Metabolism of winter-acclimatized new Holland honeyeaters
Phylidonyris novaehollandiae from Hobart, Tasmania

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摘 要 在 5 – 40℃ 温度范围内，测定了澳大利亚塔斯马尼亚黄翅澳蜜鸟（Phylidonyris novaehollandiae）（平均体重 24.1 ± 0.27 g）冬季的耗氧量。结果表明，热中性区是 25 – 35℃。基础代谢率是 4.92 ± 0.14 ml/g. h，分别比 Lasiewski and Dawson (1967) 和 Aschoff and Pohl (1970) 基于体重的关于雀型鸟类的期望值高 57% 和 77%。本研究结果同样也比已经报道的分布在澳洲大陆的该物种的代谢率高 [动物学报 51 (2): 338 – 343, 2005]。

关键词 黄翅澳蜜鸟 基础代谢率 冬季驯化

Key words New Holland honeyeaters Phylidonyris novaehollandiae, Basal metabolic rate, Winter-acclimatized

Small birds in temperate areas are confronted seasonally with the interacting problems of climate, day length and food supplies that might constrain their energy utilization. For example, during a cold winter the requirements of feeding for a diurnal bird are increased while day-length to obtain food is shortened. During summer, the conditions are markedly different, thus birds have to develop strategies to cope with climatic changes.

Adjustments of small birds to seasonal conditions have attracted considerable attention due to their limited capacities for insulative acclimatization. They develop morphological, physiological and behavioural adaptations that assist in coping with the various energy demands. These adaptations might include a reduction in the level of activity (Ambrose, 1984), selection of a suitable microclimate (Reinertsen and Haftorn, 1986), changes in body mass and lipid content (O’Connor, 1995) and shifts in basal metabolic rate (Weathers and Caccamise, 1978).

Basal metabolic rate can be defined as the minimal rate of energy used by a post-absorptive animal at rest within the zone of thermoneutrality (Blight and Johnson, 1973; Blem, 2000). The basal metabolic rate is most commonly determined from measured oxygen consumption (Lindstrom and Kvist, 1995) or rarely by carbon dioxide production (Weathers et al., 1996). The volume of oxygen consumed after correction to standard conditions of temperature (0°C) and pressure (760 mmHg) for the dry gas (STPD) and multiplied by 20.1 kJ/L convert to heat units (Daan et al., 1990).

In birds, the basal metabolic rate has been found to vary with season (Weathers and Caccamise, 1975, 1978), climate (Weathers, 1979, 1980), body mass (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970), activity phase of the bird (Aschoff and Pohl, 1970) and diet (McNab, 1988; Vitali et al., 1999). The correlation between basal metabolic rate and body mass in birds has been studied repeatedly (e.g. Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970) yielding equations to calculate the basal metabolic rate based on the bird’s body mass.

Whittow (1986) stated that the relationship between basal metabolic rate and body mass in birds differs in passerines and other birds. In the past it has
been generally accepted that passerines have a higher metabolic rate than nonpasserines (Lasiewski and Dawson 1967: Aschoff and Pohl 1970). McNab (1988) pointed out that the high basal metabolic rate of passerines in combination with their tricarial habits might have significance in permitting high post-natal growth rates and exploitation of seasonally abundant resources. High growth rates permit young to develop and to store sufficient amounts of fat to overwinter or migrate and permit adults to produce more than one brood during a short summer, perhaps contributing to the pre-dominance of passerines in temperate land environments (McNab 1988).

However, subsequent investigations using phylogenetic comparative methods have failed to substantiate BMR differences between passerines and non-passerines (Reynolds and Lee, 1996; Rezende et al., 2002). McKechnie and Wolf (2004) have produced an equation of log W = 1.461 + 0.669 log M based on 67 avian species chosen for their rigorous experimental technique. Vitali et al. (1999) have shown that members of the family Meliphagidae (Australian honeyeaters), do not have a metabolic rate that differs from other passerine birds: though they stated that ‘additional meliphegied species’ are required to confirm this finding’.

In this study, the basal metabolic rate of the New Holland honeyeater Phylidonyris novaehollandiae was observed in winter over a range of ambient temperatures. This bird is a member of the family Meliphagidae, one of Australia’s dominant passerine families (Ford and Paton, 1977). Several studies on the metabolism of this species have been conducted in mainland Australia (Paton, 1980; MacMillen, 1985) but none have been conducted in Tasmania. Weathers (1979) stated that the basal metabolic rate tends to be higher in birds from cold climates. Tasmania has a colder climate than the study sites of both earlier studies conducted (in Sydney, New South Wales and Melbourne, Victoria). As the climate in Tasmania is colder, one might reasonably conclude that the basal metabolism of the New Holland honeyeater living in Tasmania would differ from their counterparts in mainland Australia, particularly during the winter months.

