PERGAMON

Journal of Thermal Biology 24 (1999) 43–50

Journal of
THERMAL BIOLOGY

The thermoregulatory limits of an Australian Passerine, the Silvereye (*Zosterops lateralis*)

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Received 6 June 1998; received in revised form 20 August 1998; accepted 10 October 1998

Abstract

(1) The thermal capabilities of Australian silvereyes (*Zosterops lateralis*, 11 g) were investigated both at low and high ambient temperatures (T_a) during the photophase and scotophase. (2). The peak metabolic rate (PMR) induced by helium–oxygen (79:21 %, He–O_2) exposure during the photophase was 15.64 ± 1.55 mL O_2 g^{-1} h^{-1} at an effective lower survival limit T_a (T_{pmr}) of -39.7 ± 6.1°C. (3). Above the thermoneutral zone (TNZ), metabolic rate, body temperature (T_b), and thermal conductance increased steeply, but they were able to withstand a T_a of 39°C. (4). Our study shows that silvereyes are able to tolerate an impressive range of T_a from about −42°C to at least +39°C and are able to produce enough heat to maintain a thermal difference between T_b and T_a of up to 80°C.

1. Introduction

Tolerance of a wide range of ambient temperatures (T_a) permits some animals to live in a variety of habitats and to survive even in the seemingly most adverse weather conditions.

To achieve this and to maximise the time period that they can remain active, many species rely on endothermic heat production to maintain a body temperature (T_b) largely independently of T_a (Schmidt-Nielsen, 1990). However, the production of heat is energetically expensive. Particularly, small endotherms possess relatively large surface areas that facilitate dissipation of heat to a cold environment which must be compensated by an increase in metabolic rate (MR) (Schmidt-Nielsen, 1990). To allow greater tolerance of extreme thermal conditions several adaptations are commonly employed. These include increasing insulation to conserve energy at low T_a or having a high peak MR (PMR). In contrast, warm-climate species often have a low basal MR (BMR) and a high thermoneutral zone (TNZ) in order to increase heat tolerance.

Unfortunately, specialisations towards either hot or cold T_a can be disadvantageous as it will narrow the climatic range that a species can tolerate. For example, arctic passerines have high BMR and a low TNZ (West, 1972; Pohl and West, 1973; Rosenmann and Morrison, 1974; Grossman and West, 1977; Reinertsen and Haftorn, 1986), whilst arid zone birds have low BMR coupled with a high TNZ (Calder, 1974; Ambrose et al., 1996). Therefore, animals adapted for surviving extremely cold weather should have a decreased tolerance to heat, while those adapted for extremely hot conditions should have a decreased cold tolerance.

Birds that inhabit areas which experience seasonal changes in weather conditions and remain there throughout the year must be able to cope with this challenge. Many small endotherms resort to seasonal acclimatisation, adjusting MR, T_b and thermal conductance in response to T_a (Feist and White, 1989). However, if extremes of T_a are experienced on a daily basis, acclimatisation cannot occur. Therefore, survival in such a habitat requires both a high thermogenic ca-

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0306-4565/99/$ - see front matter
PII: S0306-4565(98)00036-9

pacity and thermal tolerance to adjust to both extremes.

Australian silvereyes have a wide distribution range, inhabiting areas from Queensland to Tasmania, and west to Western Australia (Blakers et al., 1985). They are resident to the extent that individuals occur throughout their range yearlong (Blakers et al., 1985) and thus are annually exposed to temperature and food fluctuations. In winter, some populations experience warm days followed by cold nights. Such short-term extremes in T_a will make acclimatisation impossible and will require energetically demanding metabolic responses. As the extremes of T_a encountered in the Armidale area in winter range from −11 to 26.3°C (minimum and maximum T_a ever recorded; P. Burr, personal communication) and daily T_a fluctuations regularly exceed 20°C, we were interested in whether silvereyes from this area were better adapted for cold conditions, hot conditions, or able to cope with both extremes. Therefore we investigated how silvereyes regulate their MR, T_b and conductance on a daily basis, and how they adjust these properties in response to T_a changes. In particular we investigated the metabolic and thermal responses to cold and heat exposure, and whether these responses varied during the photo- and scotophase.

