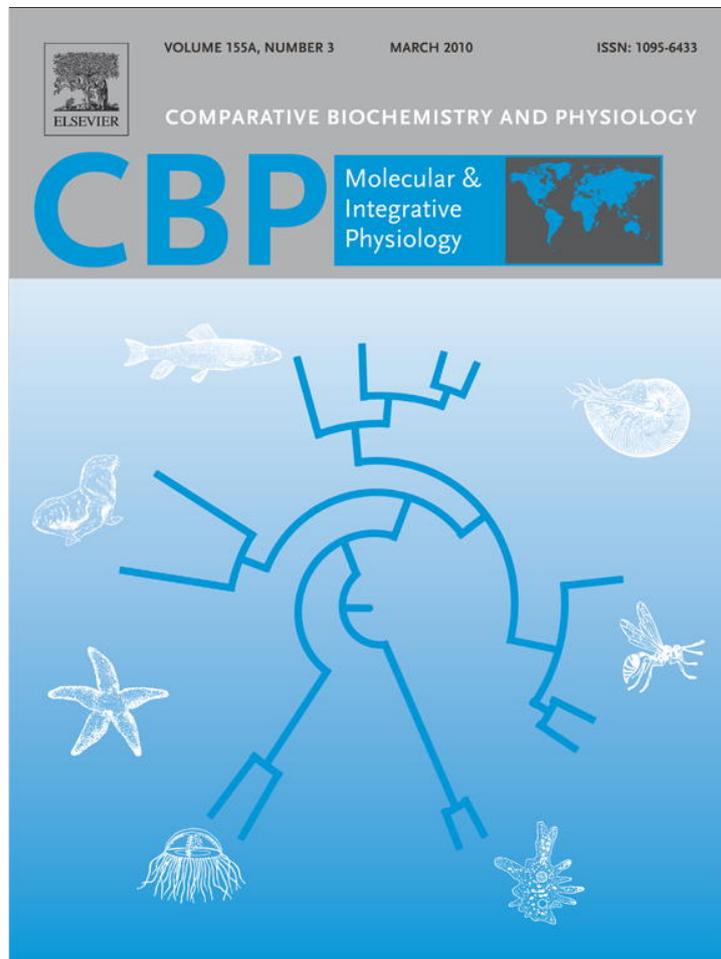


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## Seasonally constant field metabolic rates in free-ranging sugar gliders (*Petaurus breviceps*)

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### ABSTRACT

Sugar gliders, *Petaurus breviceps* (average body mass: 120 g) like other small wild mammals must cope with seasonal changes in food availability and weather and therefore thermoregulatory and energetic challenges. To determine whether free-ranging sugar gliders, an arboreal marsupial, seasonally adjust their energy expenditure and water use, we quantified field metabolic rates (FMR) and water flux at a seasonal cool-temperate site in eastern Australia. Thirty six male and female sugar gliders were labelled with doubly labelled water for this purpose in spring, summer and autumn. The mean FMR was  $159 \pm 6 \text{ kJ d}^{-1}$  (spring),  $155 \pm 8 \text{ kJ d}^{-1}$  (summer), and  $152 \pm 20 \text{ kJ d}^{-1}$  (autumn) and the mean FMR for the three seasons combined was  $158 \pm 5 \text{ kJ d}^{-1}$  (equivalent to  $1.33 \text{ kJ g}^{-1} \text{ d}^{-1}$  or  $780 \text{ kJ kg}^{-0.75} \text{ d}^{-1}$ ). The mean total body water was  $83 \pm 2 \text{ g}$ , equal to 68.5% of body weight. Mean water flux was  $29 \pm 1 \text{ mL day}^{-1}$ . Season, ambient temperature or sex did not affect any of the measured and estimated physiological variables, but body mass and total body water differed significantly between sexes and among seasons. Our study is the first to provide evidence for a constant FMR in a small mammal in three different seasons and despite different thermal conditions. This suggests that seasonal changes in climate are compensated for by behavioural and physiological adjustments such as huddling and torpor known to be employed extensively by sugar gliders in the wild.

