ENERGETICS, THERMOREGULATION AND NOCTURNAL HYPOTHERMIA IN AUSTRALIAN SILVEREYES[1]

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Abstract. We investigated whether the Silvereye, *Zosterops lateralis* (10–12 g) uses heterothermy to reduce energy expenditure when confronted with adverse environmental conditions. We also determined the thermal physiology and energetics of this species. *Z. lateralis* entered nocturnal hypothermia over a range of ambient temperatures (T_a) from 3–26°C. Below the thermoneutral zone (TNZ), metabolic rate (MR) decreased by up to 50% and this reduction was more pronounced at high T_a than at low T_a. The reduction of MR at night was accompanied by a reduction of body temperature (T_b) from 40.3 ± 0.5 to 36.9 ± 0.1°C, a decrease in the difference between T_b and T_a and a reduction in thermal conductance. Within the TNZ, basal metabolic rate (BMR) was 2.43 ± 0.41 mL O_2 g^{-1} h^{-1}, while the corresponding day RMR was significantly elevated at 3.26 ± 0.42 mL O_2 g^{-1} h^{-1}. The ability of Silvereyes to reduce daily energy expenditure by employing nocturnal hypothermia may be one reason why this species and its relatives are able to occupy a wide variety of habitats and climates.

Key words: nocturnal hypothermia, Silvereye, Zosterops lateralis, *metabolic rate, thermoregulation, thermal conductance, body temperature.*

INTRODUCTION

Endothermic animals expend much of their ingested nutrients on thermoregulation. Since climate and food availability often change with season, many endotherms use heterothermy (lowering of body temperature) during certain times of the day or the year to reduce energy expenditure. Whereas heterothermy appears to be common in mammals, it appears to be far less common in birds (Dawson and Hudson 1970, Reinertsen 1983). Ostensibly, one reason for this is the ability of birds to migrate over long distances, and thus largely avoid adverse environmental conditions and food shortages.

The three general patterns of heterothermy known to occur in birds are nocturnal hypothermia, daily torpor and hibernation. All three physiological states show the same general pattern of pronounced fluctuations of metabolic rate (MR) and body temperature (T_b) over time, but the amplitude and frequency differ. Nocturnal hypothermia is the pattern most commonly recorded in birds and is characterized by a 30–40% reduction in MR and a lowering of T_b by about 5°C (Dawson and Hudson 1970, Reinertsen 1983, French 1993). Daily torpor also has been observed in a number of bird species, and

is characterized by torpor bouts of several hours, T_b of about 20°C and MR of about 30% of the basal metabolic rate (BMR) (Dawson and Hudson 1970, French 1993, Geiser and Ruf 1995). Hibernation, commonly employed by mammals of all three subclasses (Geiser 1994) has been described in only one bird species, the Common Poorwill, *Phalaenoptilus nuttallii* (Jaeger 1949, Ligon 1970, Brigham 1992). During hibernation the MR of Poorwills is reduced by more than 90% in comparison to resting rates and T_b falls to about 5°C (Withers 1977).

While long distance migration is widely used by birds from the northern hemisphere, many Australian birds are sedentary or nomadic, and do not migrate over long distances (Ford 1989). This may be because Australia is geographically isolated and seasonal changes in climate are not as severe as those experienced in the high latitudes of the northern hemisphere. Nevertheless, food availability does change with season and weather conditions. Moreover, those Australian species which live at high altitudes or low latitudes experience harsh environmental conditions, especially during winter (Chan et al. 1990). Small passerines encountering such conditions may experience thermoregulatory and energetic difficulties caused by low ambient temperatures (T_a), reduced daylength and hence foraging opportunities, which may exaggerate

food shortages (Dawson et al. 1983b, Chan 1994). Seasonal patterns of cold tolerance have primarily concentrated on species which experience extreme winter cold (Swanson 1991). The small size and high energy requirements of many passerines might necessitate the use of cold adjustments (e.g., heterothermy) even in species inhabiting less stressful temperate regions (Dawson et al. 1983a). This would enable them to survive thermal challenges and to balance energy demand with food supply. Research on an individual Australian Nightjar, *Caprimulgus argus* (Dawson and Fisher 1969) and anecdotal evidence from field observations (Heumann 1926, Serventy 1970, Ives 1973) supports this prediction; however, little detailed information on heterothermy in Australian birds is available.