2. Material and methods

2.1. Experimental animals

Nine silvereyes were mist-netted near Armidale, NSW, Australia (30°32′S, 151°39′E, elevation 980 m) in June (winter) 1995. Groups of two or three animals were housed outdoors in wooden cages (70×40×40 cm) where they were exposed to natural photoperiod and temperature fluctuations. Water and food (artificial nectar and insect replacements, apple and *Tenebrio* larvae) were available ad libitum and were replaced daily.

2.2. Measurements of MR, T_b and T_a

MR measurements were conducted during August and the first week of September 1995. MR was measured as the rate of oxygen consumption using open-flow respirometry. Animals were individually placed in 1-L glass respirometry chambers fitted with a perch, and then positioned within a temperature-controlled cabinet (±0.5°C). For calculation of mass-specific oxygen consumption, animals were weighed before and after each testing period and body mass (BM) interpolated assuming a constant rate of mass loss. Air flow rates of approximately 300 mL min^{-1} through the chambers were controlled with rotameters and measured with a calibrated (Levy, 1964) mass flowmeter (FMA 5606, Omega Engineering, 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 three animals and a reference in succession; each channel was measured once every 12 min.

T_b was measured using implanted temperature-sensitive transmitters (Minimitter model X-M in modified, smaller capsule). These had been calibrated to the nearest 0.1°C against a precision mercury thermometer in a water bath between 30–45°C. The wax-paraffin-coated transmitters weighed 1.1–1.3 g, measured 12×8 mm and were smaller than silvereye eggs (17×13 mm). Transmitters were implanted intraperitoneally under Isoflurane anaesthesia. Animals were allowed at least a 7-day recovery period after surgical implantation before any experiments were performed. The transmitter signal was received with a ferrite rod antenna placed under each chamber and multiplexed to a receiver.

A Cu–Cn thermocouple inserted 1 cm into the respirometry chamber measured T_a (±0.1°C). Thermocouple output was amplified by a digital thermometer (Omega DP116). Measurements of T_b and T_a were taken simultaneously with MR every 12 min.

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 PC. Data acquisition and processing were performed with software written by B. Lovegrove, T. Ruf and G. Körtner. VO_2 values were calculated for STP conditions according to Eq. (3a) of Withers (1977) assuming an RQ of 0.85.

2.3. Experimental procedures

Measurements of oxygen consumption were conducted in both air and He–O_2 atmosphere. Measurements began when the birds were post-absorptive (at least 2 h since last possible feeding) and food and water were not available during MR measurements. The photoperiod within the cabinet was adjusted with a timer to coincide with the natural photoperiod (approximately L11:D13 h). Individuals were allowed at least 3 days after each measurement before being measured again.

2.4. Measurements in air

Resting MRs (RMR) were determined in air over a range of T_a from 3–40°C. For T_a < 25°C, animals were placed in the respirometry chambers at approxi-

mately 15:30 h and measured at a constant T_a for periods of 16–18 h. Above T_a 25°C, animals were placed in the respirometry chambers at approximately 09:00 h (photophase) and at least 1 h was allowed for birds to settle before measurements commenced. For the corresponding scotophase measurements, animals were placed in the respirometry chambers at approximately 16:15 h (~1.25 h prior to lights out) and measurements commenced approximately 1 h after lights out. T_a was increased every hour in 2°C steps until an acute increase in MR and/or T_b was observed, at which point the experiment was terminated. For the variable T_a measurements, birds were held in the respirometry chambers for a maximum of 8 h before they were removed and fed. All MR values were calculated as the mean of at least three 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. BMR was determined for each individual as the lowest MR value during the scotophase. The lower critical T_a (T_{lc}) of the TNZ, where RMR increases 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}), where RMR increases with increasing T_a, was determined by calculating the T_a at which the mean BMR for $n = 8$ individuals intersected the RMR vs T_a regression line above the TNZ. For the scotophase, pooled data were used for values above the TNZ because not enough data for all individuals were available. For photophase, insufficient data was available above the TNZ for the determination of T_{uc}.