1 Materials and methods

1.1 Capture and husbandry

All birds were captured near Hobart, Tasmania (S 42°54′10″, E 147°19′26″) under permit number FA 00030 from the Tasmania Parks and Wildlife Service and authority number 644 from Australian Bird and Bat Banding Scheme. For section 1, five birds (mean body mass 24.1 ± SE 0.27 g) were captured using mist nets during May 2001. The birds were banded, then were placed in an aviary (3.0 m x 1.5 m x 2.0 m) with mesh panels, thus exposing the birds to natural photoperiods and air temperatures. The aviary had branches and perches consisting of native foliage, and was cleaned daily. Birds were fed once daily on Improved Honeyeater Mixture, Bird Cake Mixture and Fly Pupae (Vaartjes, pers. comm.). Water for drinking and bathing was available ad lib.

1.2 Basal metabolic rate measurement

Measurements of oxygen consumption were conducted in winter (July to August). Birds were post-absorptive (resting, alert, and fasting) for 4 hours prior to the measurements. Oxygen consumption was measured using a dual channel oxygen analyzer (Ametek Applied Electrochemistry Oxygen Analyzer S-3A/ II, Pittsburgh). Prior to measurement the air was scrubbed of water and carbon dioxide. Body weight was recorded immediately prior to placing bird in a 2000 ml metabolic chamber enclosed within a water bath. The measurement was conducted for approximately 2 hours at night between 19.00 to 21.00 at 5°C, 15°C, 25°C, 30°C, 35°C, and 40°C. Every bird was exposed to each temperature but only one temperature each night and a different temperature every week. Airflow rate through the chamber was set to 350 ml/min using a recently calibrated Ametek R2 Flow Control. The value was taken to be the lowest stable VO2 which was maintained for at least 3 minutes in the second hour of measurement. The calculations were made using equations 4a of Withers (1977). All values were adjusted to STP. Body temperature was measured immediately after each trial with a thermocouple inserted approximately 1 cm.

Oxygen consumption and body temperature data were analyzed using repeated measures ANOVA (S-STAT 5.0) followed by Tukey’s post hoc tests. Statistical significance was accepted as P < 0.05.

2 Results

2.1 Body temperature

Mean body temperature at each ambient temperature varied between 37.82 ± 0.54°C and 41.12 ± 0.67°C. Body temperature varied considerably between individual birds and there were no significant differences before and after temperature treatments (P = 0.93) (Fig. 1).

2.2 Oxygen consumption

The relationship of oxygen consumption to ambient temperature in five winter-acclimatized New Holland honeyeaters is shown in Fig. 2.

Analysis of variance showed that there were significant differences due to the ambient temperature (F4,5 = 26.09, P<0.05). The highest oxygen consumption occurred at the ambient temperature of 5°C.
Fig. 1 Mean body temperature (± SE) of the winter-acclimatized New Holland honeyeater in Tasmania at different ambient temperatures

![Graph showing mean body temperature (± SE) over different ambient temperatures for the winter-acclimatized New Holland honeyeater in Tasmania.](image)

**Fig. 2** Oxygen consumption of the winter-acclimatized New Holland honeyeater in Tasmania at different ambient temperatures. Each data point is one animal.

![Graph showing oxygen consumption (ml/g/h) over different ambient temperatures for the winter-acclimatized New Holland honeyeater in Tasmania.](image)

(8.87 ml/g·h), decreasing gradually with increasing ambient temperature. Post hoc tests showed this value to be significantly different to all others (P < 0.05). However, the oxygen consumption was not significantly different between temperatures 25°C, 30°C and 35°C which then equates to the thermoneutral zone. The average oxygen consumption between 25°C and 35°C was 5.12 ± 0.14 ml/g·h. However, the lowest (basal) metabolic rate was 4.92 ± 11.4 at 35°C. When the ambient temperature was above thermoneutrality (40°C) the oxygen consumption increased to 6.81 ml/g·h; post hoc tests value to be significantly different from all values other than that at 15°C.

### 3 Discussion

Winter-acclimatized New Holland honeyeaters exhibit fluctuations in oxygen consumption at different ambient temperatures. Oxygen consumption was the highest at 5°C but significantly decreased as the ambient temperature increased to 25°C. Calder and King (1974) stated that the adaptation of small birds to cold commonly results in substantial increases of basal metabolic rate.