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### 1. Introduction

Ambient temperature ( $T_a$ ) strongly affects the energy requirement of small mammals. At low  $T_a$ , where the differential between body temperature and  $T_a$  is large, the substantial heat loss over the relatively large body surface of small mammals must be compensated for by a proportional amount of internally produced heat (Scholander et al., 1950). Accordingly, in essentially all species that have been investigated, resting metabolic rate (RMR) increases with decreasing  $T_a$  (Withers, 1992). Moreover, for those species for which data on daily energy expenditure are available, the average daily metabolic rate (ADMR), which includes RMR values, periods of daily activity and in some species employment of torpor, also increases with decreasing  $T_a$  (Ruf and Heldmaier, 1992; Coburn and Geiser, 1998), resulting in an increased requirement of food.

As in other small mammals, both RMR and ADMR measured in the laboratory increase substantially with decreasing  $T_a$  in the marsupial sugar glider (*Petaurus breviceps*, body mass 120 g) (Fleming, 1980; Holloway and Geiser, 2001). However, as in some other species, behaviour and particularly thermal energetics of sugar gliders differ substantially between the laboratory and the field (Körtner and Geiser, 2000; Geiser et al., 2007). Moreover, although laboratory data predict a strong seasonal change in energy expenditure according to the changing  $T_a$ , there are few data confirming that this is the case in free-ranging animals (see Humphries et al., 2005). The assumption that laboratory data are applicable to the field may not be supported for a species that, like the sugar glider, can be highly flexible in its energy use because it may remain inactive in thermally insulated tree hollows during inclement weather (e.g. during rain and low  $T_a$ ), huddles extensively and employs torpor for energy conservation in the wild (Fleming, 1980; Körtner and Geiser, 2000; Christian and Geiser, 2007).

Sugar gliders (*P. breviceps*), the smallest petaurid (~130–160 g), have a wide distribution range, spanning from New Guinea down along the east coast of Australia to Tasmania. They are nocturnal and live in social groups of 7–10 animals with a dominant male and several reproductive females and their young (Suckling, 1984; Sadler and Ward, 1999). Females give birth after 15–17 days to 1–2 young

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(Suckling, 1984). After birth the young stay for 70 days in the pouch of the mother, are weaned at approximately 120 days and reach their adult size at around 300 days (Holloway and Geiser, 2000). Sugar gliders shelter in nest and tree hollows and their diet consists mainly of plant and insect exudates, nectar, pollen and insects (Smith, 1982; Hume, 1999).

We employed the doubly labelled water method (Lifson et al., 1955) for quantifying energy expenditure and water flux of free-ranging sugar gliders in a cool-temperate region of eastern Australia. We used these data to test the hypothesis that, as predicted by ADMR measurements in the laboratory, FMR should change with season because of changes in  $T_a$ . This information is especially important because limited information is available on seasonal changes in energy expenditure in the wild and sugar gliders are known to exhibit pronounced seasonal shifts in thermal and foraging biology according to weather and food availability (Smith, 1982; Quin, 1993; Körtner and Geiser, 2000; Christian and Geiser, 2007).

## 2. Material and methods

### 2.1. Animals and management

The study was undertaken at White Gum Flat on Newholme Field Laboratory Station approximately 10 km North-West of Armidale, on the New England Tablelands, New South Wales, Australia (latitude: 30° 25' S, longitude: 151° 26' E; altitude: 1100 masl; annual rainfall: 790 mm). The region experiences a cool-temperate climate and lies in a transition zone between summer and winter dominated rainfall. The site comprises open forest and woodland dominated by Apple Box (*Eucalyptus bridgesiana*), Mountain White Gum (*E. dabrympleana*), New England Stringybark (*E. caliginosa*) and Silvertop Stringybark (*E. laevopinea*). A detailed description of the vegetation of the study site is given in Smith and Phillips (1984) and Quin et al. (1992). Daily climatic data were collected from a weather station located approximately 2 km from the trapping sites. Data were collected during field trips undertaken from October 1986 to November 1990.