2.5. Measurements in He–O_2

To avoid cold injury at low T_a, helium–oxygen gas mixture (He–O_2; 79:21% helium–oxygen) was used to facilitate heat loss and induce PMR at moderate T_as. Measurements were taken over the T_a range 5–25°C during the photophase and scotophase. Animals were initially placed in the chambers ventilated with air at a T_a of 15°C until they were determined to be resting by means of visual monitoring and/or characteristic resting MR. Air was then substituted with He–O_2 and at least 24 min were allowed to flush the air out of the system. Measurements were taken in 2°C steps, lowering the T_a at 45-min intervals, which allowed T_a to stabilise at each temperature. Animals were kept in He–O_2 until an acute decrease in MR and/or T_b was observed. MRs were calculated as the mean of two to three stable consecutive readings (i.e. over a 24–36-min interval) and the corresponding T_b and T_a values were also calculated. Additional He–O_2 measurements were conducted later at T_a of 25°C. The lowest T_a attained in He–O_2 for each individual was used to calculate the PMR from the He–O_2 MR vs T_a regression equation. This calculated PMR value was then used to calculate the effective lower survival limit T_a (T_{pmr}; Lovegrove et al., 1991) in air by extrapolating the linear regression for MR measurements in air for each individual to the intersect with the PMR.

The mass-specific apparent thermal conductance was calculated using the equation: conductance = MR/($T_b - T_a$) (Lasiewski et al., 1967).

2.6. Statistics

Data are presented as mean ± SD of the number of individuals measured (n). 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). Linear regressions were fitted using the method of least squares, and the slopes and elevations were compared using an analysis of covariance (Zar, 1984). Differences were considered significant at the 5 % level ($P < 0.05$).

3. Results

3.1. Cold exposure

The MR of silvereyes below the TNZ was negatively correlated with T_a in both air (photophase: $P < 0.001$, $r^2 = 0.73$; scotophase: $P < 0.001$, $r^2 = 0.92$) and He–O_2 (photophase: $P < 0.001$, $r^2 = 0.71$; scotophase: $P < 0.001$, $r^2 = 0.89$) (Fig. 1(a), (b)). The elevations for the MR vs T_a regressions were higher during the photophase than during the scotophase in both air ($P < 0.001$) and He–O_2 ($P < 0.001$), while the slopes were not significantly different (Fig. 1(a), (b)). However, the MR vs T_a regression slopes were significantly steeper in He–O_2 than in air both during the photophase ($P < 0.001$) (Fig. 1(a)) and scotophase ($P < 0.001$) (Fig. 1(b)). The PMR during the photophase was 15.64 ± 1.55 mL O_2 g^{-1} h^{-1} (BM = 10.99 ± 0.86 g, $n = 8$) (Fig. 1(a)) which was significantly higher than during the scotophase (13.16 ± 1.58 mL O_2 g^{-1} h^{-1}; BM = 11.08 ± 1.23 g, $n = 8$) ($P < 0.001$) (Fig. 1(b)). In contrast, T_{pmr} did not differ significantly ($P = 0.42$) between photophase and scotophase (-39.7 ± 6.1°C and -41.7 ± 9.9°C, respectively).

Below the TNZ, T_b was independent of T_a ($P = 0.82$ photophase; $P = 0.53$ scotophase), but T_b measured in air were significantly higher during the photophase (40.4 ± 0.6°C, $n = 5$) than during the scotophase (36.9 ± 0.1°C, $n = 5$) ($P < 0.001$) (Fig. 2). In He–O_2, T_b in the photophase (37.9 ± 0.8°C) was higher than in