Therefore, we investigated various aspects of energetics and thermoregulation of an Australian passerine, the Silvereye (*Zosterops lateralis*). We determined whether this species is heterothermic, and if so, which pattern of heterothermy it uses. The Australian Silvereye population resides in eastern and southern Australia, from Tasmania, north to Cape York, and west to Perth and north to Carnarvon, Western Australia (MacDonald 1973). Although a resident of Australia, the Silvereye belongs to the passerine adaptive radiation of the northern hemisphere (Sibley and Ahlquist 1985). Silvereyes are arboreal and are common in many types of habitats (Kikkawa 1985). Their diet mainly consists of nectar and insects, but may be supplemented with fruit (MacDonald 1973, Kikkawa 1985). They are relatively small, weighing 10–12 g (MacDonald 1973).

MATERIAL AND METHODS

In June (winter) 1995, nine Silvereyes were captured with mist nets near Armidale, NSW (30°35'S, 151°44'E). Shortly after capture, birds were weighed to the nearest 0.1 g and identification leg bands weighing 0.03 g were fitted. They were housed in 70 × 40 × 40 cm cages within a large outdoor aviary where they were exposed to natural photoperiod and temperature fluctuations. Each cage housed two or three birds and was cleaned twice weekly. Water for drinking and bathing, and food were available in excess. Their diet of artificial nectar and insect replacements, apple and *Tenebrio* larvae was supplied fresh daily.

MR was measured as the rate of oxygen consumption using open flow respirometry. The birds were individually placed in a 1-L respirometry chamber fitted with a perch, which was positioned within a temperature-controlled cabinet ($\pm$ 0.5°C) so that the birds could be observed, but were unable to see the observer or the other birds. Sufficient space was available for the birds to change position within the respirometry chamber, although flight was not possible. Birds were weighed before and after each testing period and a constant rate of mass loss was assumed for calculation of mass-specific MR. All individuals survived and were determined to be healthy at the termination of the experimental period. Food and water were not available during MR measurements and the birds were post-absorptive.

Air flow rate through the chambers was approximately 300 mL min^{-1} and was measured with a mass flowmeter (FMA 5606, Omega Engineering Inc.). Oxygen content of the dried expired air was measured using a single channel oxygen analyzer (Ametek Applied Electrochemistry Oxygen Analyzer S-3A/1). Solenoid valves switched channels in 3-min intervals, which permitted the measurement of up to three animals and a reference in succession; each channel was measured once every 12 min.

T_b was measured using temperature-sensitive transmitters (Minimitter model X-M in a modified, smaller capsule), which were calibrated to the nearest 0.1°C against a precision mercury thermometer in a water bath. The wax-coated transmitters weighed 1.1–1.3 g and were implanted intraperitoneally while birds were under isoflurane anesthesia. After surgical implantation, the birds were allowed a minimum of seven days to recover before any experiments were performed. Measurements of T_b were taken simultaneously with those of MR. A ferrite rod antenna was taped to the outside of the respirometry chamber, and the signal was received by a car radio.

T_a also was measured simultaneously to the nearest 0.1°C with a thermocouple inserted 1 cm into the respirometry chamber. Thermocouple output was amplified by a digital thermometer (Omega DP116). The analog outputs from the flowmeter, oxygen analyzer, car radio, and digital thermometer were interfaced via a 14 bit A/D card to an IBM compatible computer.
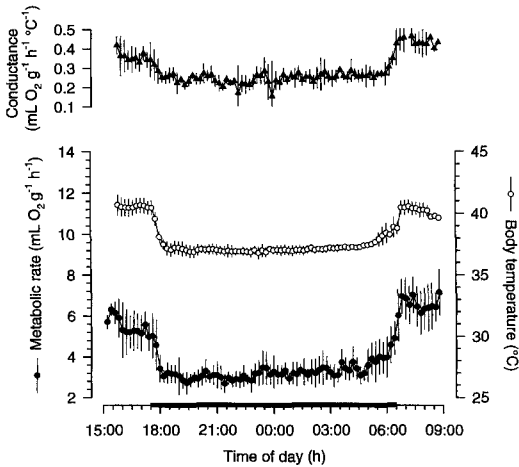
Measurements of oxygen consumption were

