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ORIGINAL PAPER

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Field metabolic rates and water uptake in the blossom-bat *Syconycteris australis* (Megachiroptera)

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Abstract Blossom-bats, *Syconycteris australis* (18 g) are known to be highly active throughout the night. Since this species frequently enters torpor, we postulated that their use of heterothermy may be related to a high energy expenditure in the field. To test this hypothesis we measured field metabolic rates (FMR) of *S. australis* at a subtropical site using the doubly labelled water (DLW) method. We also measured DLW turnover in captive animals held at constant ambient temperature (T_a) with ad libitum food to estimate whether T_a and food availability affect energy expenditure under natural conditions. The FMR of *S. australis* was 8.55 ml CO_2 g^{-1} h^{-1} or 76.87 kJ day^{-1} which is 7.04 times the basal metabolic rate (BMR) and one of the highest values reported for endotherms to date. Mass-specific energy expenditure by bats in the laboratory was about two-thirds of that of bats in the field, but some of this difference was explained by the greater body mass in captive bats. This suggests that foraging times in the field and laboratory were similar, and daily energy expenditure was not strongly affected by T_a or ad libitum food. Water uptake in the field was significantly higher than in the laboratory, most likely because nectar contained more water than the laboratory diet. Our study shows that *S. australis* has a FMR that is about double that predicted for its size although its BMR is lower than predicted. This supports the view that caution must be used in making assumptions from measurements of BMR in the laboratory about energy and other biological requirements in free-ranging animals.

Key words Doubly labelled water · Field metabolic rate/basal metabolic rate ratio · Megachiroptera · Subtropical

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Abbreviations *BM* body mass · *BMR* basal metabolic rate · *DLW* doubly labelled water · *FMR* field metabolic rate · *MR* metabolic rate · T_a ambient temperature · T_b body temperature

Introduction

Blossom-bats are small nectar and pollen eating megachiropterans found in tropical and subtropical regions of Africa, Asia and Australia (Fenton 1983). They are a highly active group of mammals and one Australian species, the common blossom-bat *Syconycteris australis*, is known to forage on the wing for much of the night (Law 1993). This activity is energetically costly and may be the reason why during their rest phase *S. australis* and other blossom-bats readily enter daily torpor to reduce metabolic rate (MR), even under mild environmental conditions (Bartholomew et al. 1970; Kulzer and Storf 1980; Coburn and Geiser 1996, 1998; Geiser et al. 1996; Bonaccorso and McNab 1997; Bartels et al. 1998; Geiser 1998a). While activity patterns of *S. australis* have been quantified in the field and MR has been measured in the laboratory, energy expenditure in the field has not been determined for this species nor to our knowledge in any other bat of the suborder Megachiroptera (henceforth megabat). In contrast, field metabolic rates (FMR) have been measured in several microchiropterans and birds (Nagy 1987; Speakman and Racey 1991; Degen and Kam 1995), and in many non-flying mammals (Nagy 1987; Degen and Kam 1995). These studies establish that energy expenditure in the field can differ substantially from that predicted from basal metabolic rate (BMR) measurements in the laboratory.

To provide information on energy expenditure and water metabolism under natural conditions in a highly active small megabat, we measured FMR and water influx for *S. australis*, using the doubly labelled water (DLW) method. The species is found in tropical and subtropical areas along the Australian east coast, roosts in rainforests or wet sclerophyll forests and forages for

nectar among native trees and bushes with a preference for *Banksia* spp. flowers (Law 1992, 1994). We conducted our study in winter, when food is most clustered and abundant (Armstrong 1991; Coburn and Geiser 1998) and the probability of recaptures was therefore highest. The daily energy expenditure by blossom-bats in the laboratory is relatively high in winter, because they have long activity periods at night and undergo only short and shallow periods of torpor during the day (Coburn and Geiser 1996, 1998).

For comparison we also measured energy expenditure using the DLW method in captive bats held in a temperature-controlled room with ample space for flight. For captive bats, food was available ad libitum to assess the magnitude of the cost of flying to or between food sources in the field. To test whether ambient temperature (T_a) is an important determinant of daily energy expenditure, T_a in the holding room was maintained at 20 °C, which was about 10 °C higher than the daily T_a minima in the field. Water intake was used to compare uptake of nectar in the field with uptake of the artificial food in the laboratory.

Materials and methods

Field study

The field study was conducted near Iluka (29°13′S, 153°21′E) on the subtropical north coast of New South Wales. Measurements were made in June 1995 and June 1996 (Australian winter). We were able to collect data for four individuals in 1995 and eight in 1996.