Animals were trapped with Elliott Scientific Type A folding box traps, covered with plastic bags and baited with a mixture of honey and sugar. The trapping technique involved placing a trap on brackets mounted to trees (>20 cm diameter at breast height) at a height of 3 to 5 m (for trapping technique see Smith and Phillips, 1984; Quin et al., 1992). After trapping, sugar gliders were removed from traps, placed in cloth bags and transported to the nearby field laboratory. The animals were sexed and weighed at the beginning and at the end of the trial after recapture. Any animals not previously captured were tagged with a numbered fingerling eartag ('FF', Salt Lake Stamp Co., Utah, USA). Unique colour combinations of Scotchlite reflective tape (3 M Australia Pty. Ltd., Mount Waverley, Victoria, Australia) were affixed to each eartag, permitting identification of individuals in a spotlight beam at night for recapture.

### 2.2. Isotope application, blood sampling and laboratory analysis

Sixty-six sugar gliders from which 36 could be recaptured (males: 14 in spring, 5 in summer, 2 in autumn; females: 10 in spring, 4 in summer, and 1 in autumn) received an intraperitoneal injection of  $^3\text{H}_2^{18}\text{O}$ .

The enrichments of the labels used were 95.0 at.% for  $^{18}\text{O}$  and 12 MBq for  $^3\text{H}$ . The amounts of dose given were 0.30–0.50 mL. The exact amount of isotope was measured gravimetrically to the nearest 0.001 g.

Blood samples of 1050–2000  $\mu\text{L}$  were collected using heparinised haematocrit tubes (i) just before the application of the isotopes for baseline analysis, (ii) after 2–3 h equilibration (Nagy and Suckling, 1985), and (iii) 2–5 days after dosing, depending on recapture of the individuals. Animals were held in cloth bags at Newholme field laboratory between baseline and equilibration sample. Blood samples were immediately flame-sealed in heparinised glass capillary tubes

and refrigerated pending laboratory analysis. In some instances, females had pouch young that were 1–2 weeks old. However they weighed only 1–2 g each, which would have had a negligible effect on the analysis in a 120 g animal (see Nagy and Suckling, 1985).

Analyses on water-distilled blood samples were carried out at the University of California, Los Angeles. Tritium activities were measured by liquid scintillation spectrometry (Nagy, 1983). Oxygen isotope ratios were measured by a cyclotron-generated-proton activation (Wood et al., 1975). Individual samples were measured 5 times and the averages calculated. In total, 108 samples (45 from females and 63 from males) were analysed for hydrogen and oxygen.

Total body water volumes (TBW) and water fluxes were calculated by equations given in Nagy (1980, 1983) and Speakman (1997). It was assumed that any changes in TBW occurred linearly through time. TBWs were estimated at the time of injection from the  $^{18}\text{O}$  dilution space.

Carbon dioxide production rates ( $\text{rCO}_2$ ) were calculated from established equations (Nagy, 1980, 1983).

Rates of energy metabolism (in  $\text{kJ d}^{-1}$ ) and metabolic water production were calculated from  $\text{rCO}_2$  production with the dietary conversion factors of 22.5 kJ per litre  $\text{CO}_2$ , and 0.655 mL water per litre  $\text{CO}_2$ , as derived by Nagy and Suckling (1985) for sugar gliders studied in Victoria. The sugar gliders studied in Victoria were feeding on similar food items (sap, pollen, insects, etc., see Smith, 1982; Quin, 1993), and experienced similar environmental conditions to those studied at Newholme. Hence, the previously measured value for conversion of food to energy and water was considered to be appropriate for our study.

### 2.3. Statistical analysis

Statistical analyses were performed with the program package SAS version 9.01 (SAS, 2001). An analyses of variance was performed using the procedure GLM as follows:  $Y_{ijk} = \mu + G_i + S_j + G_i \times S_j + e_{ijk}$ ; where:  $Y_{ijk}$  = observation value,  $\mu$  = overall mean,  $G_i$  = fixed effect of the  $i$ th gender ( $i$  = male, female),  $S_j$  = fixed effect of the  $j$ th season ( $j$  = spring, summer, autumn),  $G \times S_j$  = interaction between the  $i$ th gender and  $j$ th season,  $e_{ijk}$  = random error. Numerical values are given as means  $\pm$  SE for the number of individuals.