FIGURE 1. Daily fluctuation of conductance, T_b and MR of *Zosterops lateralis* at 26°C during winter. Animals were measured at a constant T_a for a period of 16 to 18 hours. Values shown are mean ± SD ($n = 5$ for conductance and T_b; $n = 9$ for MR measurements). The dark bar indicates the period of darkness.

used to determine BMR and resting metabolic rate (RMR). These were calculated as the mean of the three lowest consecutive readings at each T_a. The means of the corresponding readings of T_b and T_a also were calculated.

RMRs were determined over a range of T_a from 3 to 26°C which is similar to the T_a Silvereyes experience in Armidale throughout the year. Each individual was tested at approximately 5, 15 and 25°C. The birds were kept in the respirometry chamber at a constant T_a for periods of 16–18 hours (about 15:00–09:00). The photoperiod within the cabinet was adjusted with a timer to coincide with the natural photoperiod (approx. L11:D13).

BMR measurements were carried out separately. The animals were placed in respiratory chambers for a maximum of 8 hours during the night, and measured at T_a ranging from 25 to 39°C to determine the thermoneutral zone (TNZ). The T_a was progressively increased in steps of 2°C every hour. The corresponding MRs within the TNZ during the day were determined in the same manner as BMR.

Apparent thermal conductance was calculated using the equation (Schmidt-Nielsen 1990):

$$\text{Conductance} = MR/(T_b - T_a)$$

All numerical values are expressed as means ±SD of the number (n) of individuals mea-

sured. Sample variances were tested for homogeneity using F_{max}-test (Zar 1984). Paired observations underwent a paired or pooled form of Student's t-test (Zar 1984). Multiple observations were compared using a one-way analysis of variance (ANOVA). Straight lines were fitted using least squares regression analysis, slopes and elevations were compared using an analysis of covariance (Zar 1984). Differences were considered significant at $P < 0.05$.

RESULTS

Silvereyes exhibited distinct daily fluctuations in MR, T_b and conductance (Fig. 1). When placed in the chamber in the afternoon, birds usually showed brief periods of activity characterized by high MR, T_b and conductance. This was followed by a period of rest characterized by a low RMR and lower T_b and conductance. After the lights were switched off, MR, T_b and conductance decreased rapidly within about 20 min, and then marginally increased throughout the night. When the lights were switched on in the morning, a rapid increase in MR, T_b and conductance was recorded. The MR and conductance in the morning were generally higher than afternoon measurements and associated with activity.

Fluctuations of MR were observed at all T_a between night and day (Fig. 2). Within the TNZ, the MR also differed between night and day. The BMR (night) was 2.43 ± 0.41 mL O_2 g^{-1} h^{-1}, and birds had a mass of 11.78 ± 1.54 g ($n = 9$), while the corresponding day RMR was significantly elevated at 3.26 ± 0.42 mL O_2 g^{-1} h^{-1} ($P < 0.001$), and mean mass was 11.07 ± 1.72 g ($n = 7$).