Bats were netted using mist nets set in a large flowering *Banksia integrifolia* stand. A blood sample (approximately 50 µl) was taken from a wing vein to determine background radiation. Animals then received an intraperitoneal injection of 100 µl of DLW containing >95% oxygen-18, and 180 MBq/ml tritiated water. After at least 1 h, which is enough time for equilibration of the injected sample with the body water (Nagy 1983; Nagy and Gruchacz 1994) a post-injection blood sample was taken. The bats were then marked and released at the site of capture. We continued netting over several nights at the same site, increasing the number of nets and changing net position to recapture individuals. We injected 9 individuals (8 females, 1 male) in 1995 and 14 individuals (7 females, 7 males) in 1996. We recaptured four females in 1995 and eight individuals (six females, two males) in 1996 and took a recapture blood sample. Bats were weighed to the nearest 0.1 g in 1995 and to the nearest 1 g in 1996. Most individuals were recaptured only once, but one individual (5f) was recaptured twice. Analysis of blood revealed that energy turnover was usually so high that CO_2 production could be quantified only when animals were recaptured within about 1 day of the injection. For one individual (17f) however, which had a relatively low FMR, we obtained good values after 2 days. Water influx could be measured in all bats caught 1 or 2 days after the injection. The weather during the periods of field measurements was mild, with T_a measured in the *Banksia* stand ranging between minima of 10 °C at night and maxima of 21 °C during the day. In both years we recorded rainfall on several occasions.

Laboratory study

In August (winter) 1995, six individuals (males) were kept in captivity at the University of New England in a large holding room (3.5 length × 2.1 width × 3.0 height m) which provided ample space for flight. Animals were maintained under these conditions for several weeks to acclimate them to the laboratory conditions. The room was fitted with leaved branches and wide plastic mesh for roosting. Laboratory food contained about 58% water and consisted of a blended mixture of apple juice, bananas, sugars and "Infasoy" (Geiser et al. 1996). Food was provided daily ad libitum in special plastic feeders which were washed and soaked daily in antibacterial solution to discourage microbial growth. Water was available ad libitum in bird feeders, but bats appeared to drink very little if at all.

The T_a in the room was maintained at 20 ± 1 °C and relative humidity above 40%. Photoperiod was maintained at the natural photoperiod at the time of capture (10L:14D; lights on from 0700 hours to 1700 hours).

As for individuals in the field, a blood sample for background radiation was taken in several individuals before the injection of DLW. Animals then received an intraperitoneal injection of 100 µl DLW, a post-injection blood sample was taken after 1 h, and bats were released into their holding room. The final blood sample was taken 24 h after the post-injection blood sample (i.e. 25 h after the injection). Bats were weighed on both days to the nearest 0.1 g.

DLW analysis

Blood samples were analysed by B. Green and K. Newgrain at CSIRO Wildlife and Ecology in Canberra. Water was obtained by the micro distillation method (Wood et al. 1975); 2 µl of water from the sample were counted to 1% error in a Beckman LS2800 LSC using PCS (Amersham) scintillation cocktail. Samples of 20 µl of water were incubated with CO_2 in Urey tubes overnight at 60 °C and the 46:44 ratios measured in a VG Optima Mass Spectrometer. Pool sizes were calculated from standard oxygen-18 dilutions of the injectate in the single pool equation by Nagy (1980). Pool size ratios (water volumes estimated by tritium/oxygen-18) were 1.07 ± 0.02 for the field bats and 1.03 ± 0.01 for the laboratory bats and were within the range reported for other species (Speakman 1997). Rate of CO_2 production was calculated according to equations of Nagy (1980). Since energy metabolism of blossom-bats is mainly fuelled from sugars in nectar it was assumed that 1 l CO_2 produces the equivalent of 21.9 kJ heat.

Numerical values are expressed as means ±1 SD. Analysis of Covariance (ANCOVA) with body mass as covariate was used to compare slopes and intercepts of linear regressions. Linear regressions were performed using the method of least squares. Differences between means were assessed using a Student's *t*-test.

