

Seasonal variations in thermal energetics of Australian silvereyes (*Zosterops lateralis*)

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Abstract

Most Australian birds do not migrate over long distances and therefore have to cope with seasonal changes in weather and food availability. We investigated whether the small (11 g) silvereye *Zosterops lateralis* changes its thermal tolerance from winter to summer. Body mass and body temperature of silvereyes exhibited little seasonal variability. However, metabolic rates (MR) and thermal conductance showed significant changes. Below the thermoneutral zone (TNZ), winter-acclimatized birds had significantly lower resting MR and thermal conductance than summer-acclimatized birds. Within the TNZ (~27.0–33.6 °C winter; ~25.4–33.5 °C summer) basal MR of winter-acclimatized birds (2.30 ± 0.29 mL O₂ g⁻¹ h⁻¹) was significantly lower than that of summer-acclimatized birds (2.88 ± 0.43 mL O₂ g⁻¹ h⁻¹). The average daily MR also differed significantly between summer and winter largely due to a greater reduction of MR at night and the decreased conductance. Our study shows that small passerines such as silvereyes exhibit seasonal variability in physiology and thermal energetics, even when they live in areas with a relatively mild climate, to help overcome seasonal changes in weather conditions and food availability.

Key words: birds, thermal energetics, season, metabolic rate, body temperature, *Zosterops lateralis*

INTRODUCTION

Seasonal changes in climate represent potential increases in energetic stress for small diurnal birds. During summer they are exposed to hot temperatures which may result in dehydration and heat stress. During winter, conditions may be even more unfavourable as the interacting problems of inclement weather, long nights and restricted food supplies, and high energetic costs for thermoregulation may push them to their energetic limit. To cope with these stressors, many birds exhibit seasonal changes in their physiology. In passerines, such changes have been investigated primarily in species from North America and Europe, with the major physiological changes involving body mass (BM), metabolic rate (MR) and insulation (Hart, 1962; Mugaas & Templeton, 1970; Dawson & Carey, 1976; Dawson *et al.*, 1983; Swanson, 1991; Cooper & Swanson, 1994; Saarela, Klapper & Heldmaier, 1995).

Nevertheless, seasonal adjustments might also be required in small passerines living in the less climatically stressful areas such as Australia due to their small size and high energy requirements. Although most of the Australian continent experiences relatively minor

seasonal changes in climate and less harsh winter conditions than many areas in the northern hemisphere, weather conditions are highly unpredictable and may make acquiring food difficult and/or energetically demanding. Moreover, in contrast to many birds from the northern hemisphere, most Australian birds are nomadic or sedentary and do not migrate over long distances (Ford, 1989). To survive changing environmental conditions, small birds living in Australia therefore require some survival mechanisms and/or seasonal acclimatization, although these are likely to be less pronounced than in species from the northern hemisphere.

Although seasonal changes in physiology seem likely in Australian birds, little is known about the subject. The only information available is restricted to seasonal changes in basal MR (BMR) of Australian scrubwrens (Ambrose & Bradshaw, 1988) and resting MR (RMR) of honeyeaters (Collins & Briffa, 1983). There is no detailed information that encompasses seasonal variation of BM, RMR, BMR and conductance, nor how diurnal variations in body temperature (T_b) and MR change with season.

We were interested in whether the silvereye (*Zosterops lateralis*), an Australian passerine, exhibits seasonal acclimatization in morphology and/or thermal energetics. Australian silvereyes have a wide distribution,

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which extends from Queensland to Tasmania and west to Western Australia (Blakers, Davies & Reilly, 1985). They are resident to the extent that some individuals are present throughout their range in all seasons and thus are annually exposed to fluctuations in temperature and food availability. Silvereyes are known to significantly reduce MR and T_b at night in winter (Maddocks & Geiser, 1997, 1999). To determine whether they exhibit seasonal acclimatization, we investigated the seasonal changes in BM, MR, T_b and thermal conductance over a range of ambient temperatures (T_a). We also determined whether daily fluctuations of MR and T_b change with season.

MATERIALS AND METHODS

Nine silvereyes were captured with mist nets near Armidale, NSW, Australia (30°32'S, 151°39'E) in June (winter) 1995. As some of these birds were used in another experiment and were not available for summer measurements, a further 4 birds were captured in September. After capture, birds were weighed to the nearest 0.1 g. They were housed outdoors in wooden cages, where they were exposed to natural photoperiod and temperature fluctuations. Water and food (artificial nectar and insect replacements, apple and *Tenebrio* larvae) were available in excess and supplied fresh daily.