During cold stress, birds enhance thermogenesis through shivering and/or non-shivering mechanisms. During non-shivering thermogenesis, Calder and King (1974) stated that birds conserve heat through piloerection, retracting extremities within plumage, peripheral vasoconstriction, and counter-current heat exchange. They also maximize water conservation and/or heat production is augmented as necessary.

During shivering thermogenesis, the thermogenic capacity of birds depends mainly on muscle activity (Marsh and Dawson 1982). Both pectoral and non-pectoral muscles play a role in heat production through shivering. In birds, shivering is the primary source of heat production during cold stress (Barnett, 1970), though more recent research suggest the importance of non-shivering thermogenesis in birds and its location in skeletal muscle (Duchamp and Barre, 1993).

Winter-acclimatized birds tolerate cold stress far better than summer-acclimatized birds. Cooper and Swanson (1994) found that cold tolerance in winter-acclimatized Black-capped Chickadee *Parus atricapillus* was improved over their summer counterparts. Adjustments in insulation may assist the birds in winter improvement of cold tolerance. Saarela et al. (1995) found that thermal insulation of *Carduelis chloris* was significantly better in winter than in summer. However, Swanson (2001) stated that metabolic adjustments associated with enhanced shivering endurance are the major responsible factor for improved cold tolerance in winter. This was also supported by Saarela et al. (1995) who showed that winter-acclimatized Greenfinches *Carduelis chloris* maintained a high level (greater than 60% of maximum) of shivering thermogenesis during extreme cold.

The oxygen consumption of the New Holland honeyeater remains stable between a temperature of 25°C and 35°C. This temperature range is in agreement with Hissa and Palokangas (1970), who stated that the thermoneutral zone in most Passerines birds is from 25°C to 35°C. MacMillen (1985) stated that the thermoneutral zone for Meliphagid species is at 30°C ± 1°C which is exactly mid-way between the values found in this study. The mean of metabolic rates between 25 – 35°C was 5.12 ± 0.14 ml/h. However, the lowest mean was at 35°C hence the basal metabolic rate in this study was taken as 4.92 ± 0.14 ml/h. Table 1 presents data from the literature on basal metabolic rate of the New Holland honeyeater together with rates predicted from the bird’s
mass by appropriate equation of Lasiewski and Dawson (1976), Aschoff and Pohl (1970) and McKechnie and Wolf (2004).

**Table 1 Metabolic rate of the New Holland honeyeater calculated from Lasiewski and Dawson (1967), Aschoff and Pohl (1970) and McKechnie and Wolf (2004) equations together with measured data from earlier studies from mainland Australia and the present study**

<table>
<thead>
<tr>
<th>Author</th>
<th>Body mass (g)</th>
<th>BMR (ml o2/g*hr)</th>
<th>Study sites</th>
<th>Latitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>1967 Lasiewski and Dawson</td>
<td>24</td>
<td>3.13</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>1970 Aschoff and Pohl</td>
<td>24</td>
<td>2.77</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>2004 McKechnie and Wolf</td>
<td>24</td>
<td>3.11</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>1980 Paton</td>
<td>20</td>
<td>3.3 ± 0.30</td>
<td>Victoria</td>
<td>S 37.81°</td>
</tr>
<tr>
<td>1985 MacMillen</td>
<td>19.5 ± 1.4</td>
<td>2.51 ± 0.55</td>
<td>Sydney</td>
<td>S 33.86°</td>
</tr>
<tr>
<td>2002 This study</td>
<td>24.1 ± 0.27</td>
<td>4.92 ± 0.14</td>
<td>Tasmania</td>
<td>S 42.89°</td>
</tr>
</tbody>
</table>

Factors influencing the basal metabolic rate include time of day (Pohl, 1969), season (Weathers and Caccamise, 1978; Cooper and Swanson, 1994), length of time in captivity (Pohl, 1977), and type of diet (McNab, 1988). Unfortunately, Paton (1980) and MacMillen (1985) did not state the season during which their measurements were made. There are several factors that might explain why their calculated basal metabolic rate differs from that of this study. The first factor is the study sites. Our research was conducted in Tasmania which has a colder climate compared to the study sites in which both earlier studies were conducted. Weathers (1979) stated that higher basal metabolic rates in colder climate birds were related to increased rates of their endogenous heat production. Studies on the winter-acclimatized Black-capped chickadee by Sharbaugh (2001) in Alaska and Chaplin (1974) in New York also revealed that the basal metabolic rate of the birds in a colder climate (Alaska) was higher than that of their counterparts inhabiting a less cold area (New York).