While the daily patterns of MR fluctuations at different T_a were similar, the level of MR was significantly dependent on T_a (Fig. 2). MR increased with a reduction in T_a with the relationship: RMR (day) = 9.43 − (0.166 × T_a), $r^2 = 0.73$, $P < 0.001$ and RMR (night) = 6.62 − (0.158 × T_a), $r^2 = 0.92$, $P < 0.001$. Between 3 and 26°C, RMR ranged from 7.77 ± 0.67 mL O_2 g^{-1} h^{-1} (mass = 11.55 ± 0.78 g, $n = 8$) to 5.06 ± 0.82 mL O_2 g^{-1} h^{-1} (mass = 11.15 ± 1.20 g, $n = 9$) during the day, and from 5.58 ± 0.32 mL O_2 g^{-1} h^{-1} (mass = 11.39 ± 1.11 g, $n = 9$) to 2.60 ± 0.30 mL O_2 g^{-1} h^{-1} (mass 10.79 ± 1.14 g, $n = 9$) at night. This represents a decrease of 29% at 7°C up to 49% at 25°C in RMR from day to night. Below the
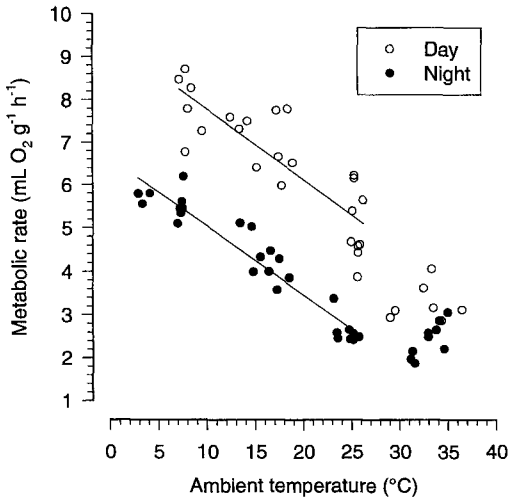
FIGURE 2. MR measured as the rate of oxygen consumption in *Zosterops lateralis* as a function of T_a. Measurements were conducted during winter and each point is the mean of the lowest three or more consecutive readings for each individual. Below the TNZ (3–29°C), lines were fitted by least squares regression, and showed a negative correlation with T_a ($P < 0.001$ day; $P < 0.001$ night). The slopes of the lines were not significantly different ($F_{1,43} = 0.136$, $P > 0.5$), but the elevations were ($F_{1,48} = 247.84$, $P < 0.001$). Within the TNZ the difference between the BMR and minimum RMR (day) values were highly significant ($t = 8.47$, $n = 9$, $P < 0.001$).

TNZ, the highest RMR (8.70 mL O_2 g^{-1} h^{-1}) recorded was during the day at 7.8°C and the lowest RMR (2.41 mL O_2 g^{-1} h^{-1}) recorded was during the night at 25.2°C.

Similar to MR, T_b differed between night and day (Figs. 1 and 3). Below the TNZ, there was a significant decrease from day to night ($P < 0.001$), independent of T_a ($P = 0.56$, day; $P = 0.53$, night) (Fig. 3). During the day, mean T_b was 40.3 ± 0.5°C ($n = 5$) decreasing at night, on average by 3.4°C to 36.9 ± 0.1°C ($n = 5$). The lowest T_b measured for an individual was 35.2°C at a T_a of 7.3°C. The T_b within and below the TNZ were similar during the day ($P = 0.53$), but during the night T_b increased somewhat within the TNZ in comparison to values below the TNZ ($P = 0.004$). Nevertheless, the T_b difference from day to night was significant both within ($P = 0.001$) and below ($P < 0.001$) the TNZ.

Thermal conductance also was strongly affected by T_a and differed between night and day (Figs. 1 and 4). The minimum conduc-
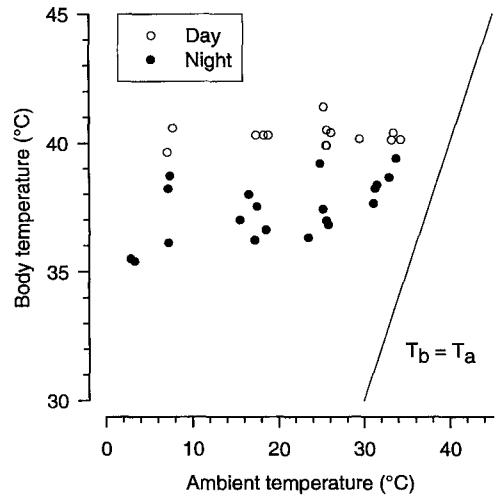

FIGURE 3. T_b as a function of T_a in *Zosterops lateralis*. Measurements were conducted during winter and each point is the mean of the lowest three or more consecutive readings for each individual. T_b was independent of T_a ($P = 0.56$ day; $P = 0.53$ night). The day/night difference in T_b was highly significant below the TNZ ($t = 11.0$, $n = 5$, $P < 0.001$), and within the TNZ (29–36.5°C) ($t = 5.24$, $n = 5$, $P = 0.001$).