Winter measurements were carried out during August and the first week in September (T_a range approx. 0 to 13°C; Bureau of Meteorology, 1988), and summer measurements during December and January (T_a range approx. 13 to 27°C; Bureau of Meteorology, 1988). MR was measured as the rate of oxygen consumption using open flow respirometry. The respirometry chamber (1L glass jar fitted with a perch) was positioned within a temperature-controlled cabinet ($\pm 0.5^\circ\text{C}$). Birds could not see each other during measurement periods. Air flow rates of about 300 mL min⁻¹ through the chambers were controlled with rotameters and measured with a mass flowmeter (FMA 5606, Omega Engineering Inc. Stamford, USA). Oxygen content of the air entering and leaving the metabolic chamber was measured using a single channel oxygen analyser (Ametek Applied Electrochemistry Oxygen Analyser S-3A/1, Pittsburgh). Solenoid valves switched channels in 3 min intervals, which permitted the measurement of up to 3 animals and a reference in succession, each channel was measured once every 12 min. 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 remained healthy during the course of the experimental period.

Implanted temperature-sensitive transmitters (Mini-mitter model X-M, in modified, smaller capsule) were used to measure T_b ($\pm 0.1^\circ\text{C}$). The wax-paraffin coated transmitters weighed 1.1–1.3 g and measured 12 × 8 mm and were smaller than silvereye eggs (17 × 13 mm). Several days after batteries were replaced, transmitters were calibrated to the nearest 0.1°C against a precision

mercury thermometer in a waterbath over a T_a range of 30–50°C. The transmitters were implanted intraperitoneally under Isoflurane anaesthesia. Animals were allowed at least 7 days to recover before any experiments were performed. The transmitter signal was received with a ferrite rod antenna placed under each chamber and multiplexed to a receiver.

Ambient temperature (T_a) was measured to the nearest 0.1°C with a calibrated Cu-Constantan thermocouple inserted 1 cm into the respirometry chamber. Thermocouple output was amplified by a digital thermometer (Omega DP116). Measurements of T_b and T_a were taken simultaneously with MR every 12 mins.

Analog outputs from the flowmeter, oxygen analyser, transmitter receiver and digital thermometer were interfaced via a 14 bit analog to digital converter card to a computer. Data acquisition and processing were performed with software written by B. Lovegrove, T. Ruf and G. Körtner. MR values were calculated for STP conditions according to equation 3a of Withers (1977) assuming an RQ of 0.85.

During MR measurements, birds were post-absorptive (at least 2 h since last possible meal) and food and water were not available. RMR were determined over a range of T_a from 3 to 26°C which is approximately the range between average daily minimum in winter and average daily maximum in summer in the Armidale area. Birds were placed in the respirometry chambers at approx. 15:00 and kept at constant T_a for periods of 16–18 h. The photoperiod within the cabinet was adjusted with a timer to coincide with the natural photoperiod at that time of year (approx. L11:D13 winter; L14:D10 summer).

Measurements of oxygen consumption were used to determine RMR, BMR and average daily MR (ADMR) during winter and summer. MR values were calculated as the mean of at least 3 low consecutive readings (i.e. over at least a 36 min interval) at each T_a . The means of the corresponding readings of T_b and T_a were also calculated.

For MR measurements within the thermoneutral zone (TNZ), animals were placed in respirometry chambers at approx. 16:00 and kept for a maximum of 8 h. Measurements were taken over a T_a range of 25 to 40°C to determine the TNZ. Starting at 25°C the T_a was progressively increased in steps of 2°C every hour until a sharp rise in MR and T_b was observed. If an acute rise was evident for 1 individual, all birds being measured at that time were removed because the removal of 1 would disturb the others. Therefore, for some individuals, data above TNZ may be lacking due to premature termination of the experiment. BMR was determined for each individual as the lowest MR value over 36 min during the scotophase. The lower critical T_a (T_{lc}) of the TNZ, at which RMR begins to increase with decreasing T_a , was determined by calculating the T_a of the RMR/BMR intersect of each individual using the RMR vs. T_a regression line below the TNZ. The upper critical T_a (T_{uc}) was determined by calculating the T_a of the RMR/BMR intersect using the RMR vs. T_a

