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ORIGINAL PAPER

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Seasonal changes in the thermoenergetics of the marsupial sugar glider, *Petaurus breviceps*

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Abstract Little information is available on seasonal changes in thermal physiology and energy expenditure in marsupials. To provide new information on the subject, we quantified how body mass, body composition, metabolic rate, maximum heat production, body temperature and thermal conductance change with season in sugar gliders (*Petaurus breviceps*) held in outdoor aviaries. Sugar gliders increased body mass in autumn to a peak in May/June, which was caused to a large extent by an increase in body fat content. Body mass then declined to minimum values in August/September. Resting metabolic rate both below and above the thermoneutral zone (TNZ) was higher in summer than in winter and the lower critical temperature of the TNZ occurred at a higher ambient temperature (T_a) in summer. The basal metabolic rate was as much as 45% below that predicted from allometric equations for placental mammals and was about 15% lower in winter than in summer. In contrast, maximum heat production was raised significantly by about 20% in winter. This, together with an approximately 20% decrease in thermal conductance, resulted in a 13°C reduction of the minimum effective T_a gliders were able to withstand. Our study provides the first evidence that, despite the apparent lack of functional brown adipose tissue, sugar gliders are able to significantly increase heat production in winter. Moreover, the lower thermoregulatory heat production at most T_as in winter, when food in the wild is scarce, should allow them to reduce energy expenditure.

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Abbreviations *ADMR* average daily metabolic rate · *BAT* brown adipose tissue · *BMR* basal metabolic rate · HP_{max} maximum heat production · *NST* nonshivering thermogenesis · *RMR* resting metabolic rate · T_a ambient temperature · T_b body temperature · T_{lc} lower critical temperature of thermoneutral zone · *TNZ* thermoneutral zone · T_{uc} upper critical temperature of thermoneutral zone

Introduction

Seasonal changes in climate are generally associated with changes in food availability. Such seasonal challenges can be problematic for small endotherms because their relative large surface area results in high rates of heat and thus energy loss, and their capacity to store energy is limited. Especially in winter, the decrease in T_a (ambient temperature) often results in high rates of heat loss, and thus food requirements, and a reduction in food availability. To overcome these challenges, small endotherms must make morphological, physiological and/or behavioural adjustments that increase their chance of survival.

Although seasonal physiological changes are crucial for survival in the wild, they are not widely studied. Instead, studies on short-term acclimation to one environmental variable in the laboratory are most common, despite the potential difficulty of interpreting the ecological significance of the elicited physiological response (Grodzinski and Wunder 1975; Wunder 1979). In some instances, acclimation to continuous cold temperatures has sometimes resulted in physiological responses (e.g. body mass, metabolic rate) that are entirely different to those of animals acclimatised to natural conditions (Lynch 1973; Hyvärinen 1984). Further, animals acclimated to constant photoperiod may not respond at all as some physiological variables are apparently caused by the rate of change of photoperiod rather than absolute photoperiodic length per se (McAllan and Dickman 1986). Although physiological responses of seasonally acclimatised animals are likely to provide ecologically more relevant results, detailed laboratory studies on the physiology of seasonal acclimatisation in mammals are few. This is especially true for marsupials, which are interesting in this respect because they appear to lack functional brown adipose tissue (BAT; Nicol et al. 1997; Rose et al. 1999). It is known that in small placental mammals, on which most work on thermal physiology has been performed, the major change in thermogenic capacity in winter is achieved by a profound proliferation in BAT (Feist and White 1989). Since marsupials do not appear to have this option, they must use a different approach to cope with seasonal challenges.

To resolve whether and how small marsupials alter thermoenergetics with season, we quantified metabolic rates and body temperature (T_b) of the sugar glider, *Petaurus breviceps* (115–160 g), in summer and winter over a wide range of T_as. Sugar gliders were selected for the study because they have a wide distribution along the east coast of Australia (Suckling 1995) including cool-temperate regions, with relatively pronounced seasonal changes in T_a (Fig. 1) that cause energetic stress in winter (Körtner and Geiser 2000; Geiser and Stapp 2001). Field metabolic rates of gliders in a cool-temperate region indicate that, despite the change of T_a, metabolism is similar throughout the year (Quin 1993), suggesting that they must undergo some morphological, thermoregulatory or behavioural adjustments. To determine whether this is the case, we investigated how body mass, body composition, metabolic rates, T_b, thermal tolerance, and thermal conductance of sugar gliders change with season.