tance below the TNZ during the day was 0.31 ± 0.04 mL O_2 g^{-1} h^{-1} °C^{-1} ($n = 5$) and at night decreased by about 50% to 0.20 ± 0.02 mL O_2 g^{-1} h^{-1} °C^{-1} (Fig. 4). During the night, conductance was dependent on T_a (Conductance = 0.17 + (0.002 × T_a), $r^2 = 0.72$, $P < 0.001$) but during the day, although a similar trend occurred, the regression was not significant ($P = 0.06$). Within the TNZ, the conductance values were greater than those below the TNZ ($P = 0.002$ day; $P < 0.001$ night), and they were independent of T_a ($P = 0.18$ day; $P = 0.14$ night). Also, within the TNZ, the day and night values of conductance were not significantly different ($P = 0.19$).

DISCUSSION

Our study demonstrates that *Zosterops lateralis* shows nocturnal hypothermia. It provides the first detailed data on nocturnal hypothermia in an Australian bird. Silvereyes decreased RMR and conductance from day to night by up to 50% and T_b fluctuated by as much as 5.5°C. This decrease in MR and T_b is similar to that recorded for nocturnal hypothermia in other small passerines such as tits (Steen 1958, Reinertsen and Haftorn 1983, 1984, 1986) and finches (Saarela
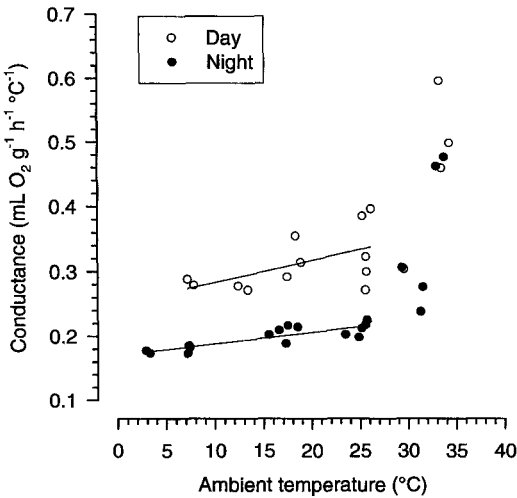
FIGURE 4. Conductance as a function of T_a in *Zosterops lateralis*. Measurements were conducted during winter and each point is the mean of the lowest three or more consecutive readings for each individual. Below the TNZ, conductance was dependent on Ta during the night ($P < 0.001$), but not during the day ($P = 0.063$). The day/night difference was highly significant below ($t = 9.24$, $n = 5$, $P < 0.001$), but not within ($t = 1.46$, $n = 5$, $P = 0.19$) the TNZ.

et al. 1995). These species, however, were all measured over a wider T_a range, and were subjected to much colder T_a ($< -25°C$) than were the birds in our study. They also would be naturally acclimatized to colder temperatures, as they inhabit areas which experience T_a well below zero during winter. It is interesting, in this respect then, that Silvereyes should display the same pattern of nocturnal hypothermia although they do not experience extremely cold temperatures. During winter in Armidale the average daily minimum and maximum T_a are 0 and 12.7°C, respectively. Nevertheless, the weather is unpredictable and adverse conditions presumably reduce foraging time and food supply making birds energetically stressed. In addition, their small size, limited capacity to store fat, and high rate of metabolism make Silvereyes susceptible to the effects of cold T_a and resource depletion. Hence, Silvereyes might experience difficulties meeting their daily energy requirements if they did not resort to nocturnal hypothermia. The pattern of nocturnal hypothermia seen in Silvereyes differs, however, from that observed in such species as hummingbirds

(Lasiewski et al. 1967, Hainsworth and Wolf 1970, Carpenter 1974, Krüger et al. 1982, Hiebert 1990), the Housemartin (Prinzinger and Siedle 1988) and the Poorwill (Jaeger 1949, Ligon 1970, Withers 1977, Brigham 1992). These birds are known to enter a more pronounced form of hypothermia, where T_b can be lowered by 20–35°C and MR falls below BMR, which was not the case for Silvereyes.