Results

Body mass (BM) of *S. australis* in the field ranged between 16.0 g and 19.6 g with a mean of 17.4 ± 1.2 g (Table 1). Mean BM of males (17.0 ± 1.4 g) did not differ from that of females (17.4 ± 1.2 g). BM of captive individuals (20.0 ± 1.5 g) was significantly greater ($P < 0.001$) than that of field individuals (Tables 1, 2), but capture mass of laboratory bats (mean 17.5 g) was similar to that of field individuals. Mass change over 1 day was −0.28 ± 0.53 g ($n = 4$) for bats measured in the field in 1995, which was similar to that measured in the laboratory (−0.03 ± 1.22 g, $n = 6$). In 1996, when a balance with a 1-g resolution was used, no differences could be detected between first and second capture masses in the field. Body water content was 67 ± 4% in the field bats which was significantly higher ($P < 0.001$) than the 58 ± 2% in the laboratory bats, most likely because of a greater fat content in the latter. Both values measured here were within the range reported for microbats (Speakman 1997).

Table 1 Metabolic rates and water influx of *Syconycteris australis* in the field (*BM* body mass, *m* male, *f* female, *FMR* field metabolic rate)

No.	BM (g)	CO_2 out (ml g^{-1} h^{-1})	CO_2 out (l day^{-1})	FMR (kJ day^{-1})	H_2O in (ml g^{-1} day^{-1})	H_2O in (ml day^{-1})
1m	16.0	10.51	4.04	88.38	1.89	30.24
2f	17.0				2.12	35.96
3f	16.0	9.52	3.65	80.02	1.72	27.52
4f	17.0	8.62	3.52	76.99	1.83	31.16
5f	16.0	10.05	3.86	84.52	1.97	31.47
6m	18.0				1.88	33.75
7f	16.0				2.43	38.88
10f	18.7	7.53	3.38	74.05	1.09	20.31
13f	18.1				1.87	33.85
14f	18.0				2.30	41.44
16f	18.9	7.40	3.36	73.51	1.01	19.11
17f	18.6	6.20	2.77	60.61	1.46	27.19
Mean	17.36	8.55	3.51	76.87	1.80	30.91
SD	1.16	1.58	0.41	8.99	0.43	6.70

S. australis had a very high FMR. The average CO_2 production was 8.55 ± 1.58 CO_2 g^{-1} h^{-1}, which amounts to a daily energy expenditure of 4.45 kJ g^{-1} day^{-1} or 76.9 kJ day^{-1} (Table 1). The average daily FMR was 7.04 times the BMR (10.92 kJ day^{-1}) of this species in winter (Coburn and Geiser 1998). FMR did not appear to differ between the sexes. Although bats in the field had an almost 1.5-fold higher average mass-specific CO_2 production than bats in the laboratory (8.55 ml CO_2 g^{-1} h^{-1} vs 5.89 ml CO_2 g^{-1} h^{-1}; Table 2), this difference appears to be at least partially due to BM (Fig 1). ANCOVA indicated that the data point of bat 20 m (22.6 g; Table 2) is an outlier for this BM by having a large standardised residual. Exclusion of this point suggests the two data sets are the same (ANCOVA; $P > 0.9$), and when mass-specific CO_2 production rates of field and laboratory bats were regressed together against BM a highly significant correlation was obtained ($r^2 = 0.92$; $P < 0.001$). Similarly, ANCOVA suggested that total CO_2 production of field and laboratory bats are indistinguishable ($P > 0.5$) when expressed as a function of BM. A single linear regression of total CO_2 production against BM was also highly significant ($r^2 = 0.80$; $P < 0.001$). Thus, apparent differences in energy expenditure between laboratory and field bats may to some extent be explained by size differences and scaling effects (Fig. 1).

Daily water turnover in the field was also very high. Water intake of bats amounted to 1.80 ± 0.43 ml g^{-1} day^{-1} and thus a total daily water uptake of 30.91 ml, which is 1.77 times BM. On average the daily water uptake of laboratory individuals was only 35% of that of field animals (Tables 1, 2). In the field, no correlation could be observed between total daily water uptake and BM, whereas in the laboratory, total daily water uptake increased with mass (Fig. 2).

Discussion

The FMR of *S. australis* we report here are among the highest values known for a mammal of its size and to the best of our knowledge are the first FMR data for any megabat. The energy requirements in the field were about 7 times the BMR and the FMR/BMR ratio was about twice the value predicted for a similar sized placental mammal (Nagy 1987; Degen and Kam 1995).