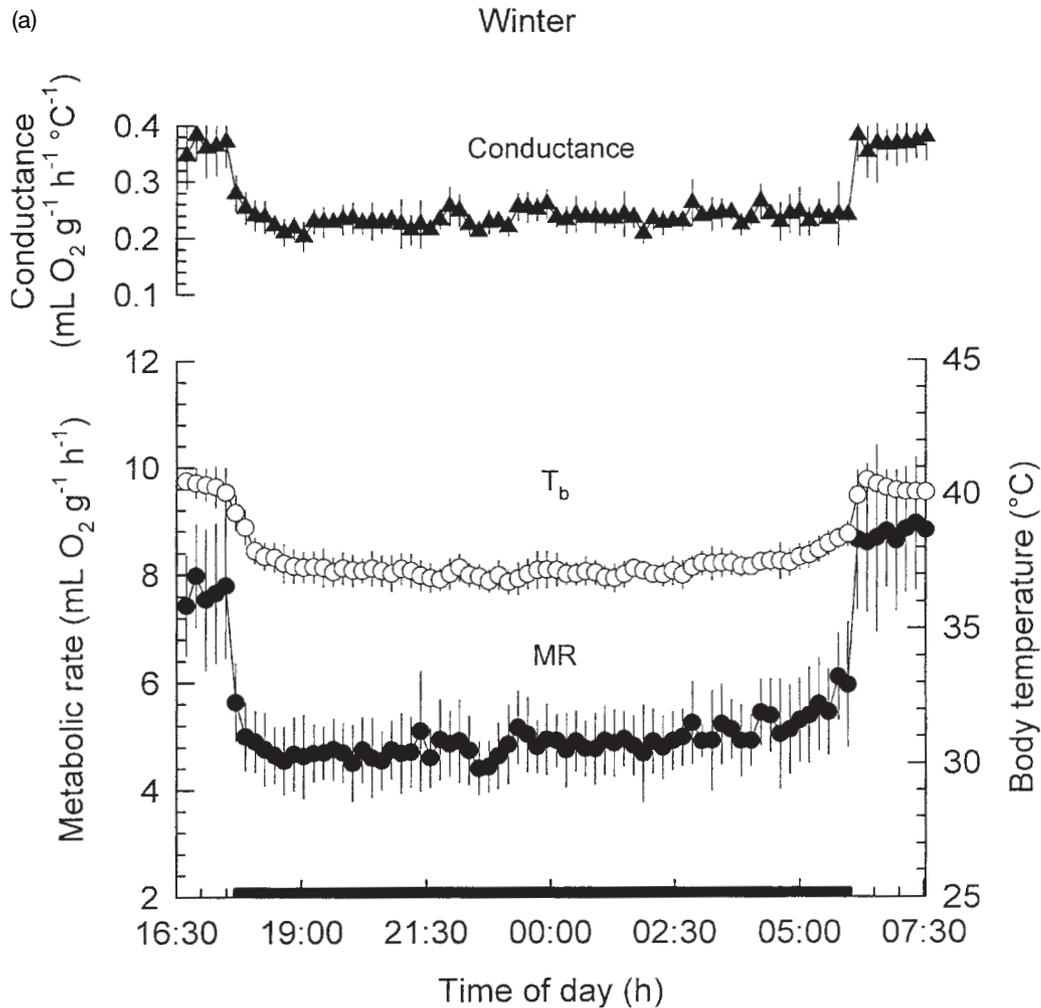


Fig. 1(a). Daily fluctuation of metabolic rate (MR), body temperature (T_b) and conductance of *Zosterops lateralis* at ambient temperature (T_a) 16°C during winter. Animals were measured at a constant T_a for a period of 16–18 h. Values shown are mean \pm SD of $n=9$ (MR), $n=4$ (T_b and conductance). Dark bar indicates period of darkness.

regression line above the TNZ of pooled data as there was insufficient data above the TNZ to calculate T_{uc} for each individual.

The ADMR was calculated for each individual integrating total MR at each T_a measured. An average for both the photophase and scotophase was determined, which was then multiplied by the duration of the phase for each season (L11:D13 winter; L14:D10 summer). Data were converted to kJ (1L $O_2 = 20.08$ kJ; Schmidt-Nielsen, 1997). For each measurement T_a was also averaged, and data for each season were grouped according to T_a . For each group, T_a data were then rounded to the nearest 0.1°C. Mass-specific thermal conductance was calculated using the equation: $\text{Conductance} = \text{MR}/(T_b - T_a)$ (Lasiewski, Weathers & Bernstein, 1967).

Data are presented as mean \pm SD of the number of individuals measured (n). Sample variances were tested for homogeneity using F_{\max} test. Paired observations were compared using a paired or pooled Student's t -test. Linear regressions were fitted using the method of least

squares, and the slopes and elevations were compared using an analysis of covariance. Differences were considered significant at the 5% level ($P < 0.05$).

RESULTS

The BM of silvereyes varied little seasonally. The average BM during winter (11.22 ± 0.96 g, $n=9$) did not differ significantly ($P=0.26$) from the average summer BM (10.90 ± 1.04 g, $n=9$).

Daily oscillations of MR, T_b and conductance were triggered by the light phase both during winter (Fig. 1a) and summer (Fig. 1b). The three variables decreased significantly immediately after the light was switched off (approx. 17:30 winter; 18:50 summer), but then gradually increased throughout the scotophase. A significant and rapid increase of MR, T_b and conductance occurred when the light was switched on (approx. 06:25 winter; 04:50 summer).