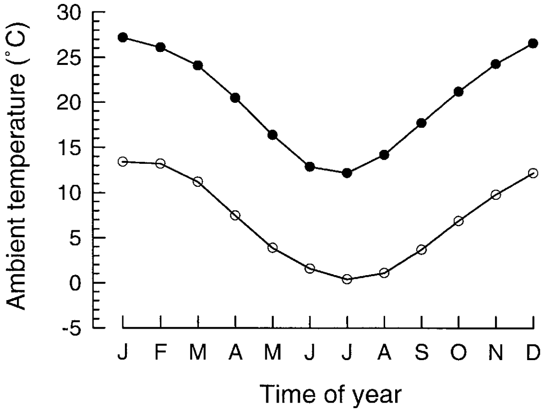

Fig. 1. Average monthly minimum and maximum ambient temperature (T_a) for Armidale, New South Wales. Average T_a range from 0.4–12.2 °C in July (winter) and 13.4–27.2 °C in January (summer)

Materials and methods

A total of 13 sugar gliders (6 males, 7 females) were used. Of these, 11 were wild-caught, using nest boxes, in the New England Tablelands region of NSW, near Armidale, Australia, at about 1000 m altitude. Most of these gliders were used throughout the study. The other two gliders were born in captivity. As sugar gliders are territorial, they were maintained in their three family groups within outdoor aviaries under natural photoperiod and temperature conditions at the University of New England. Each aviary contained two nest boxes, and fresh leafy branches were supplied weekly. Excess food and water were provided daily. Food consisted of a mixture of high-protein cereal, honey and water, which was occasionally supplemented with vitamins (Pentavite infant vitamins). In addition, fresh apple and carrot were given every 2nd day, while mealworms (*Tenebrio* larvae) were also provided occasionally.

The study was conducted between June 1994 and May 1997. Only adult gliders were used, and no female was included that was known to be either pregnant or lactating. To ensure that seasonal response was detected, rather than individual variation, the same individuals were used in the seasonal comparisons.

Resting metabolic rates (RMR) were measured as rate of oxygen consumption using open-flow respirometry during summer (December–February) and winter (June–August). Animals were placed individually into 3-l respirometry chambers within a temperature-controlled cabinet (±0.5 °C). The gliders could move freely within the chambers, and their metabolic rates during the scotophase were almost double those during the day when the animals were observed to be resting. Photoperiod within the cabinet matched that outside. Flow rates of dried air, 40–50 l h^{-1}, were controlled with rotameters and measured with mass-flowmeters (Omega, FMA 5606, Stamford). With these flow rates and the size of the chambers, the system was in 99% equilibrium after 17–20 min. Oxygen content of the dried expired air was measured with a single-channel oxygen analyser (Ametek Applied Electrochemistry S-3A/I, Pittsburgh) fitted with a high-resolution output board. Solenoid valves switched channels in 3-min intervals. This permitted the measurement of up to three animals and a reference (outside air) in succession, with each channel measured once every 12 min when all chambers were occupied.

Animals were placed in the respirometry chambers late in the afternoon (16.00–17.00 hours), at T_as of between 10 °C and 25 °C, and allowed to settle overnight. The following morning, during the gliders' inactive phase, T_a was either raised or lowered to the desired T_a and RMR was determined. T_a was then raised or lowered in 2–5 °C steps, and the process repeated. RMR was determined at no more than four T_as (usually two or three) during 1 day. Animals were in the chamber for a maximum of 23 h. For the extreme high and low T_as, RMRs were measured in the morning and the gliders were removed by 12.00 hours. Food and water were not available to the gliders during the measurements. At least 5 days were allowed for gliders to recover between measurements. The whole process was repeated for each animal over a T_a range of at least 5–38 °C. The gliders were weighed before and after each testing period and a constant rate of mass loss was assumed for calculation of mass-specific RMR.

RMRs were calculated from the mean of at least three consecutive lowest diurnal VO_2 values (i.e. over at least 36 min) in normothermic resting individuals at each T_a. Basal metabolic rates (BMR) were determined as the minimum RMR within the range of T_as measured. Maximum metabolic rates (HP_{max}) were defined as the point where RMR and/or T_b could be maintained for at least 1 h and were just above the T_a where hypothermia, as demonstrated by either a falling RMR or T_b, was induced. HP_{max} was induced by substituting air with helox (approx. 79% helium, 21% oxygen), a more conductive medium (Rosenmann et al. 1975; Thomas et al. 1998), to increase heat loss, thus enabling us to quantify HP_{max} without thermally damaging the gliders (Holloway and Geiser 2001). The effective T_a at which HP_{max} occurred was derived by extrapolating the regression line for an individual's

RMR in air to the intercept with its HP_{max} value. Metabolic scope was determined by dividing mean HP_{max} by BMR (Dawson and Dawson 1982).

