that in owlet-nightjars, low BMR contributes to low energy expenditure, which together with its extensive use of torpor (Brigham et al., 2000; Doucette, 2007b), permits a sedentary life despite its small size and insectivorous diet.

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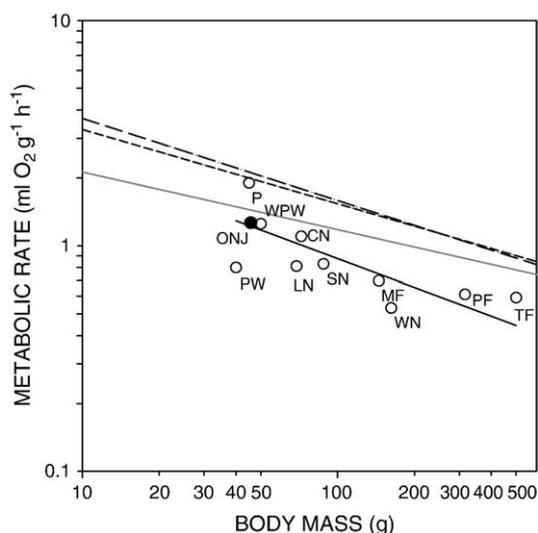


Fig. 4. Basal metabolic rate (BMR) of nightjars (○) (Caprimulgiformes) as a function of \log_{10} body mass (BM). The solid black line represents the resulting significant regression ($\text{BMR} = 6.13 \text{ BM}^{-0.422}$; $F_{1,9} = 6.95$, $P < 0.05$, $R^2 = 0.46$, $n = 10$, excluding owlet-nightjars). The published BMR values and corresponding BM values of the Caprimulgiformes plotted, and the full species names for the abbreviated data labels, are given in Table 1. The mean of both summer and winter BMR values obtained for Australian owlet-nightjars (●) in the current study ($1.27 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$) was 3% higher than that predicted by the nightjar regression line ($1.23 \text{ mL O}_2 \text{ g}^{-1} \text{ h}^{-1}$). The regression for Caprimulgiformes including owlet-nightjars is $\text{BMR} = 6.38 \text{ BM}^{-0.431}$ ($F_{1,10} = 9.05$, $P < 0.05$, $R^2 = 0.50$, $n = 11$). The BMR values for nightjars, with the possible exception of the tropical pauraque (*Nyctidromus albicollis*), are below those predicted by recent equations for scaling of avian metabolism by Reynolds and Lee (1996; short dashed line; $\text{BMR} = 7.01 \text{ BM}^{-0.330}$), Rezende et al. (2002; long dashed line; $\text{BMR} = 8.51 \text{ BM}^{-0.365}$), and McKechnie et al.'s (2006) equation for wild-caught birds (solid grey line; $\text{BMR} = 3.83 \text{ BM}^{-0.256}$).

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