RMR was negatively correlated with T_a during both

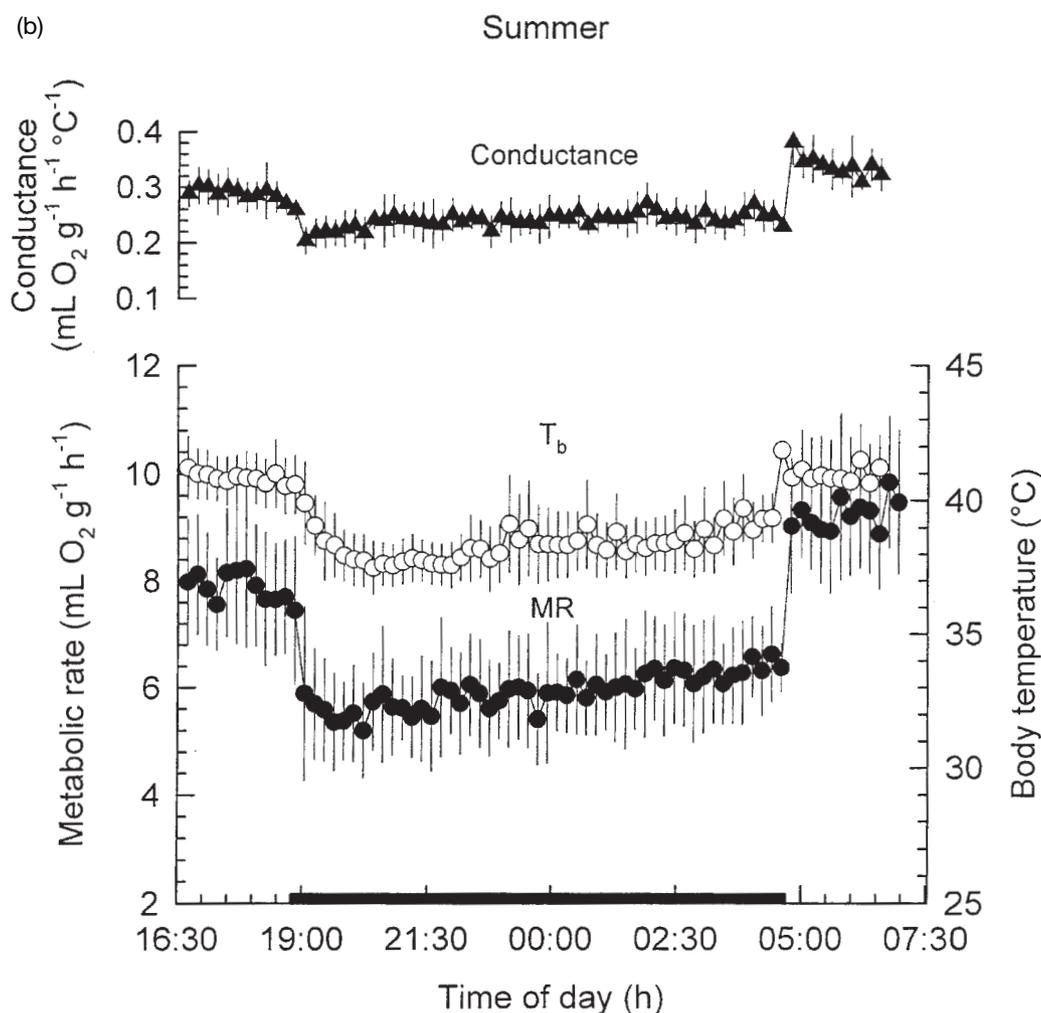


Fig. 1(b). Daily fluctuation of metabolic rate (MR), body temperature (T_b) and conductance of *Zosterops lateralis* at ambient temperature (T_a) 16°C during summer. Animals were measured at a constant T_a for a period of 16–18 h. Values shown are mean \pm SD of $n=9$ (MR), $n=4$ (T_b and conductance). Dark bar indicates period of darkness.

the scotophase ($r^2=0.92$, $P<0.001$; $r^2=0.87$, $P<0.001$; Fig. 2) and photophase ($r^2=0.73$, $P<0.001$; $r^2=0.67$, $P<0.001$) during winter and summer, respectively. However, winter RMRs were significantly lower than those measured during summer for both photophase ($P=0.02$) and scotophase ($P<0.001$). Between T_a 3°C and 26°C during winter, RMR ranged from 7.77 ± 0.67 mL O₂ g⁻¹ h⁻¹ ($n=9$) to 5.06 ± 0.82 mL O₂ g⁻¹ h⁻¹ ($n=9$) during the photophase, and from 5.58 ± 0.32 mL O₂ g⁻¹ h⁻¹ ($n=9$) to 2.60 ± 0.30 mL O₂ g⁻¹ h⁻¹ ($n=9$) during the scotophase. This is a decrease in MR of up to 49.4% from photo- to scotophase in winter. During summer the RMR ranged from 9.46 ± 0.87 mL O₂ g⁻¹ h⁻¹ ($n=7$) to 5.84 ± 0.88 mL O₂ g⁻¹ h⁻¹ ($n=9$) during the photophase, and from 7.35 ± 0.58 mL O₂ g⁻¹ h⁻¹ ($n=8$) to 3.26 ± 0.55 mL O₂ g⁻¹ h⁻¹ ($n=9$) during the scotophase. This is a decrease in MR of up to 44.4% from photo- to scotophase in summer.