For average daily metabolic rates (ADMR), gliders were maintained at a constant T_a (range 10–25 °C) for 23 h. ADMR was then calculated by integrating oxygen consumption over this entire 23-h period. It was assumed that 1-l oxygen produced the equivalent of 20.083 kJ heat. No animal entered torpor during these measurements.

T_b was measured simultaneously with RMR using temperature-sensitive transmitters (single-stage FM, model EPX76, Sirtrack). These transmitters were calibrated to the nearest 0.1 °C against a precision mercury thermometer in a water bath. The wax-coated transmitters weighed 2.5–4.5 g (battery life approximately 9 months), and were implanted intraperitoneally under isoflurane anaesthesia at least 2 weeks before measurements. Transmitter mass was subtracted from glider mass for all mass-specific calculations. Transmitter signals were received using a VHF/UHF scanning receiver (Yaesu, FRG-9600), T_a was measured to the nearest 0.1 °C with a calibrated thermocouple inserted 1 cm into the respirometry chamber, and the thermocouple output was amplified by a digital thermometer (Omega DP116).

The analog outputs from the mass-flowmeter, oxygen analyser, scanning receiver and digital thermometer were interfaced to a personal computer where data acquisition and processing were performed using software written by G. Körtner, B. Lovegrove and T. Ruf. Rates of oxygen consumption were calculated, after dry standard temperature and pressure gas values were calculated, using Eq. 3a of Withers (1977).

Thermal conductance is often calculated from the slope of the regression line of RMR versus T_a below the lower critical temperature (T_{lc}). This method requires that conductance is minimal and constant below the thermoneutral zone (TNZ), T_b is constant, and the regression line extrapolates to T_b at the intersection of the abscissa (Bradley and Deavers 1980). However, for sugar gliders only one of these assumptions, constant T_b, was valid. Therefore, apparent thermal conductance was calculated using the equation:

$$\text{Thermal conductance (ml O}_2\text{ g}^{-1}\text{ h}^{-1}\text{ °C}^{-1}) = \text{RMR(ml O}_2\text{ g}^{-1}\text{ h}^{-1})/(\mathrm{T_b} - \mathrm{T_a})(\text{°C})$$

To determine if body composition differed between seasons, CAT scans were performed on five individuals in mid-March (late summer/early autumn), late May (late autumn/early winter), mid-September (early spring) and mid-December (early summer). Animals were restrained individually in cardboard tubes, secured at each end with a piece of calico fastened with elastic bands, and scanned using a Hitachi CT-W400 CAT scanner. Scans of 2-mm thickness were taken at 15-mm increments, moving from the head to the tail of each glider. The resulting images were processed with a specialised software package (Autocat; Neville Jopson, AgResearch, NZ) to determine the area of each tissue group. The software works on the principle of a 256 grey scale and allows separation of tissues using gates set to only include the desired tissue groups. For the present study these groups were fat, muscle and organs, and bone. Unfortunately, muscle and organ tissue could not be differentiated by the grey scales. The gates were determined by plotting the number of pixels from a range of images and comparing these histograms to the positions of the desired tissue groups from the same sites in a deceased animal. Masses of the tissue groups were then determined using the computer program, Autocalc (Neville Jopson, AgResearch, NZ).

Sugar gliders are sexually dimorphic in body mass (Suckling 1995). However, when all data other than mass were analysed for differences due to gender, no significant differences were observed. Therefore, all data were pooled for the analyses, with the exception of body mass.

All numerical values are expressed as means ± SD for the number of individuals *n* measured. Differences were considered significant at $P \leq 0.05$. Sample variances were tested for homogeneity using an F_{max}-test (Zar 1984). Two means were compared using either student's (HP_{max}, critical T_a for T_b) or paired *t*-tests [BMR, T_{lc}, upper critical temperature of the TNZ (T_{uc}), mean T_b, thermal conductance]. Multiple observations of body mass between April 1996 and March 1997, the time when continuous data on a large sample size were available, first underwent a repeated-measures ANOVA prior to stepwise polynomial regression analysis. Seasonal changes in body composition were analysed using repeated-measures ANOVA and Tukey's tests. After standardised residuals were plotted to ensure homoscedasticity, lines were fitted using least squares regression analysis (Zar 1984). Slopes and elevations were compared using analysis of covariance (ANCOVA). Physiological variables as a function of body mass could not be analysed this way because the small body mass range usually rendered the regressions non-significant. The T_{lc} and T_{uc} at which RMR showed a significant increase were determined by calculating a regression equation for the increasing values for each individual and determining the intercept with the mean BMR for that individual. The critical T_a at which T_b began to increase was determined as the intercept of the regression for the increase in T_b at high T_as and the mean T_b of individuals below a T_a of 25 °C.