Other data on the new Holland honeyeater in Tasmania (Kusuma Yuni, 2003) shows that there were not significant differences in basal metabolic rates between the various seasons indicating that our differences are likely to be due to climatic and not just seasonal differences between Tasmania and the rest of mainland Australia.

Other contributing factors could be the length of time in captivity and type of diet. Our birds were in captivity for about two months prior to the experiment and were fed on an artificial diet. It is unclear whether Paton (1980) and/or MacMillen (1985) conducted their measurements on freshly caught birds or on captives. However, the basal metabolic rate of five freshly caught New Holland honeyeater during winter were also measured and it was found that their BMR were even higher (6.47 ± 0.31) (unpublished observations) than captives. This result suggest captivity alone could not explain differences in basal metabolic rate between birds from Tasmania and mainland Australia.

Within the thermoneutral zone, heat production depends also on the level of food intake prior to the measurement. Whittow (1986) stated that the higher the level of food intake, the higher heat production would be. However, this would not apply in our measurement as the birds were fasted for 4 hours prior to the experiment. The choice of this period of time was based on the finding of Wooler et al. (1988) that the total gut elimination in Meliphagidae takes about 4–5 hours.

The basal metabolic rate in this study was found not to be in agreement with the values calculated from Lasiewski and Dawson (1976) and Aschoff and Pohl (1970) equations. The BMR measured was 57% and 77% higher than those calculated from Lasiewski and Dawson (1976) and Aschoff and Pohl (1970) equations respectively. Several other workers also found higher basal metabolic rate than those calculated value from Lasiewski and Dawson (1967) and Aschoff and Pohl (1970) equations e.g. West (1972), Dawson and Carey (1976), Weathers (1979), Reinertsen and Haftorn (1986), Swanson (1993), Cooper and Swanson (1994), Leon and Nicolson (1997), Sharbaugh (2001). Weathers (1979) found that the basal metabolic rate tends to be higher in birds from high latitude or cold climates and lower in tropical forms than would be expected from the equations of Lasiewski and Dawson (1967) and Aschoff and Pohl (1970).

Although both Lasiewski and Dawson (1967) and Aschoff and Pohl (1970) had separate equations for passerines and non-passerines, there are other factors known to affect the basal metabolic rate not considered in those equations. One factor is the diet. McNab (1988) stated that passerines feeding mostly on nectar have a much higher basal metabolic rate than other birds. Several species of honeyeaters feed mostly on insect e.g. the helmeted honeyeater *Lichenostomus melanops cassidix* (Moysey, 1997) while others feed mostly on nectar and others carbohydrates e.g. the western spinebills *Acanthorhyncus superciliiosis* (Collins and Newland, 1986), the Regent honeyeaters *Xanthomyza phrygia* (Oliver, 2000). The New Holland honeyeater in this study was found to feed mostly on nectar and spent little of its foraging time catching small flying insects to satisfy protein and nutrient requirements (unpublished observations). Therefore, it might be reasonable to ex-
pect that the basal metabolic rate obtained in the present study differs from values calculated from the equations of Lasiewski and Dawson (1967) and Aschoff and Pohl (1970). A study by MacMillen (1985) also demonstrated that factors other than body mass affected the basal metabolic rate. He found that the basal metabolic rate of two birds from the same family (Meliphagidae) with similar body mass, namely the yellow-faced honeyeater Meliphaga chrysops (16.0 g) was 23% higher than the white-cheeked honeyeater Phylidonyris niger (16.3 g).

Reynolds and Lee (1996) found no significant differences in basal metabolic rate between passerine and non-passerine species; once both phylogeny and body mass effects were accounted for. Furthermore, Rezende et al. (2002) also found no statistical differences in the scaling of metabolic rate between passerines and non-passerines. As a consequence, they suggested the use of a single allometric regression for these birds.

In conclusion, the range of the thermoneutral zone of the winter-acclimatized Phylidonyris novaehollandiae from Tasmania extended from at least 25°C to 35°C. This zone is similar to that put forward by Hissa and Palokangas (1970) and MacMillen (1985) for the Passerines and Meliphagidae species respectively. Conversely, the basal metabolic rate was found to be higher than the same species from mainland Australia. The colder climate in Tasmania is more energetically demanding, therefore the birds enhance their thermogenesis with an increased basal metabolic rate.

References
568–575.