Our observations support the view that energy is a very important currency for *S. australis* as has been predicted by Law (1992, 1994, 1995). The data suggest that a reduction in food availability, as for example when few flowers are blossoming or after rain when nectar is diluted or washed away, will restrict the ability of blossom-bats to collect enough food to remain normothermic throughout the day and thus they may resort to the use of torpor to reduce energy expenditure during the rest phase (Geiser et al. 1996). Since food is more abundant and clustered in winter and the time available for foraging in summer is short, energy con-

Table 2 Metabolic rates and water influx of *S. australis* in the laboratory (*MR* metabolic rate)

No.	BM (g)	CO_2 out (ml g^{-1} h^{-1})	CO_2 out (l day^{-1})	MR (kJ day^{-1})	H_2O in (ml g^{-1} day^{-1})	H_2O in (ml day^{-1})
19m	20.0	5.00	2.40	52.53	0.57	11.40
20m	22.6	6.79	3.68	80.62	0.71	16.07
21m	20.1	5.56	2.68	58.77	0.62	12.36
22m	18.2	7.61	3.32	72.78	0.42	7.61
25m	19.1	5.26	2.42	52.99	0.42	7.93
27m	20.1	5.12	2.47	54.13	0.46	9.29
Mean	20.02	5.89	2.83	61.97	0.53	10.78
SD	1.47	1.06	0.54	11.88	0.12	3.2

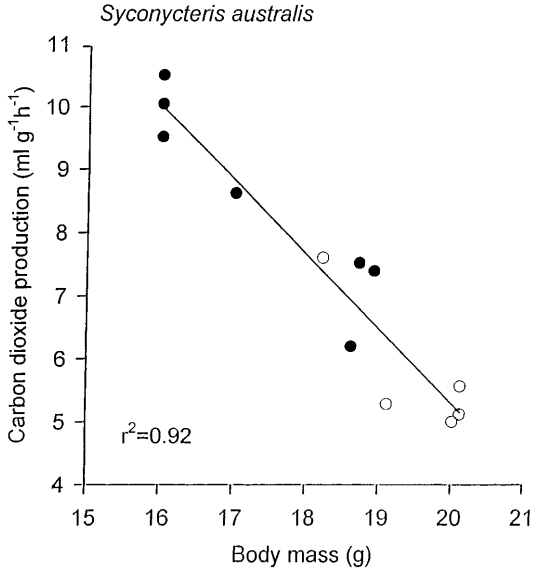

Fig. 1 CO_2 production as a function of body mass in *Syconycteris australis* in the field (*closed symbols*) and in a large holding room in the laboratory at ambient temperature (T_a) 20 °C (*open symbols*). The data of field and laboratory individuals are best described by a single regression: CO_2 (ml g^{-1} h^{-1}) = 28.92 – 1.18 mass (g); r^2 = 0.92; $P < 0.001$

straints are likely greatest in summer which coincides with the time when blossom-bats use torpor most extensively in the laboratory (Coburn and Geiser 1998). Food availability in summer may be further limited by rainfall because most precipitation along the Australian east coast occurs during this time.

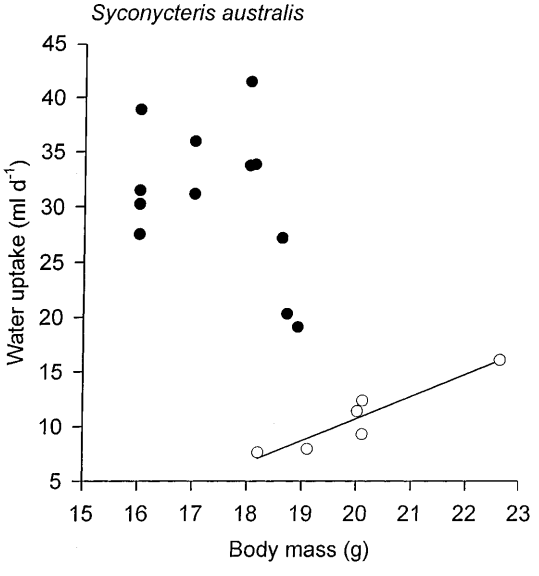

Fig. 2 Water uptake as a function of body mass in *S. australis* in the field (*closed symbols*) and in a large holding room in the laboratory at T_a 20 °C (*open symbols*). Only individuals in the laboratory showed a correlation between water uptake and body mass (BM): H_2O (ml day^{-1}) = 29.95 + 2.03 mass (g); r^2 = 0.87; $P < 0.01$

Similar to energy expenditure, daily water uptake of blossom-bats was high. In the field, daily-water uptake was about 1.8 times the BM of bats. As for hummingbirds (Calder and Hiebert 1983) and other nectar feeders, water can be a nuisance. Nectar contains between 60% and 87% water (Richards 1997) which is much more than metabolically required, but it must be ingested and processed if requirements for energy and nutrients are to be met. In the laboratory, daily water uptake was only slightly above 50% of the BM. The difference between laboratory and field data can be explained largely by differences in water content of the diets and differences in energy expenditure. *Banksia* nectar, a major dietary item of *S. australis*, contains on average about 73% water (Law 1992), but this percentage could increase during wet weather as during the present study. The on average 1.5-fold greater energy expenditure of animals in the field would further increase the demand of nectar intake. In contrast, the laboratory diet contained only about 58% water and bats did not appear to drink free water which was available to them, or did so in very small quantities.