Comparison of sugar glider BMR to those of other marsupials was performed using phylogenetically independent linear contrasts, which were adequately standardised (see Garland et al. 1992). Phyletic topology and branch lengths were obtained from Kirsch et al. (1997). The tree was constructed and contrasts calculated using the Phylogenetic Diversity Analysis Program (PDAP, Garland et al. 1992). Garland and Ives (2000) was the source for the calculation of the phylogenetically independent regression intercept and prediction intervals mapped back to the original data.

Results

Body mass of adult gliders fluctuated with season ($P < 0.001$), and ranged in males from 126.5 ± 3.5 g to 168.0 ± 16.9 g (in spring and late autumn, respectively) and in females from 115.8 ± 6.7 g to 157.5 ± 12.5 g (in summer and late autumn, respectively). Individuals of both sexes displayed a similar and predictable increase or decrease in body mass with time of year ($P < 0.05$; $n = 5$ males, 5 females; Fig. 2). Body mass of gliders peaked during May and June (late autumn/early winter), followed by a pronounced decrease, of about 20–30 g, to a minimum during August and September. Mass also increased in early summer, and this became more pronounced during consecutive years, followed by a decrease in February and March prior to increasing to the peak in May.

The increase in mean body mass during the course of the study was most likely due to ad libitum feeding. However, this was a necessary measure to ensure all animals, in particular the subordinates and juveniles in the groups, obtained enough food to maintain body mass. Despite the excess food provided, the mass of a few individuals ($n = 5$) did remain near average and did not display any substantial increase over the 3 years, other than those seasonal increases mentioned above.

Body composition of sugar gliders, in particular fat content, changed with season. The absolute amount of fat observed in the gliders was highest in May (late autumn) compared to the same animals during September, December and March ($P = 0.004$; Table 1). All individuals underwent an increase in fat content, however, the amount of fat deposited was quite variable. The percentage of body mass consisting of fat also differed with

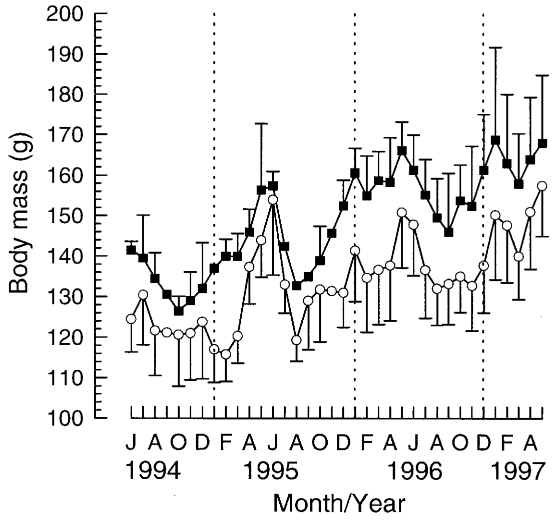

Fig. 2 Mean (±SD) body mass of adult male (*filled symbols*) and female (*unfilled symbols*) *Petaurus breviceps* from June 1994 to May 1997. The number of individuals (1–7 males; 3–7 females) varied throughout the study as animals were caught, attained adult mass or died. Repeated measures ANOVA and stepwise polynomial regressions were performed on data from April 1996–March 1997 ($n = 5$ males, 5 females). Both male and female gliders displayed a peak in body mass during May and June