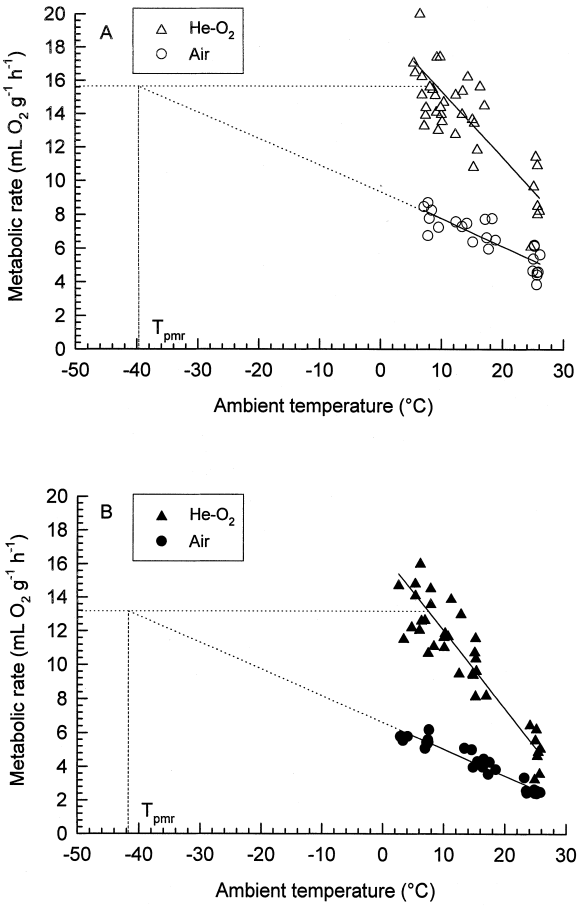

Fig. 1. Mass-specific metabolic rate of resting *Z. lateralis* below the TNZ during the photo- (A) and scotophase (B). Measurements were taken in air and in He–O_2, and each point represents a measurement for one individual. MR showed a negative linear relationship with T_a both during the photophase (air: MR = 9.43 − 0.17 T_a, $P < 0.001$, $r^2 = 0.73$; He–O_2: MR = 19.4 − 0.40 T_a, $P < 0.001$, $r^2 = 0.71$) and scotophase (air: MR = 6.62 − 0.16 T_a, $P < 0.001$, $r^2 = 0.92$; He–O_2: MR = 16.6 − 0.46 T_a, $P < 0.001$, $r^2 = 0.89$). Dashed lines represent the mean PMR and effective T_{pmr} for eight individuals.

the scotophase (35.5 ± 0.6°C) ($P < 0.001$) and both means were lower than those in air ($P < 0.001$).

As expected, in He–O_2 the thermal conductance below the TNZ was significantly higher than in air (Fig. 3), and was also higher during the photophase than during the scotophase in both He–O_2 and air (Fig. 3). In air, thermal conductance was dependent on T_a during the scotophase (conductance = 0.17 + 0.002 T_a, $P < 0.001$, $r^2 = 0.72$), but not during the photophase (conductance = 0.249 + 0.003 T_a, $P = 0.06$, $r^2 = 0.31$; mean conductance = 0.31 ± 0.04 mL O_2 g^{-1} h^{-1} °C^{-1}, $n = 5$) (Fig. 3). Thermal conductance in He–O_2 was independent of T_a during the scotophase (conductance = 0.45 ± 0.001 T_a, $P = 0.52$,

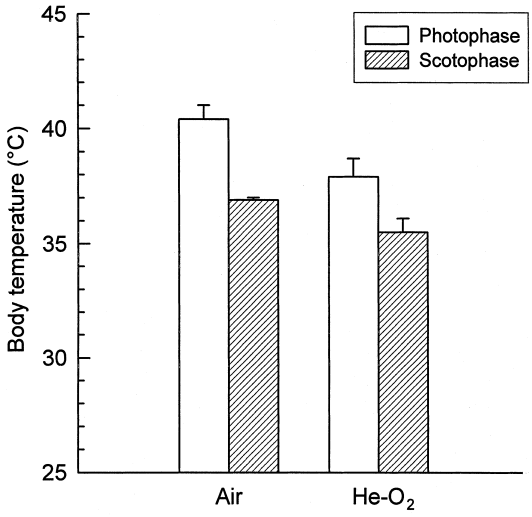

Fig. 2. Mean ± SD T_b of *Z. lateralis* ($n = 5$) during the photo- and scotophase in air and He–O_2 measured below the TNZ (T_a range 3–26°C). T_b was significantly higher during the photophase in both air ($P < 0.001$) and He–O_2 ($P < 0.001$). T_b was also significantly higher in air than in He–O_2 during both photo- ($P < 0.001$) and scotophase ($P < 0.001$).