When plotted against BM, daily energy expenditure by bats in the field and laboratory could be described by a single linear regression equation. This suggests that bats in the laboratory foraged throughout the night even though they had easy access to food. However, since bats in the field were measured in winter when flowers with nectar were clustered, the relatively small difference between laboratory and field energy expenditure may be explained by the abundance of food. This observation should, however, not be used to deduce that energy is not a limiting commodity. Our data simply indicate that when food is freely available in the laboratory and bats have room to fly they use almost as much energy as under natural conditions. However, when animals are confined to metabolic chambers which prevent flight, the average daily MR is only about half of that measured in the holding room (Coburn and Geiser 1996).

The rather small differences in energy expenditure between the laboratory and field also suggest that little of the daily energy costs are for thermoregulation per se. Bats in captivity were maintained at a constant T_a of 20 °C, which is about 10 °C below the lower critical temperature of the thermoneutral zone, requiring only a small increase of the MR of resting animals for regulation of a normothermic body temperature (T_b) (Geiser et al. 1996). In the field, bats foraged at as low as T_a 10 °C, which should have resulted in a significant increase in MR if it was used for thermoregulation. However, since during flight MR of small bats increases to about 20 times the BMR (Speakman and Racey 1991; Winter and von Helversen 1998), it is likely that high activity at night produces enough heat as a by-product so that there is little need for thermoregulatory heat production. During the daytime, when bats are at rest, energy expenditure should be low. At T_a 20 °C, the average daily maximum T_a in winter, MR at rest is about twice the BMR when bats are normothermic and

about 50% of the BMR when they are torpid (Geiser et al. 1996). Thus daytime energy expenditure should account for only a small part of the overall daily energy expenditure.

Nevertheless, calculation of a daily energy budget from predicted energy expenditure during flight by bats (Speakman and Racey 1991), activity patterns (Law 1993), average daily MR (Coburn and Geiser 1996) and resting energy expenditure (Geiser et al. 1996) of *S. australis* suggests that use of torpor may be important for free-ranging blossom-bats even in winter. Energy expenditure for an 18-g bat during a 14-h night should be 71.5 kJ, based on 45% flight activity (54 kJ) and 55% rest at 10 °C (17.5 kJ; the average daily MR was used for calculation because it is similar to that of resting bats at night). Assuming that bats were resting but normothermic throughout the 10-h day at 20 °C (9 kJ) they would consume 80.5 kJ day^{-1} and exceed their daily energy expenditure measured in the field by almost 4 kJ day^{-1}. If, however, bats entered torpor for 5.5 h, as observed in the laboratory in winter (Coburn and Geiser 1998), daily energy expenditure would be reduced to 77 kJ day^{-1} which is almost exactly the value for FMR we measured.

BMR is often used to make predictions about energy expenditure by animals in the field. Commonly factors between two and three are used to derive energy expenditure in the field from BMR. Others have taken the argument further and have used BMR to make general predictions about nutritional ecology, thermal physiology and energetics (e.g. McNab 1983). However, BMR of endotherms is not always a reliable predictor for energy expenditure in the field (Nagy 1987; Koteja 1991); the ratio of FMR/BMR differs among taxa and is inversely related to BM (Degen and Kam 1995). Therefore generalisations based on BMR alone should be viewed with some scepticism.

In placental mammals the FMR/BMR ratio is about 2 in 5-kg species, and increases to values of 4–5 in 10-g species (Degen and Kam 1995). Thus the FMR/BMR ratio of 7 in *S. australis* is higher than that presently known for any other placental mammal (Fig. 3). The main reason for this high value lies in the relatively low BMR although the FMR of *S. australis* is also near the upper limit for some similarly sized species (Nagy 1987). In this aspect *S. australis* is similar to some small Australian marsupials (Fig. 3) which also have a high FMR, a high thermogenic capacity despite a low BMR and many enter daily torpor (Hume 1982; Dawson 1983; Geiser 1994; Degen and Kam 1995). As bats and marsupials diverged over 100 million years ago (Dawson 1983; Geiser 1998b), metabolic similarities between the two groups strongly suggest that environmental constraints are at least as important in determining energy metabolism as is taxonomic affiliation (Lovegrove 1996).