The TNZ extended over about 7–8°C, ranging from 27.0 ± 2.4 °C to 33.6 °C during winter and from 25.4 ± 1.9 °C to 33.5 °C during summer (Fig. 2). How-

ever, the T_{ic} for winter- and summer-acclimatized birds did not differ significantly ($P=0.20$). Within the TNZ, BMR of winter birds (2.30 ± 0.29 mL O₂ g⁻¹ h⁻¹, $n=8$) was significantly lower ($P=0.006$) than that of summer birds (2.88 ± 0.43 mL O₂ g⁻¹ h⁻¹, $n=9$) (Fig. 2).

Below the TNZ, the scotophase T_b in both seasons was more or less stable until T_a declined below 5°C, and thus was not correlated with T_a ($P=0.53$ winter; $P=0.13$ summer) (Fig. 3). The mean T_b of birds both below (36.92 ± 0.95 °C, $n=5$, winter; 37.6 ± 0.87 °C, $n=4$, summer) and within the TNZ (38.41 ± 0.75 °C, $n=4$, winter; 39.9 °C, $n=2$, summer) were indistinguishable ($P=0.07$ and $P=0.13$, respectively) (Fig. 3).

Thermal conductance below the TNZ during the scotophase was significantly lower in winter than in summer ($P=0.001$) (Fig. 4). Thermal conductance was a significant linear function of T_a during winter ($P<0.001$), though not in summer ($P=0.73$). The mean thermal conductance within the TNZ during winter (0.38 ± 0.10 mL O₂ g⁻¹ h⁻¹ °C⁻¹, $n=4$) was not significantly higher ($P=0.33$) than the mean for summer

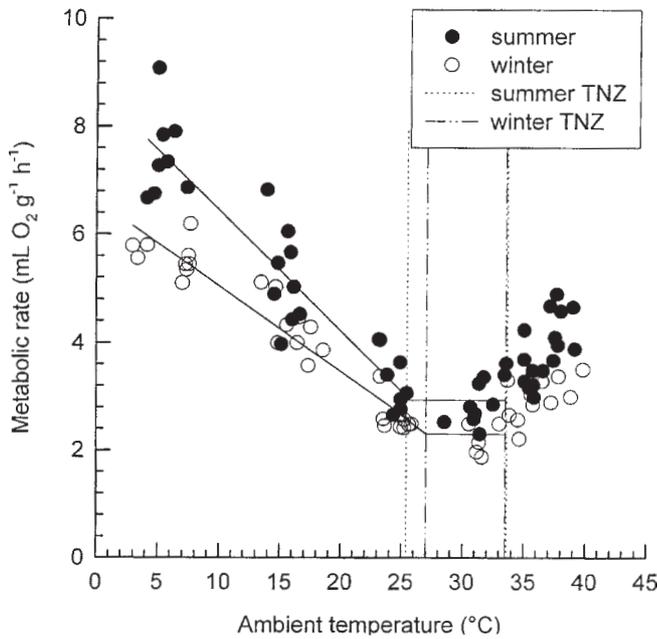


Fig. 2. Mass-specific metabolic rate of resting *Zosterops lateralis* over a range of ambient temperature (T_a) during the scotophase. Measurements were taken in summer (closed symbols) and in winter (open symbols), and each point represents a measurement for one individual. Dashed and broken lines represent the lower critical and upper critical temperatures (T_{lc} and T_{uc}) of the thermoneutral zone (TNZ) for summer and winter, respectively. Below the TNZ the MR showed a negative linear relationship with T_a (summer: $MR = 8.50 - 0.22 T_a$, $P < 0.001$, $r^2 = 0.87$; winter: $MR = 6.62 - 0.16 T_a$, $P < 0.001$, $r^2 = 0.92$). Within the TNZ (25.4–33.5 °C summer; 27.0–33.6 °C winter) the BMR was 2.88 ± 0.43 mL O_2 g^{-1} h^{-1} in summer-acclimatized birds and 2.30 ± 0.29 mL O_2 g^{-1} h^{-1} in winter-acclimatized birds.

(0.29 mL O_2 g^{-1} h^{-1} $^{\circ}C^{-1}$, $n = 2$) (Fig. 4). However, due to the low sample size, these results within the TNZ must be viewed with caution.

ADMR differed significantly between summer and winter largely due to the greater reduction of MR at night and the decreased conductance in winter (Fig. 5). As winter RMRs were lower than summer RMRs, and the duration of the scotophase during winter is longer (i.e. winter 13 h, summer 10 h), the ADMR in winter was reduced. At T_a 6.3 °C, 15.8 °C and 24.9 °C winter-acclimatized birds used significantly less energy per day than summer-acclimatized birds ($P = 0.0001$, $P = 0.008$, and $P = 0.002$, respectively) (Fig. 5).