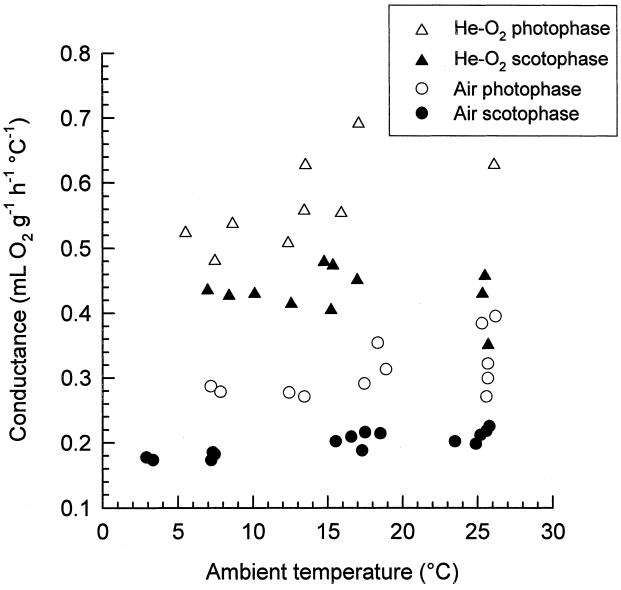

Fig. 3. Thermal conductance of *Z. lateralis* as a function of T_a during the photo- and scotophase in air and He–O_2. Each point represents a measurement for one individual. During the photophase, T_a and conductance were not related in air (conductance = 0.249 + 0.003 T_a, $P = 0.063$, $r^2 = 0.31$), however, in He–O_2 there was a positive linear relationship (conductance = 0.467 + 0.008 T_a, $P = 0.04$, $r^2 = 0.46$). During the scotophase in air conductance and T_a showed a positive linear relationship (conductance = 0.170 + 0.002 T_a, $P < 0.001$, $r^2 = 0.72$); in He–O_2 the relationship was not significant (conductance = 0.450 + 0.001 T_a, $P = 0.52$, $r^2 = 0.05$).

$r^2 = 0.05$; mean conductance = 0.43 ± 0.04 mL O_2 g^{-1} h^{-1} $°C^{-1}$, $n = 5$), but dependent during the photophase (conductance = $0.467 + 0.008\ T_a$, $P = 0.04$, $r^2 = 0.46$) .

3.2. Thermoneutral zone

The TNZ for silvereyes was situated between T_a 27.0 ± 2.4 to 33.6°C (Fig. 4). Within this zone, the mean BMR (scotophase) was 2.30 ± 0.29 mL g^{-1} h^{-1} ($n = 8$, BM = 11.30 ± 1.26 g), and the corresponding T_b was 38.4 ± 0.8°C ($n = 4$). In contrast, during the photophase the MR (3.26 ± 0.42 mL O_2 g^{-1} h^{-1}, $n = 7$, BM = 11.07 ± 1.72 g) and the T_b (40.2 ± 0.1°C, $n = 4$) were significantly elevated ($P < 0.001$) (Fig. 4). When compared with measurements below the TNZ (see previous section), the T_b within and below the TNZ were similar during the photophase ($P = 0.53$), but the scotophase T_b was significantly higher within the TNZ (38.4 ± 0.8°C, $n = 4$) than below (36.9 ± 1.0°C, $n = 5$) ($P = 0.01$) (Fig. 4).

The mean thermal conductance was similar during the scotophase (0.38 ± 0.1 mL O_2 g^{-1} h^{-1} $°C^{-1}$, $n = 4$) and photophase (0.46 ± 0.12 mL O_2 g^{-1} h^{-1} $°C^{-1}$, $n = 4$) ($P = 0.32$). However, conductance should increase with T_a within the TNZ, and accordingly it was higher than below the TNZ ($P = 0.002$ photophase; $P < 0.001$ scotophase) (Fig. 4), but because the TNZ was narrow and the sample size was small, regressions were not significant.

3.3. Heat exposure

Above the TNZ in air, the MR and T_b increased steeply with only minor increases in T_a (Fig. 4). During the scotophase at T_a 38.7 ± 0.7°C, the mean MR (3.917 ± 1.07 mL O_2 g^{-1} h^{-1}, $n = 4$) was about 1.7 times that of BMR, and the T_b was significantly elevated to 42.0 ± 0.79°C ($n = 3$, $P < 0.01$). The corresponding thermal conductance also showed a substantial increase (1.23 ± 0.20 mL O_2 g^{-1} h^{-1} $°C^{-1}$, $n = 3$) being over three times that within the TNZ. For photophase, the determination of T_{uc} and analysis of thermal responses above TNZ were not performed due to insufficient data above the TNZ.

4. Discussion

Our study provides the first detailed information about the thermoregulatory limits of an Australian passerine exposed to both extreme cold and heat.