The decrease in RMR of up to 50% represents the difference between the RMR values from day to the minimum at night. However, the MR decrease over the duration of the scotophase (~ 11 hr) accrues a net saving to birds of approximately 15%, 21% and 24% at T_a of 7, 16 and 25°C, respectively when compared to the RMR during the day. Thus, nocturnal hypothermia is most effective in terms of energy saving at higher T_a. This is possibly one reason why Silvereyes use it on a regular basis, even though they do not experience T_a as low as birds in parts of the northern hemisphere. Our results support those previously recorded for other passerine species, that at lower T_a the energy savings during nocturnal hypothermia are smaller than they are at higher T_a (Reinertsen and Haftorn 1986, Saarela et al. 1995). The energy savings gained from nocturnal hypothermia in Silvereyes are not as great as they would be if they allowed their T_b to fall to lower temperatures. However, the risk of predation increases when a bird is in an unresponsive state (Hainsworth et al. 1977, Hiebert 1991), and the lower the T_b falls, the less capable it is of responding to the threat of predation (Heller 1988, French 1993).

The reduction of MR during nocturnal hypothermia we observed is likely due to several factors. At night, Silvereyes decreased T_b by, on average, 3.4°C irrespective of T_a. A lower T_b should slow biochemical reactions and reduce energy metabolism, and reduce the thermal gradient between the body and the environment (ΔT), which reduces heat loss and thus permits a reduced heat production. This is in contrast to daily torpor at a T_a above the set point for T_b, where ΔT does not affect the MR during torpor (Song et al. 1995). However, below the set point for T_b when the torpid animal is thermoregulating, the ΔT and MR are related (Song et al. 1995), similar to our observations in *Z. lateralis* (Fig. 5). Therefore, nocturnal hypothermia resembles daily torpor below the set point for

T_b where animals start to thermoregulate although at a much higher T_b.

The decrease in T_b is equivalent to an increase in T_a as it causes the same effect on ΔT. In Silvereyes, the 3.4°C decrease in ΔT accounts for only 1/3 to 1/4 of the diurnal change in MR (Fig. 5). For ΔT to explain the entire MR decrease, there would have to be a more significant decrease, of about 12 to 14°C. In addition to ΔT, a reduction of conductance facilitates the nocturnal reduction of MR. Silvereyes, like other bird species (Aschoff 1981), are able to significantly decrease conductance at night, thus reducing energy expenditure for thermoregulation. A reduction in conductance decreases the heat loss from the body to the environment, and thereby reduces the amount of internal heat production required to maintain a stable T_b. In Silvereyes, conductance below the TNZ was positively correlated with T_a. This permitted them to maintain a relatively high T_b, and although the MR did increase linearly with decreasing T_a, a steeper increase would be required if conductance was not significantly reduced.

Silvereyes exhibited nocturnal hypothermia over the range of T_a measured (3 to 26°C). However, T_b reduction was independent of T_a ($P = 0.56$, day; $P = 0.53$, night). Our findings that T_b during nocturnal hypothermia was independent of T_a are similar to the results recorded for some avian species (Steen 1958, Lasiewski and Dawson 1964, Prinzinger et al. 1981, Hohtola et al. 1991, Brigham 1992), but are in direct contrast to others (West 1972, Reinertsen and Haftorn 1983, 1984, 1986, Swanson 1991, McNab and Bonaccorso 1995). This conflict may be due to a number of factors, not excluding the different response of different species. Discrepancies may also be due to different experimental procedures, such as the range of T_a measured, how close this range is to that experienced by the species naturally, whether the birds were acclimatized to T_a, and the method of measuring T_b.

The ability of some avian species to use nocturnal hypothermia and torpor is likely influenced by a number of factors, including body size and feeding habits. Larger animals are less likely to use nocturnal hypothermia or torpor than smaller animals. The variations in the depth and duration of torpor can be correlated with the size of the bird (Calder and King
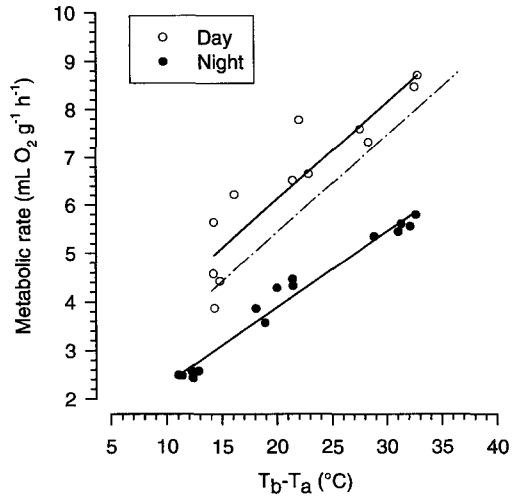