DISCUSSION

Our study demonstrates that silvereyes undergo distinct daily fluctuations in MR, T_b and conductance on a regular basis during both winter and summer. These fluctuations, especially that of MR, are more pronounced in winter than in summer resulting, together with decreases in conductance, in lower ADMR during

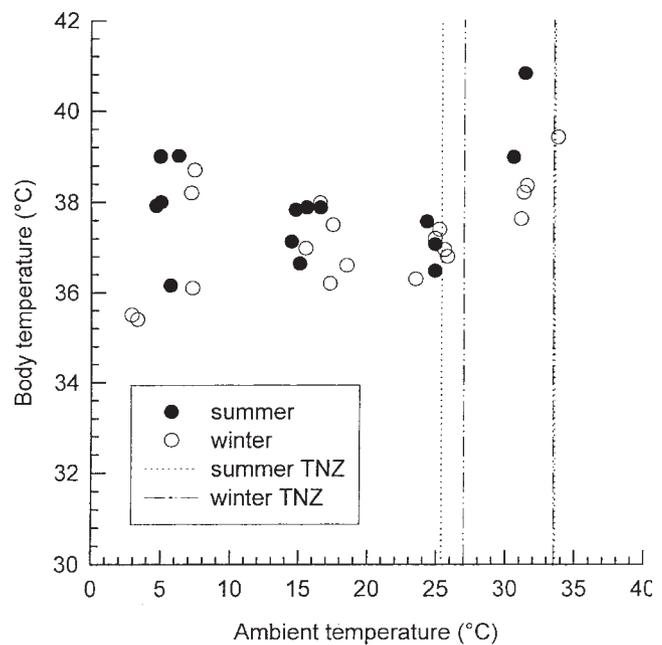


Fig. 3. Body temperature (T_b) of *Zosterops lateralis* as a function of ambient temperature (T_a) during summer (closed symbols) and winter (open symbols) during the scotophase. Each point represents a measurement for one individual. The dashed and broken lines represent the lower critical and upper critical temperatures (T_{lc} and T_{uc}) of the thermoneutral zone (TNZ) for winter and summer, respectively. Below the TNZ the T_b showed no relationship to T_a in either summer ($P = 0.13$) or winter ($P = 0.53$). Within the TNZ, T_b for winter birds (38.4 ± 0.75 °C) was lower, but not significantly, than summer birds (39.9 ± 1.3 °C).

winter. This phenomenon of controlled reduction of T_b by several degrees for energy conservation at night is not uncommon, and has been recorded for many small passerines from North America and Europe (Mugaas & Templeton, 1970; West, 1972; Pohl & West, 1973; Reinertsen & Haftorn, 1983; Berger & Phillips, 1993; Saarela *et al.*, 1995). However, our study is the first to demonstrate the seasonal change of thermal energetics in an Australian passerine. Altering thermoregulatory patterns with season should maximize energy use and increase the probability of survival.

Seasonal acclimatization by birds commonly involves altering a number of morphological and physiological variables, including BM, MR, T_b and conductance. Increases in BM in winter are largely due to an increase in the amount of fat stores (Marsh & Dawson, 1989). Increased fat stores are common for avian winter acclimatization, as fat can be used to help fulfil the high energy demand that is required for thermoregulation, because it can function as a high energy content reserve during foraging restrictions (Dawson & Marsh, 1986), and, especially when stored subcutaneously, also increases insulation. Seasonal changes in BM appear to be common for ground foraging birds, however, tree foraging species (such as silvereyes) show less change (Rogers, 1987; Blem, 1990). This may be because the

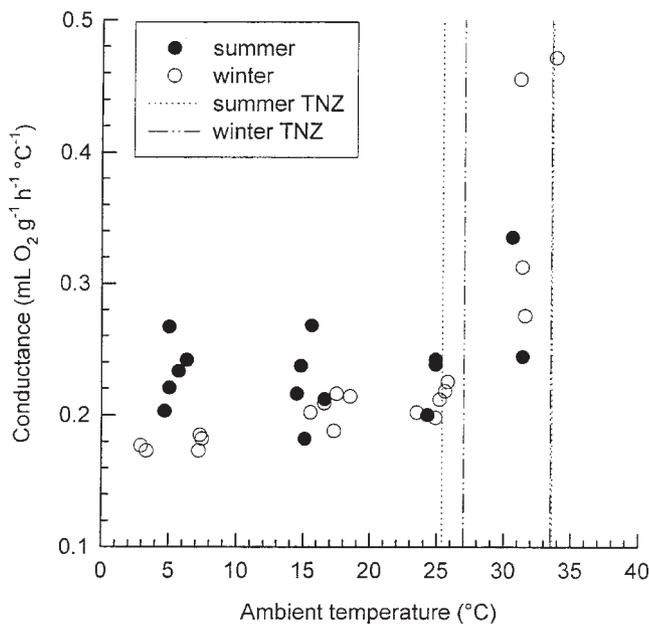


Fig. 4. Thermal conductance of *Zosterops lateralis* as a function of ambient temperature (T_a) during the scotophase in summer (closed symbols) and winter (open symbols). Each point represents a measurement for one individual. Dashed and broken lines represent the lower critical and upper critical temperatures (T_{lc} and T_{uc}) of the thermoneutral zone (TNZ) for winter and summer, respectively. Below the TNZ, conductance values and T_a showed a positive linear relationship in winter (conductance = $0.170 + 0.002T_a$, $P < 0.001$, $r^2 = 0.72$), though not in summer (conductance = $0.232 - 0.0003T_a$, $P = 0.73$, $r^2 = 0.01$).

food supply is more predictable for tree foraging birds (Rogers, 1987; Rogers & Smith, 1993). Like some other small passerines (West, 1972; Cooper & Swanson, 1994), the silvereyes in our study did not significantly increase BM during winter, indicating that altering fat stores during seasonal acclimatization is of minor consequence and may reflect the limitations imposed by their small body size and requirements for locomotion.