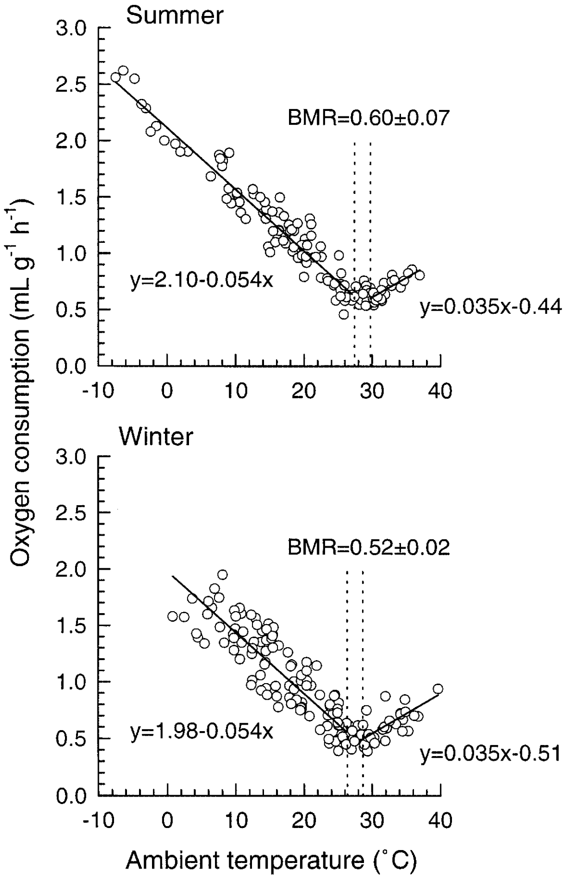

Fig. 3 Resting metabolic rates (RMR) over entire range of T_as measured for *P. breviceps* in summer and winter. *Broken lines* indicate the thermoneutral zones (TNZ). Basal metabolic rate (BMR) of gliders was lower ($P = 0.001$) in winter. Further, the elevations for the regression lines of RMR above and below the TNZ were both significantly lower for animals in winter ($P = 0.006$ and $P < 0.001$, respectively) than in summer. Pooled r^2 for regressions were 0.86 and 0.55 below and above the TNZ, respectively

season and was also highest in May ($P = 0.007$). The CAT scans revealed that extra fat was primarily deposited subcutaneously, as the layer of fat surrounding the body was substantially thicker in May than in all other scanning periods.

Although not significant, the mean amount of muscle/organ mass increased by almost 10 g between March and May (51.4 ± 4.6 g to 62.0 ± 15.3 g). However, the percentage of muscles and organs remained unchanged throughout the year (around 41% of body mass), despite a mean increase in body mass of approximately 25 g. The amount of bone did not change significantly throughout the year.

The metabolic response of *P. breviceps* over the range of T_as measured in both summer and winter was similar to that of other small endotherms. A distinct TNZ was bordered on both sides by increasing RMR (Fig. 3). The mean T_{lc} differed significantly between summer (27.4 ± 1.7 °C; $n = 12$) and winter (26.4 ± 1.7 °C, $n = 12$; $P < 0.05$). In contrast, the mean T_{uc} of summer (29.8 ± 1.1 °C; $n = 6$) and winter (28.7 ± 1.7 °C; $n = 6$) did not differ, and when the data from both seasons were pooled the mean T_{uc} was T_a 29.2 ± 0.9 °C ($n = 6$).

The BMR of gliders also changed with season (Fig. 3). The mean mass-specific BMR in winter was 0.519 ± 0.018 ml g^{-1} h^{-1} (mass 135.6 ± 17.0 g, $n = 13$), which was 13% lower than that of the same individuals in summer, 0.598 ± 0.067 ml g^{-1} h^{-1} (mass 127.7 ± 12.9 g, $n = 13$) ($P = 0.001$). The total BMR of gliders was

Table 1 Fat content, as mass (g) and as a percentage of body mass, of *Petaurus breviceps*, as derived from CAT scans at different times of the year

Animal no.	March		May		September		December	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
1	35	25.00	39	27.27	34	24.64	32	23.36
6	22	17.46	37	25.87	14	11.76	17	13.71
10	30	27.27	64	41.59	25	20.83	45	12.98
11	29	23.39	39	26.17	20	14.29	25	19.38
12	21	15.22	25	15.06	14	9.79	21	12.98
Mean	27.4	21.67	40.8	27.19	21.4	16.26	28.0	16.48
SD	5.9	5.12	14.2	9.45	8.4	6.27	11.0	4.69

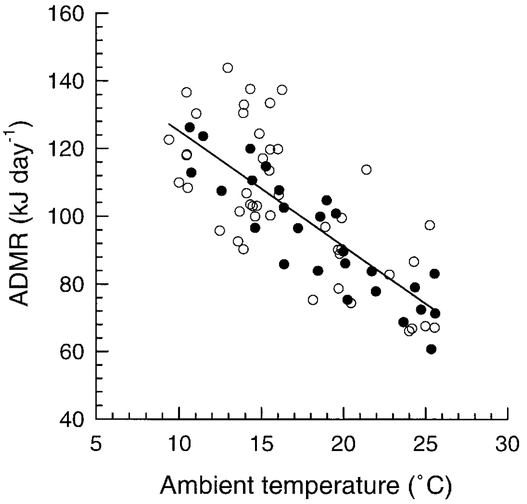

Fig. 4 Average daily metabolic rates (ADMR) for *P. breviceps* during summer (*filled symbols*) and winter (*unfilled symbols*). No significant difference was found between seasons and the common equation was y = 159.3–3.40x ($P < 0.001$, $r^2 = 0.60$)

69.82 ± 7.37 ml h^{-1} (winter) and 76.20 ± 10.85 ml h^{-1} (summer) and the means differed ($P = 0.05$).