## 3. Results

Maximum  $T_a$  varied from 11.4 °C in autumn to 27.1 °C in summer. Mean minimum  $T_a$  varied from  $-2.2$  °C in autumn to 14.3 °C in summer. Intermittent light rainfall occurred throughout the study, but usually accounted for <1 mm per day in total. Minimum  $T_a$  over which gliders were active ranged from  $-2.2$  °C in autumn to 16.5 °C in summer. Mean seasonal  $T_a$ 's for spring, summer and autumn were 13.9, 19.9 and 10.3 °C, respectively (Australian Bureau of Meteorology). Maximum  $T_a$  over which gliders were active (i.e. at night) varied from 0 °C in autumn to 21.2 °C in summer. Given that the lower critical temperature of a 120 g sugar glider (mean mass for this study) is 29.0 °C (Fleming, 1980), individuals were always below thermoneutrality.

Body masses at the time of injection (male:  $126.9 \pm 2.9$  g, female  $114.5 \pm 2.5$  g, all  $121.8 \pm 2.3$  g) and at the time of recapture (male:  $121.7 \pm 3.1$  g, female  $111.1 \pm 2.9$  g, all  $117.3 \pm 2.3$  g) did not differ (paired sampled  $t$ -test, all:  $P = 0.17$ ,  $n = 36$ ; male:  $P = 0.23$ ,  $n = 21$ ; female:  $P = 0.37$ ,  $n = 15$ ), therefore further calculations were carried out using the average body masses across both measurements (Table 1).

Absolute FMR of male and female sugar gliders averaged 159 and 158  $\text{kJ d}^{-1}$  for spring, 161 and 147  $\text{kJ d}^{-1}$  for summer and 168 and 119  $\text{kJ d}^{-1}$  for autumn. Mass-specific FMR of male and female sugar gliders throughout the study averaged 1.36 and 1.41  $\text{kJ g}^{-1} \text{d}^{-1}$  for spring, 1.12 and 1.32  $\text{kJ g}^{-1} \text{d}^{-1}$  for summer and 1.47 and 1.07  $\text{kJ g}^{-1} \text{d}^{-1}$  for autumn. The overall mean for absolute and mass-specific FMR was  $158 \pm 5$   $\text{kJ d}^{-1}$  and  $1.33 \pm 0.05$   $\text{kJ g}^{-1} \text{d}^{-1}$  (mean mass  $120 \pm 2$  g), respectively (Table 1, for single animal data see Appendix A).

**Table 1**  
Average body mass (BM), total body water, CO<sub>2</sub> production, field metabolic rate and water flux rates of doubly labelled free-ranging male (M) and female (F) sugar gliders (*Petaurus breviceps*) in different seasons.