Seasonal effects on BMR also differs widely among small birds. The silvereyes displayed an elevated BMR in summer which may be related to increased energy demands for reproductive organs. However, other similar-sized passerines elevate BMR in winter (Pohl & West, 1973; Swanson, 1991), or show no significant change (Dawson & Carey, 1976). A reduced BMR in winter, such as that displayed by silvereyes, lowers energy requirements for maintenance and may enhance individual survival over winter (Feist & White, 1989).

Silvereye MR changes include not only a seasonal change in BMR, but also a more pronounced nocturnal decrease in winter RMR which results in a lower ADMR in comparison to summer. RMR during the scotophase, in comparison to photophase, decreased by up to 49% in winter and by 44% in summer, which is particularly advantageous during the long winter nights when thermoregulatory responses are most likely to be most costly. Moreover, scotophase RMR of winter-

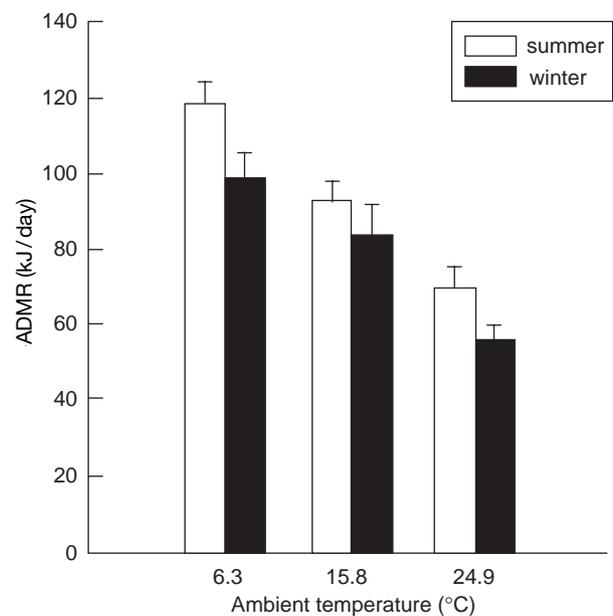


Fig. 5. Average daily metabolic rate (ADMR, kJ/day) of *Zosterops lateralis* during summer (open) and winter (solid). Energy consumption was calculated for each individual using total MR at each ambient temperature (T_a) measured. Data were converted to kJ and an average for both the photophase and scotophase was determined, which was then multiplied by the duration of the phase for each season (L11:D13 winter; L14:D10 summer). For each measurement T_a was also averaged, and data for each season were grouped according to T_a . For each group, T_a data were then rounded to the nearest 0.1 °C. Summer energy consumption was 27%, 10.6% and 11.4 % greater than winter energy consumption at T_a 6.3 °C, 15.8 °C and 24.9 °C, respectively.

acclimatized silvereyes were up to 21.5% lower than summer-acclimatized birds. Winter reduction in RMR has been recorded for a number of small passerines from the northern hemisphere, from areas that experience extremely cold winters (Dawson & Carey, 1976; Saarela *et al.*, 1995), and also those that have relatively mild winters (Swanson, 1991; Cooper & Swanson, 1994). Thus, it appears that RMR reduction in winter is a common adaptation in small passerines. The low RMR of silvereyes coupled with the extended period of hypometabolism in winter accrues significant savings in the ADMR (kJ/day) when compared to summer-acclimatized birds. Thus, the reduction of scotophase MR in winter allows for better use of energy reserves for maintaining T_b over the longer scotophase. However, the overall nightly energy consumption for the period of the scotophase (winter 13 h; summer 10 h) in winter birds is greater than in summer. Nocturnal decreases in MR were, to some extent, due to decreases in conductance. This reduction in conductance lowers the amount of heat lost to the environment, and as such, reduces the energy required to maintain a stable T_b . The greater reduction of conductance at night in comparison to daytime values in winter (42%) compared to summer (30%), reflects the greater reduction in MR which allows

extended availability of energy reserves. Moreover, in conjunction with RMR, winter-acclimatized birds had significantly lower thermal conductances when compared to summer-acclimatized birds, though their T_{bs} did not differ significantly. This is probably due to the better insulating plumage that birds tend to acquire in winter (Marsh & Dawson, 1989), which would reduce the thermal conductance.

In conclusion, our findings of seasonal acclimatization in Australian silvereyes show that even for birds exposed to a relatively mild climate, changes in thermal energetics are used to overcome potential energetic constraints. It suggests that such adaptations are commonly used by small passerines and other birds, and not just in species that inhabit areas of harsh, cold climates.