Above the T_{uc}, RMR increased linearly within the T_{a} range measured (Fig. 3). While the slope of the regression equations showed no significant seasonal response, the elevation of summer RMR was significantly greater than that during winter ($P = 0.006$). Gliders at T_{a}s above the T_{uc} lay sprawled on their back with their limbs extended and the patagium, or gliding membrane, exposed. The gliders also licked their paws and waved them slowly in the air, and at the highest T_{a} had wet faces indicating extensive salivation.

Below the T_{lc}, the RMR increased linearly with decreasing T_{a} (Fig. 3). The elevation of RMR below the T_{lc} in winter was significantly less than that in summer ($P < 0.001$). Gliders at T_{a}s below the T_{lc} usually adopted a ball shape, with the head, limbs and patagium tucked under the body and the head covered by the tail. As the T_{a} decreased, this "ball" posture appeared to get tighter, and was accompanied by occasional bouts of shivering.

Despite the lower RMR and BMR in winter, the ADMR of gliders did not differ between the two seasons (Fig. 4). This was probably due to the higher energy expenditure during the longer scotophase, and thus activity phase, in winter. Similar to the RMR, the ADMR increased linearly below the T_{lc} with decreasing T_{a} (y = 159.3–3.40x; $P < 0.001$, $r^2 = 0.60$; Fig. 4).

The mean $\mathrm{HP}_{\mathrm{max}}$ attained under a helox atmosphere differed between the two seasons (Fig. 5). The mean winter $\mathrm{HP}_{\mathrm{max}}$, 3.27 ± 0.12 ml g^{-1} h^{-1} (range: 3.12–3.41 ml g^{-1} h^{-1}; $n = 5$), was almost 17% greater than that measured during summer, 2.81 ± 0.35 ml g^{-1} h^{-1} (range: 2.29–3.34 ml g^{-1} h^{-1}; $n = 7$, $P = 0.018$). The total mean $\mathrm{HP}_{\mathrm{max}}$ of the gliders was also significantly greater in winter (425.9 ± 44.1 ml h^{-1}) than in summer (348.8 ± 45.8 ml h^{-1}; $P = 0.015$). With the lower BMR and higher $\mathrm{HP}_{\mathrm{max}}$, the metabolic scope of animals in winter (6.55 ± 0.61) was significantly greater than that of animals in summer (5.28 ± 1.05; $P = 0.037$). The mean effective T_{a} at which $\mathrm{HP}_{\mathrm{max}}$ occurred also differed significantly between the seasons (Fig. 5). Animals in winter could tolerate a mean effective T_{a} (–25.7 ± 2.2 °C; $n = 5$) more than 13 °C lower than those in summer (–12.5 ± 6.4 °C; $n = 7$, $P = 0.001$).

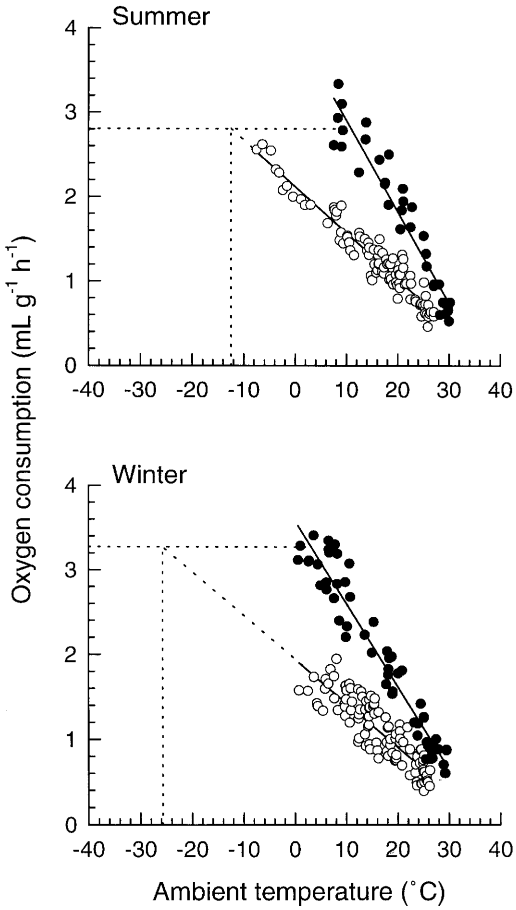

Fig. 5 Maximum metabolic rates ($\mathrm{HP}_{\mathrm{max}}$), measured in helox (*filled symbols*), for *P. breviceps* in summer and winter. Mean $\mathrm{HP}_{\mathrm{max}}$ (*horizontal broken line*) was substituted into the regression lines for resting metabolic rates in air (*unfilled symbols*) to determine the effective T_{a} (*vertical broken line*) the gliders could tolerate. $\mathrm{HP}_{\mathrm{max}}$ was higher ($P = 0.018$), resulting in a lower effective T_{a} ($P = 0.001$), in animals during winter