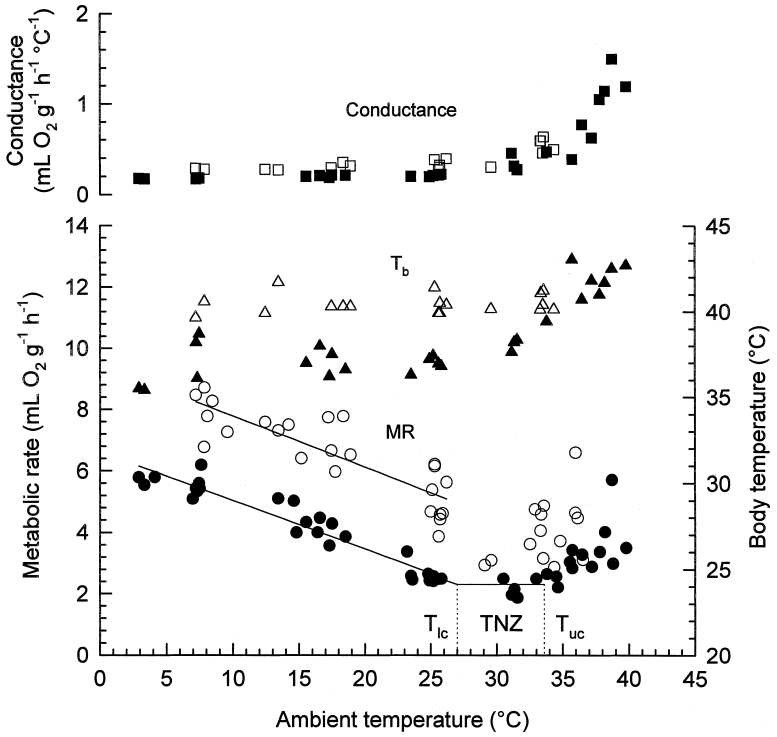

Fig. 4. Thermal conductance, T_b and MR of *Z. lateralis* as a function of T_a. Each point represents a measurement for one individual ($n = 5$ for conductance and T_b; $n = 9$ for MR) taken during the photophase and scotophase. Dashed lines display the lower critical T_a (T_{lc}) and the upper critical T_a (T_{uc}).

Silvereyes are able to tolerate a range of T_a of 81°C from about −42°C to +39°C and possess a thermogenic capacity to produce heat which is sufficient to maintain a differential between T_b and T_a (ΔT) of up to 80°C.

Cold tolerance of silvereyes is well developed, although the PMR recorded for silvereyes was somewhat lower than those recorded for other similar-sized passerines (Dawson and Smith, 1986; Dutenhoffer and Swanson, 1996). However, studies of PMR have been primarily conducted on birds from colder climates, which would be expected to have a more pronounced cold tolerance. When the metabolic scope (PMR/BMR) is considered, the PMR for silvereyes is approximately seven times BMR. This is at the upper end of the metabolic scope values (4.7–7.5) reported for passerines of similar size during winter (Rosenmann and Morrison, 1974; Dawson and Carey, 1976; Dawson and Smith, 1986; Cooper and Swanson, 1994; Saarela et al., 1995; Dutenhoffer and Swanson, 1996).

However, this high metabolic scope is primarily due to the low BMR of silvereyes. BMRs lower than predicted have also been recorded for other passerines from arid Australia (Williams and Main, 1976; Ambrose et al., 1996) and from the humid tropics (see reviews in Hails, 1983; Weathers, 1997). In contrast, many cold-climate birds have a BMR that is higher than predicted. Consequently, the BMR of many small birds inhabiting cold climates is greater than that of the silvereye (Mugaas and Templeton, 1970; Pohl and West, 1973; Rosenmann and Morrison, 1974; Dawson and Carey, 1976; Grossman and West, 1977; Weathers, 1977; Reinertsen and Haftorn, 1986) and therefore their metabolic scope is similar to that of silvereyes although PMR may be greater.