Acknowledgments

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REFERENCES

- Ambrose, S. J. & Bradshaw, D. (1988). Seasonal changes in standard metabolic rates in the white-browed scrubwren *Sericornis frontalis* (Acanthizidae) from arid, semi-arid and mesic environments. *Comp. Biochem. Physiol.* **89A**: 79–83.
- Berger, J. B. & Phillips, N. H. (1993). Sleep and energy conservation. *News in Physiol. Sci.* **8**: 276–281.
- Blakers, M., Davies, S. J. J. F. & Reilly, P. N. (1985). *The atlas of Australian birds*. Carlton: Melbourne University Press.
- Blem, C. R. (1990). Avian energy storage. In *Current Ornithology*: 59–113. Johnson, R. F. (Ed.). New York: Plenum.
- Bureau of Meteorology (1988). *Climatic averages Australia*. Canberra: Australian Government Publishing Service.
- Collins, B. G. & Briffa, P. (1983). Seasonal variations in the energetics of an Australian nectarivorous bird, *Lichmera indistincta*. *Comp. Biochem. Physiol.* **74A**: 731–738.
- Cooper, S. J. & Swanson, D. L. (1994). Seasonal acclimatization of thermoregulation in the black-capped chickadee. *Condor* **96**: 638–646.
- Dawson, W. R. & Carey, C. (1976). Seasonal acclimatization to temperature in Cardueline finches. *J. Comp. Physiol.* **112**: 317–333.
- Dawson, W. R., Marsh, R. L., Buttemer, W. A. & Carey, C. (1983). Seasonal and geographic variation of cold resistance in house finches *Carpodacus mexicanus*. *Physiol. Zool.* **56**: 353–369.
- Dawson, W. R. & Marsh, R. L. (1986). Winter fattening in the American goldfinch and the possible role of temperature in its regulation. *Physiol. Zool.* **59**: 357–368.
- Feist, D. D. & White, R. G. (1989). Terrestrial mammals in cold. In *Advances in comparative and environmental physiology*: 327–354. Wang, L. C. H. (Ed.). Heidelberg: Springer-Verlag.
- Ford, H. A. (1989). *Ecology of Birds: an Australian Perspective*. Chipping Norton: Surrey Beatty and Sons.
- Hart, J. S. (1962). Seasonal acclimatization in four species of small wild birds. *Physiol. Zool.* **35**: 224–235.
- Lasiewski, R. C., Weathers, W. W. & Bernstein, M. H. (1967). Physiological responses of the giant hummingbird, *Patagona gigas*. *Comp. Biochem. Physiol.* **23**: 797–813.
- Maddocks, T. A. & Geiser, F. (1997). Energetics, thermoregulation and nocturnal hypothermia in Australian silvereyes. *Condor* **99**: 104–112.
- Maddocks, T. A. & Geiser, F. (1999). Thermoregulatory limits of an Australian Passerine, the Silvereye (*Zosterops lateralis*). *J. Therm. Biol.* **24**: 43–50.
- Marsh, R. L. & Dawson, W. R. (1989). Avian Adjustments to Cold. In *Advances in comparative and environmental physiology*: 205–253. Wang, L. C. H. (Ed.). Heidelberg: Springer-Verlag.
- Mugaas, J. N. & Templeton, J. R. (1970). Thermoregulation in the red-breasted nuthatch (*Sitta canadensis*). *Condor* **72**: 125–132.
- Pohl, H. & West, G. C. (1973). Daily and seasonal variation in metabolic response to cold during rest and forced exercise in the common redpoll. *Comp. Biochem. Physiol.* **45A**: 851–867.
- Reinertsen, R. E. & Haftorn, S. (1983). Nocturnal hypothermia and metabolism in the willow tit *Parus montanus* at 63° N. *J. Comp. Physiol. B* **151**: 109–118.
- Rogers, C. M. (1987). Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology* **68**: 1051–1061.
- Rogers, C. M. & Smith, J. N. (1993). Life-history theory in the non-breeding period: trade-offs in avian fat reserves. *Ecology* **74**: 419–426.
- Saarela, S., Klapper, B. & Heldmaier, G. (1995). Daily rhythm of oxygen consumption and thermoregulatory responses in some European winter- or summer-acclimatized finches at different ambient temperatures. *J. Comp. Physiol. B* **165**: 366–376.
- Schmidt-Nielsen, K. (1997). *Animal physiology: adaptation and environment*. 5th edn. New York: Cambridge University Press.
- Swanson, D. L. (1991). Seasonal adjustments in metabolism and insulation in the dark-eyed junco. *Condor* **93**: 538–545.
- West, G. C. (1972). The effect of acclimation and acclimatization on the resting metabolic rate of the common redpoll. *Comp. Biochem. Physiol.* **43A**: 293–310.
- Withers, P. C. (1977). Measurement of V_{O_2} , V_{CO_2} , and evaporative water loss with a flow-through mask. *J. Appl. Physiol.* **42**: 120–123.