Mean T_{b} of gliders below the critical T_{a}, where T_{b} began to increase due to heat load, did not differ between the seasons, and the overall mean T_{b} was 35.5 ± 0.5 °C ($n = 10$; Fig. 6). However, the critical T_{a} for the increase in T_{b} occurred at a higher T_{a} in summer (28.4 ± 0.4 °C; $n = 4$) than in winter (26.3 ± 0.8 °C; $n = 5$, $P = 0.003$). Above these critical T_{a}s, T_{b} increased linearly with increasing T_{a}. There was no significant seasonal difference between the slopes or intercepts for T_{b} vs. T_{a} above the critical T_{a}, and the overall regression equation was: y = 23.3 + 0.43x ($P < 0.001$, $r^2 = 0.79$).

The thermal conductance of sugar gliders displayed a curvilinear relationship with T_{a}, with conductance increasing markedly beyond the T_{lc} in both seasons,

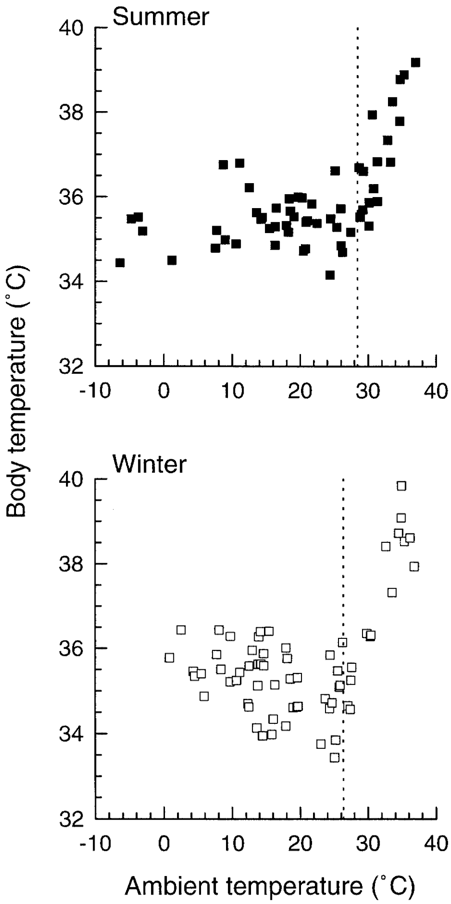

Fig. 6 Body temperatures (T_b) of *P. breviceps* during summer (*filled symbols*) and winter (*unfilled symbols*). The *broken line* indicates the critical T_a at which T_b started to rise in response to increasing T_a. The critical T_a for animals in winter (26.3 ± 0.8 °C) was lower ($P = 0.003$) than for animals in summer (28.4 ± 0.4 °C). Mean T_b below the critical T_a did not differ and the overall mean was 35.5 ± 0.5 °C

probably due to the use of evaporative cooling at higher T_as. Mean thermal conductance below the TNZ, where it was not related with T_a, was higher ($P = 0.001$) during summer (0.064 ± 0.006 ml g^{-1} h^{-1} °C^{-1}, $n = 6$) than winter (0.053 ± 0.005 ml g^{-1} h^{-1} °C^{-1}, $n = 6$).

Discussion

Our study shows that sugar gliders undergo distinct morphological and physiological changes during the year. It is the first to show that the thermogenic capacity of marsupials changes with season. Body mass, body composition, thermal tolerance, thermal conductance, and RMR, both within and below the TNZ, also changed from summer to winter. Daily energy expenditure in winter was, however, similar to that in summer, despite a longer scotophase and thus longer period of activity, likely because of the morphological and physiological adjustments.

Seasonal changes in body mass similar to those observed here have also been observed in sugar gliders in the wild (Suckling 1984; Quin 1993). Presumably, the mass increase occurs at a time when food is most abundant and is a result of fat deposition. However, the seasonal change of body mass in captivity despite ad libitum feeding throughout the year (present study) suggests that the body mass set point fluctuates and regulates food intake or activity patterns to at least some extent independent of food availability.

The increased fat storage before winter observed here would assist the survival of sugar gliders in a number of ways. Clearly, gliders can rely on the fat reserves throughout periods of limited food. Since fat storage was predominantly subcutaneous it should also improve insulation and reduce heat loss and, consequently, thermoregulatory energy expenditure. However, the mass increase during autumn may also be related to reproductive success, but given that all gliders in the present study increased their mass, including the small and presumably subordinate, non-reproducing individuals, it is likely that the primary reason for fat storage is to improve winter survival.