Although able to tolerate a T_a of −42°C, this appears to be far beyond any T_a that the Australian silvereyes would experience naturally, even for the relatively cool winters in Armidale (average minimum and maximum T_a are 0.2 and 12.6°C, respectively; Bureau of Meteorology, 1988 and the lowest T_a recorded was −11°C, P. Burr, personal communication). However, the compounding effects of adverse conditions, such as wind and rain, will necessitate a substantial increase in MR beyond that induced by T_a alone. Wind, for example, significantly increases heat loss and its effect, expressed as the standard operating temperature, follows the equation: $T_{es} = T_b - (1 + 0.26\sqrt{u})(T_b - T_a)$, where T_{es} = standard operating temperature, u = windspeed (Bakken, 1990). For T_a of 0.2°C, even a light wind of 19.3 m/s would result in a T_{es} of −41.7°C (scotophase effective T_{pmr}). Consequently, windy conditions in conjunction with moderately low T_a can demand MRs close to the PMR. Moist conditions may have an even greater effect on thermoregulation because water has a higher heat capacity than air (Schmidt-Nielsen, 1990) and in addition, decreases feather insulation.

The limited body-fat stores of small birds and the high energy turnover raises the question of how long silvereyes can survive under adverse weather conditions. The measured oxygen consumption value required to maintain a stable T_b over the 13 h scotophase at T_a −41.7°C would be equivalent to 38.1 kJ (1L O_2 = 20.08 kJ; Schmidt-Nielsen, 1990). Given that 1 g of fat yields approximately 39.3 kJ (Schmidt-Nielsen, 1990), silvereyes would need to metabolise 0.97 g of fat over a 13 h scotophase. The mass loss of silvereyes during MR measurements was negatively correlated with T_a. Therefore, if we assume a constant rate of mass loss, at −41.7°C the estimated reduction in mass would be 1.6 g, resulting in a body mass of ~9.4 g around dawn, which is not lethal. Consequently, a silvereye in good condition should be able to endure extremely cold T_as which require maximum heat production for the duration of the scotophase. However, if they were to experience such extreme conditions over a period of several days, it is unlikely that they would be able to sustain the high MR required, nor be able to find sufficient food to restore fat deposits, in order to survive.

Silvereyes were far less tolerant of extreme high T_a than they were of cold T_a. Above the TNZ there was an acute increase in MR and T_b with a small increase in T_a. Due to the decreasing ΔT, heat loss from the animal is reduced and T_b rises. The cost of thermoregulation and the Q_{10} effect of a raised T_b produce an increase in MR which, in turn, causes a further increase in T_b. Therefore, in order to facilitate heat loss, conductance of silvereyes also increased acutely. The T_{uc} of Australian passerines are variable. While similar-sized Australian arid zone passerines generally have a T_{uc} that is higher than that of the silvereye (Calder, 1964; Ambrose et al., 1996), cold-climate species may have a T_{uc} that is comparable or lower (West, 1972; Dawson and Carey, 1976; Grossman and West, 1977; Dawson and Smith, 1986; Reinertsen and Haftorn, 1986). A high T_{uc} is beneficial to species living in warmer climates as it raises the T_a at which hyperthermia begins, and this provides a greater heat tolerance. However, the silvereyes used in this study were from a population that would rarely experience T_a above the T_{uc} in winter and therefore their low BMR, which was 32% lower than predicted (Aschoff and Pohl, 1970), is probably a sufficient adaptation to heat. Other populations that inhabit hotter climates may have even lower BMR and higher T_{uc} affording them greater heat tolerance. The reduced heat production associated with a low BMR makes this an ideal adaptation for birds living in warmer climates, as it reduces the risk of heat stress.

The results of this study indicate that silvereyes are adapted to cope with both hot and cold T_a. They are in little danger of dying due to the effects of cold weather in their natural environments, provided there is sufficient food for them to refuel and recover the weight lost during the scotophase. Further, they can use nocturnal hypothermia which even helps them to overcome food shortages (Maddocks and Geiser, 1997). They are more vulnerable to heat stress, however, but are unlikely to be exposed to prolonged periods of extremely high T_a in their natural habitat. Silvereyes have been successful in occupying many types of habitats, and different environmental conditions. Their low BMR coupled with a relatively high PMR and the ability to withstand extremely cold temperatures allows them to tolerate a wide range of T_a, and this may be one reason for the extensive distribution range of this species.

Acknowledgements

This study was supported by a University of New England Internal Research Grant to T. Maddocks and a grant of the Australian Research Council to F. Geiser. We would like to thank Stuart Cairns for his assistance with statistics, Hugh Ford for his advice on various aspects of this study, Uschi Munroe for her advice on silvereyes, Gerhard Körtner for his help with equipment and Peter Burr for weather data. We are grateful to Gerhard Körtner and Jo Holloway for their comments on this manuscript.

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