		n	BM		Total body water		CO <sub>2</sub> production		Field metabolic rate		Water influx rate	
			(g)	(g)	(%)	(l d <sup>-1</sup> )	(mL g <sup>-1</sup> h <sup>-1</sup> )	(kJ d <sup>-1</sup> )	(kJ g <sup>-1</sup> d <sup>-1</sup> )	(mL d <sup>-1</sup> )	(mL kg <sup>-1</sup> d <sup>-1</sup> )	
Spring	Male	14	119 ± 3	81 ± 2	67.7 ± 1.2	7.1 ± 0.4	2.5 ± 0.2	159 ± 9	1.36 ± 0.09	27 ± 2	228 ± 15	
	Female	10	113 ± 4	78 ± 4	68.5 ± 2.1	7.1 ± 0.3	2.6 ± 0.1	158 ± 8	1.41 ± 0.07	32 ± 2	287 ± 25	
	All	24	117 ± 2	80 ± 2	68.0 ± 1.1	7.1 ± 0.3	2.6 ± 0.1	159 ± 6	1.38 ± 0.06	25 ± 2	253 ± 14	
Summer	Male	5	142 ± 2	106 ± 4	72.4 ± 2.7	7.1 ± 0.5	2.1 ± 0.2	161 ± 11	1.12 ± 0.08	24 ± 3	165 ± 20	
	Female	4	112 ± 3	84 ± 7	71.6 ± 4.6	6.6 ± 0.5	2.4 ± 0.2	147 ± 12	1.32 ± 0.11	26 ± 4	228 ± 36	
	All	9	129 ± 6	96 ± 5	72.0 ± 2.4	6.9 ± 0.4	2.2 ± 0.1	155 ± 8	1.21 ± 0.07	25 ± 2	193 ± 21	
Autumn	Male	2	115	74	62.5	7.5	2.7	168	1.47	34	298	
	Female	1	112	66	59.8	5.3	2	119	1.07	35	312	
	All	3	114 ± 3	71 ± 3	61.6 ± 2.6	6.7 ± 0.9	2.5 ± 0.3	152 ± 20	1.33 ± 0.15	34 ± 5	303 ± 49	
All seasons	Male	21	124 ± 3	87 ± 3	68.3 ± 1.2	7.1 ± 0.3	2.4 ± 0.1	161 ± 7	1.31 ± 0.07	27 ± 2	220 ± 15	
	Female	15	113 ± 3	79 ± 3	68.7 ± 1.9	6.8 ± 0.3	2.5 ± 0.1	153 ± 6	1.36 ± 0.06	30 ± 2	273 ± 20	
	All	36	120 ± 2	83 ± 2	68.5 ± 1.1	7.0 ± 0.2	2.5 ± 0.1	158 ± 5	1.33 ± 0.05	29 ± 1	242 ± 13	
Effect	Season		P < 0.01	P < 0.01	P < 0.05	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
	Gender		P < 0.01	P < 0.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	
	Season*Gender		P < 0.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	

The mass-specific FMR (kJ g<sup>-1</sup> d<sup>-1</sup>) for gliders was negatively correlated with body mass ( $\log_{10} \text{FMR (kJ g}^{-1} \text{d}^{-1}) = 1.875 - 0.848 \log_{10} \text{BM (g)}$ ,  $n = 36$ ,  $R^2 = 0.222$ ,  $P = 0.004$ ; Fig. 1). Although the mean mass differed between males (124 ± 3 g) and females (113 ± 3 g) ( $t$ -test,  $P = 0.003$ ), absolute and mass-specific FMR did not differ significantly among seasons or sexes (Table 1). Even when body mass was included as a covariate and only values for spring and summer were analysed, season and gender and their interaction had no effect on absolute (season:  $P = 0.717$ , gender:  $P = 0.634$ , season\*gender:  $P = 0.645$ ) or mass-specific FMR (season:  $P = 0.878$ , gender:  $P = 0.429$ , season\*gender:  $P = 0.462$ ). Importantly, FMR was not correlated with the mean  $T_a$  experienced by the animals during the measurement period at different seasons ( $\text{FMR (kJ d}^{-1}) = 127.5 + 1.87 T_a$  (°C),  $F_{1, 34} = 0.98$ ,  $n = 36$ ,  $R^2 = 0.029$ ,  $P = 0.329$ ; Fig. 2). However, body mass and hence TBW were significantly affected by season. Estimated TBW averaged 68.5% of body mass. Water fluxes averaged 29 ± 1 mL day<sup>-1</sup> or 242–245 mL kg<sup>-1</sup> d<sup>-1</sup> on a mass-specific basis (Table 1).