FIGURE 5. MR measured as rate of oxygen consumption in *Zosterops lateralis* as a function of $T_b - T_a$ (ΔT) below the TNZ. Lines were fitted by least squares regression, the equations are: RMR (day) $= 2.07 + (0.203 \times \Delta T)$, $r^2 = 0.83$, $P < 0.001$; RMR (night) $= 0.78 + (0.156 \times \Delta T)$, $r^2 = 0.97$, $P < 0.001$. The slopes of the lines were not significantly different ($F_{1,23} = 3.24$, $P > 0.05$), but the elevations were ($F_{1,24} = 284.2$, $P < 0.001$). The dashed line represents the MR predicted from the average 3.4°C reduction in ΔT from day to night.

1974). All birds reported to use nocturnal hypothermia and torpor are small to medium sized. The rate of rewarming by birds during arousal is known to be inversely related to their mass (Lasiewski and Lasiewski 1967, Bartholomew 1972, Reinertsen and Haftorn 1984). Slow cooling and rewarming rates not only become impractical for larger animals, but also puts them at greater risk of predation because of a delayed response time. Large animals also have a relatively lower MR than small animals when normothermic, and a greater capacity to store energy as fat deposits, and can therefore survive for longer periods of food deprivation (French 1986). Nevertheless, some medium to large size birds can use hypothermia after prolonged starvation (Walker et al. 1983, Graf et al. 1989a, 1989b, Phillips and Berger 1989, Rashotte et al. 1989). Starvation also has been shown to lead to an increase in the day-night difference in the T_b of some bird species (Prinzinger et al. 1981). It is possible that the Silvereyes in our experiments were slightly food-deprived due to the early commencement of afternoon measurement which may have pre-

cluded an afternoon feeding bout. The regime used was necessary to ensure post-absorptive, resting afternoon measurements and, on average, there was less than 10% reduction in body mass during an overnight measurement.

Heterothermy in birds also appears to be affected by diet and feeding habits. Although granivores and frugivores experience seasonal food variations, these represent a gradual and predictable resource change which can be avoided by migrating, and therefore heterothermy in granivorous and frugivorous birds seems to be uncommon (Bartholomew et al. 1983). Most heterothermic birds eat flying insects or nectar, resources which are particularly susceptible to weather changes (Dawson and Hudson 1970). Variation in food abundance is unpredictable and sudden, and often a depleted supply coincides with times when the birds also experience other environmental stresses. Since their MR is already high, the energy required for heat production at very low T_a, especially at night, would be costly. To survive these conditions, huddling and heterothermy appear to be the only options available. Silvereyes primarily feed on nectar and insects, although they may supplement their diet with fruit (MacDonald 1973). During winter, nectar is the most important food source, as few insects are available (Paton and Ford 1977). However, although nectar is often abundant in winter, the short photoperiod allows less time for feeding (Collins and Briffa 1984).

In conclusion, we demonstrated that Silvereyes reduce energy expenditures by using nocturnal hypothermia on a regular basis. This presumably increases their ability to balance energy expenditure with the available food resources, enabling them to be more tolerant of adverse environmental conditions and abrupt changes in food availability. Considering their small size, Silvereyes are extremely successful in reaching and colonizing new areas. There are about 85 species in the family Zosteropidae, divided among 12 genera (Austin 1961, Rutgers et al. 1977, Kikkawa 1985). They range throughout Africa, Asia and Australasia (Austin 1961, Rutgers et al. 1977, Kikkawa 1985). Following introduction by humans to Hawaii, they have successfully spread from island to island (Austin 1961, Kikkawa 1985) and one group has managed to colonize the Antarctic outpost, Macquarie Island (Austin 1961). The ability to balance energy expenditure with availability is particularly important for those groups living in areas with harsh weather conditions, especially during the winter months, and the successful occupation of such habitats may be partially due to the ability of Silvereyes to use nocturnal hypothermia.

ACKNOWLEDGMENTS

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