The BMR of an animal reflects the energetic requirements for maintenance of vital functions. It is commonly assumed that marsupial BMRs are about 30% lower than those of placentals (Dawson and Hulbert 1970; Hayssen and Lacy 1985), but recent evidence suggests that they may not differ from some placental taxa and from placentals in certain geographical regions (Hayssen and Lacy 1985; Lovegrove 2000). Nevertheless, the BMR of *P. breviceps* measured here was significantly lower (16% summer; 26% winter, using phylogenetically independent linear contrast analysis) than predicted by Dawson and Hulbert (1970), and thus substantially below those of most placentals.

A seasonal change of BMR, as in sugar gliders, has also been observed in a number of small placental species (Heldmaier and Steinlechner 1981; Wunder 1984; Merritt 1986, 2001; McDevitt and Andrews 1995; McDevitt and Speakman 1996). However, in contrast to sugar gliders, most have elevated BMRs under winter conditions, as do cold-acclimated marsupials *Dasyuroides byrnei* (Smith and Dawson 1984) and *Monodelphis domestica* (Dawson and Olson 1988). The increase in mass-specific BMR in many species is, however, related to a decline of body mass in winter, whereas the total energy expenditure in thermoneutrality usually declines (Degen 1997). In contrast, although body mass of sugar gliders increased in winter, both mass-specific and total BMR decreased.

A contributing factor to the decrease in the BMR of gliders during winter may be changes in body composition (Lynch 1973; Stewart and Barnett 1983; McDevitt and Speakman 1994). Compared to body organs, which are metabolically active and expensive to maintain, fat is relatively inactive (Piersma and Lindström 1997).

Therefore, by increasing the proportion of the body comprising fat during winter, sugar gliders are able to reduce their mass-specific metabolic expenditure. However, as whole-animal BMR also decreased it appears that some other physiological changes do occur. Unfortunately, as the CAT scans did not differentiate between muscle and other organs, we were unable to determine if specific organs with different metabolic activities varied with season.

Seasonal changes in BMR are often concurrent with shifts in the range or transposition of the TNZ. In a number of species T_{lc} is lowered during winter (Heldmaier and Steinlechner 1981; Reynolds and Lavigne 1988; Corp et al. 1997), often due to the seasonal elevation in BMR. This is not the case in sugar gliders, in which the lowering of T_{lc} in winter is most likely explained by the decrease in thermal conductance, which enabled them to maintain T_{b} at lower T_{a}s without the need for thermoregulatory heat production. Sugar gliders reduced thermal conductance by approximately 20% from summer to winter, likely due to the deposition of subcutaneous fat to some degree. However, seasonal changes in fur properties may also contribute, but these were not quantified as overt differences were not apparent.

In addition to decreasing heat loss, sugar gliders significantly increased $\mathrm{HP}_{\mathrm{max}}$ during winter. To our knowledge, this is the first account of a seasonal change in thermogenic capacity observed in a marsupial. In placental mammals, on the other hand, seasonal changes in peak metabolism have been observed in a number of species (Rosenmann et al. 1975; Andrews and Belknap 1985; McDevitt and Speakman 1996). Small placentals appear to increase $\mathrm{HP}_{\mathrm{max}}$ primarily due to an increase in non-shivering thermogenesis (NST) in BAT. The amount of BAT, the primary source of NST in placentals, substantially increases in winter (Feist and White 1989). As functional BAT has not been found in marsupials (Nicol et al. 1997; Rose et al. 1999), other sources of NST, such as skeletal muscle or uncoupling proteins in non-BAT tissues (Eldershaw et al. 1996; Clements et al. 1998), may explain some of the seasonal change in $\mathrm{HP}_{\mathrm{max}}$ observed here.

Sugar gliders in winter were able to withstand an effective T_{a} as low as –26 °C, which is over 13 °C lower than in summer. As the lowest recorded minimum T_{a} in Armidale (New England Tablelands) is approximately –11 °C, sugar gliders are well adapted to cope thermogenically with the cold T_{a}s experienced in this region. This cold limit also allows them a certain amount of latitude to withstand the effects of wind-chill and rain, which can substantially reduce the effective T_{a}. Moreover, it is likely that, during gliding episodes, heat loss is substantial.

Seasonal changes in thermal physiology allow captive sugar gliders to maintain their daily energy expenditure during winter at similar levels to those in summer, despite the much longer nights. However, as winter T_{a}s in the wild are substantially lower than in summer, daily energy expenditure of free-ranging gliders should be greater. Surprisingly, this is not the case, and sugar gliders appear to have similar field metabolic rates in summer and winter (Quin 1993). Therefore, it is likely that wild gliders employ additional strategies, such as torpor (Geiser et al. 2000; Körtner and Geiser 2000), to further lower their energy requirements in winter.

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