**4. Discussion**

Our study shows that sugar gliders, despite pronounced seasonal changes in  $T_a$  and food availability, seem to be able to maintain a seasonally constant rate of energy expenditure and water use. Even

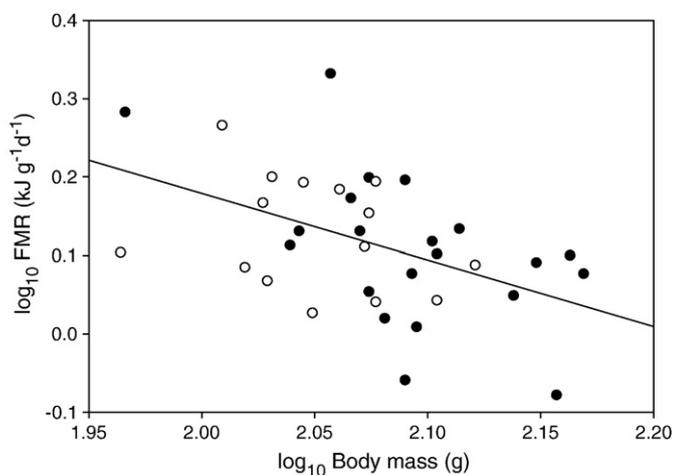
though the sample size for autumn was small, this suggests that behavioural (activity patterns, nest use, huddling and foraging) and physiological adjustments (torpor use) known to be employed by the species in the wild (Fleming, 1980; Körtner and Geiser, 2000) enable sugar gliders to maintain energy and water requirements at similar levels for much of the year.

**4.1. Body mass and total body water**

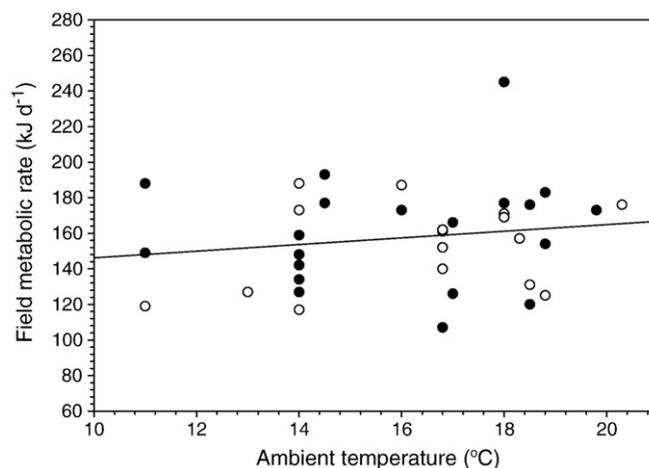
In our study TBW was on average 68.5% of body mass, which is very similar to the only other reported value of 67.4% for sugar gliders (Nagy and Suckling, 1985). Body weight and TBW volumes, were influenced by season and sex. Patterns of weight changes in demographic studies suggested that gliders are heaviest in summer and autumn, and lightest in winter and spring (Quin, 1993). However, in our study, female body mass stayed fairly constant throughout the seasons whereas male body mass increased from spring to summer. It is known that sugar gliders build up fat reserves in summer when food appears to be most abundant, and  $T_a$ 's least harsh (Quin, 1993).

**4.2. Water fluxes**

An allometric equation on standard water turnover in captive mammals derived by Nicol (1978) predicts 18 mL of water influx per



**Fig. 1.** Relationship between body mass and mass-specific field metabolic rate (FMR) in male (dots) and female (circles) sugar gliders ( $\log_{10} \text{FMR} = 1.875 - 0.848 \log_{10} \text{BM}$ ,  $n = 36$ ,  $R^2 = 0.222$ ,  $P = 0.004$ ).



**Fig. 2.** Relationship between mean ambient temperature ( $T_a$ ) and field metabolic rate (FMR) in male (dots) and female (circles) sugar gliders during the measurement period at different seasons ( $\text{FMR (kJ d}^{-1}) = 127.5 + 1.87 T_a$  (°C),  $F_{1, 34} = 0.98$ ,  $n = 36$ ,  $R^2 = 0.029$ ,  $P = 0.329$ ).

day for a 120 g mammal. Water influx rates at Newholme averaged  $29 \text{ mL d}^{-1}$ , 62% above the predicted value, suggesting that sugar gliders at Newholme, similar to their conspecifics and Leadbeater's possums in Victoria (Smith et al., 1982; Nagy and Suckling, 1985), ingested water in excess of their daily needs.

Nagy and Peterson (1988) provide allometric equations for predicting water flux rates of various taxa, from studies involving doubly labelled water measurements on field and captive mammals. Their allometric equation for field water flux rates predicts a value of 45 mL/day for a 120 g marsupial, 55% above that measured here for sugar gliders. As equations by Nagy and Peterson (1988) were derived for animals studied under various environmental conditions, (including wet and dry climates), it is likely that differences between measured and predicted water fluxes for sugar gliders reflect differences in diet, habitat and climate known to affect field water fluxes.

#### 4.3. Field metabolic rates

The seasonally constant FMR observed here raises the question as to how metabolic requirements could be adjusted considering the pronounced seasonal differences in weather and therefore thermoregulatory requirements. Contrary to measurements in the laboratory where ADMR increased substantially with decreasing  $T_a$  in sugar gliders (Holloway and Geiser, 2001), results from the present study suggest that FMR does not change significantly with  $T_a$  in free-ranging sugar gliders. Employing the equation developed by Holloway and Geiser (2001) on sugar gliders in captivity ( $\text{ADMR} (\text{kJ d}^{-1}) = 159.3 - 3.40 T_a (\text{°C})$ ), the ADMR at the different  $T_a$ 's experienced by the animals of the present study in spring, summer and autumn would have been equivalent to a decrease in energy expenditure of 18% from spring to summer and an increase in energy expenditure of 26% from summer to autumn. However, as results from the present study show, we did not observe any significant change in energy expenditure in free-ranging animals, emphasising that results obtained in captivity cannot be directly applied to free-ranging animals.

Similar constant FMR's measured in the wild have been observed for the much larger (~3 kg) rufous rat-kangaroos (*Aepyrynus rufescens*) (Wallis and Green, 1992). Their energy expenditure differed little between winter and spring despite a 20 °C difference in mean ambient temperature between seasons. The authors suggested that rufous rat-kangaroos must respond to low winter temperatures by

changes in coat, activity patterns or posture. In contrast, Green et al. (1991) found marked seasonal differences in energy and water use in the small carnivorous *Antechinus stuartii* (16–43 g), which was explained by their unusual breeding cycle in which all males die at the end of the annual mating period.

Nagy and Suckling (1985) found that absolute FMRs of larger male sugar gliders were significantly higher than in females, but on a mass-specific basis, FMR was similar. In the present study, both absolute and mass-specific FMR were similar between the sexes, but we did observe a significant negative correlation between mass-specific FMR and body mass (Fig. 1).

Sugar gliders are known to employ several behavioural adjustments to changing weather. During cold and inclement weather, the species substantially decreases foraging activity (i.e. activity outside the nest) and therefore energy costs (Quin, 1993; Körtner and Geiser, 2000; Christian and Geiser, 2007), similar to red squirrels (Humphries et al., 2005). Moreover, sugar gliders increase group sizes in winter and thus the effectiveness of huddling during cold weather, which can reduce thermoregulatory energy expenditure by up to 50% (Fleming, 1980). Sugar gliders also increase body mass and thermal insulation in autumn (Holloway and Geiser, 2001), which will further decrease thermoregulatory requirements. Finally, and perhaps most importantly, sugar gliders are able to use daily torpor for energy conservation during inclement weather (Körtner and Geiser, 2000). Assuming a mean torpor bout duration of 13.1 h as expressed in the field (Körtner and Geiser, 2000), sugar gliders can reduce daily energy expenditure by 50% in comparison to gliders remaining normothermic which by far exceeds the required seasonal change of ADMR for thermoregulatory energy expenditure (Geiser et al., 2007). Thus, a combination of behavioural and functional adjustments appears to allow sugar gliders to attune energy expenditure appropriately to thermal and trophic seasonal conditions.

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#### Appendix A

Average body mass (BM), total body water, CO<sub>2</sub> production, field metabolic rate and water flux rates of doubly labelled free-ranging male (M) and female (F) sugar gliders (*Petaurus breviceps*) at different seasons.

Animal No.	Season	BM	Total body water		CO <sub>2</sub> production		Field metabolic rate		Water influx	
		(g)	(g)	(%)	(L d <sup>-1</sup> )	(mL g <sup>-1</sup> h <sup>-1</sup> )	(kJ d <sup>-1</sup> )	(kJ g <sup>-1</sup> d <sup>-1</sup> )	(mL d <sup>-1</sup> )	(mL kg <sup>-1</sup> d <sup>-1</sup> )
M1	Spring	93	60	60.9	7.9	3.6	177	1.92	17	188
M2	Spring	123	78	63.1	8.6	2.9	193	1.57	20	163
M3	Autumn	111	75	66.7	6.6	2.5	149	1.35	42	383
M4	Autumn	119	72	58.3	8.3	2.9	188	1.58	25	214
M5	Spring	121	73	59.7	5.6	1.9	126	1.05	24	195
M6	Spring	127	87	64.2	7.4	2.4	166	1.31	36	284
M7	Spring	127	94	74.8	7.1	2.3	161	1.26	25	200
M8	Spring	123	82	67.5	4.8	1.6	107	0.87	17	140
M9	Summer	146	118	77.3	8.1	2.3	183	1.26	27	187
M10	Summer	138	102	71.7	6.9	2.1	154	1.12	19	135
M11	Summer	117	90	73.1	7.7	2.8	173	1.49	20	173
M12	Summer	148	105	70.3	7.8	2.2	176	1.19	34	227
M13	Summer	144	95	63.9	5.1	1.5	120	0.84	23	160
M14	Summer	141	114	78.9	7.7	2.3	173	1.23	16	115
M15	Spring	125	80	68.3	5.6	1.9	127	1.02	34	273

## Appendix A (continued)

Animal No.	Season	BM (g)	Total body water		CO <sub>2</sub> production		Field metabolic rate		Water influx	
			(g)	(%)	(L d <sup>-1</sup> )	(mL g <sup>-1</sup> h <sup>-1</sup> )	(kJ d <sup>-1</sup> )	(kJ g <sup>-1</sup> d <sup>-1</sup> )	(mL d <sup>-1</sup> )	(mL kg <sup>-1</sup> d <sup>-1</sup> )
M16	Spring	118	81	67.3	7.1	2.5	159	1.35	35	301
M17	Spring	119	81	67.8	6.0	2.1	134	1.13	25	212
M18	Spring	124	87	71.2	6.6	2.2	148	1.20	27	219
M19	Spring	110	78	68.8	6.3	2.4	142	1.30	29	267
M20	Spring	130	86	67.0	7.9	2.5	177	1.36	36	280
M21	Spring	114	90	74.4	10.9	4.0	245	2.15	35	303
F22	Summer	107	67	59.9	7.0	2.7	157	1.47	19	175
F23	Autumn	112	66	59.8	5.3	2.0	119	1.07	35	312
F24	Spring	132	107	81.0	7.2	2.3	162	1.23	37	277
F25	Spring	105	62	57.1	5.7	2.3	127	1.22	24	229
F26	Spring	127	82	64.3	6.2	2.0	140	1.10	24	191
F27	Spring	118	82	68.1	6.8	2.4	152	1.29	30	256
F28	Summer	115	100	82.4	7.8	2.8	176	1.53	38	327
F29	Summer	107	81	72.2	5.6	2.2	125	1.17	25	231
F30	Spring	120	90	76.4	8.3	2.9	187	1.56	22	180
F31	Summer	120	87	71.8	5.8	2.0	131	1.10	21	178
F32	Spring	111	72	65.0	7.7	2.9	173	1.56	31	279
F33	Spring	102	70	67.7	8.4	3.4	188	1.84	44	426
F34	Spring	92	65	70.4	5.2	2.4	117	1.27	34	365
F35	Spring	108	75	68.5	7.6	2.9	171	1.59	37	343
F36	Spring	119	78	66.1	7.5	2.6	169	1.42	39	332

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