McNab (1983) hypothesised that endotherms with a BMR below that predicted for their BM are poor thermoregulators and therefore must enter torpor. Our data for thermal physiology and energetics in *S. australis* do not support this tenet. Without question, *S. australis* have an enormous metabolic scope, and are able to regulate T_b over a wide range of T_a even when resting, although their thermoregulation is not especially precise (Geiser et al. 1996). However, their imprecise regulation of T_b does not appear to be a result of a poor thermoregulation or low thermogenic capacity, but is a mechanism that together with torpor and their low BMR is used for energy conservation (Geiser et al. 1996). It is thus more cogent to argue that animals with a low BMR often also enter daily torpor because they live in an environment that requires frugal use of energy during the inactive phase when fuels are not replenished.

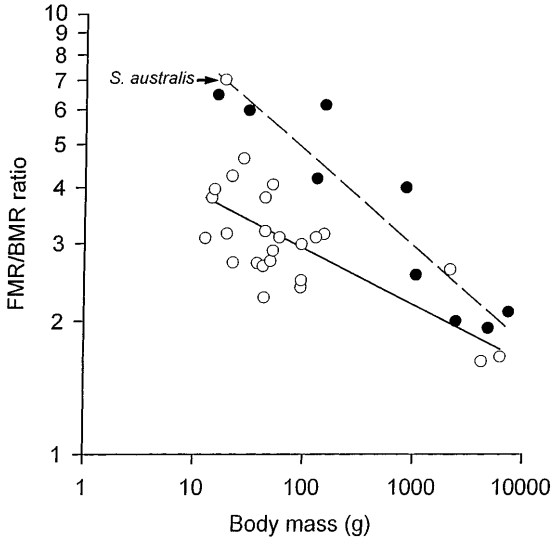

Fig. 3 The ratio of field metabolic rate (FMR) and basal metabolic rate (BMR) as a function of BM in marsupial (*closed symbols*, *broken line*) and placental mammals (*open symbols*, *solid line*). Values are taken from Degen and Kam (1995), the present study, and Coburn and Geiser (1998). Equations for the regressions are:
Marsupials FMR/BMR = $13.06BM^{-0.216}$; $r^2 = 0.87$
Placentals FMR/BMR = $5.24BM^{-0.127}$; $r^2 = 0.47$

Our study shows that energy expenditure and water uptake in blossom-bats are high. It supports the view that energy is a limiting commodity for free-living blossom bats and may be the reason why they have evolved a high proclivity to enter torpor even though they only live in areas with warm climates.

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References

Armstrong DP (1991) Nectar depletion and its implication for honeyeaters in heathland near Sydney. Aust J Ecol 16: 99–109

Bartholomew GA, Dawson WR, Lasiewski RC (1970) Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. Z Vgl Physiol 70: 196–209

Bartels W, Law BS, Geiser F (1998) Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera). J Comp Physiol B 168: 233–239

Bonaccorso FJ, McNab BK (1997) Plasticity of energetics in blossom-bats (Pteropodidae): impact on distribution. J Mammal 78: 1073–1088

Calder WA, Hiebert SM (1983) Nectar feeding, diuresis, and electrolyte replacement of hummingbirds. Physiol Zool 56: 325–334

Coburn DK, Geiser F (1996) Daily torpor and energy savings in a subtropical blossom-bat, *Syconycteris australis* (Megachiroptera). In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale, pp 39–45

Coburn DK, Geiser F (1998) Seasonal changes in energetics and torpor patterns in the subtropical blossom-bat *Syconycteris australis* (Megachiroptera). Oecologia 113: 467–473

Dawson TJ (1983) Monotremes and marsupials: the other mammals. Edward Arnold, London

Degen AA, Kam M (1995) Scaling of field metabolic rate to basal metabolic ratio in homeotherms. Ecoscience 2: 48–54

Fenton MB (1983) Just bats. University of Toronto Press, Toronto

Geiser F (1994) Hibernation and daily torpor in marsupials: a review. Aust J Zool 42: 1–42

Geiser F (1998a) Cool bats. Nat Aust 26: 56–63

Geiser F (1998b) Evolution of daily torpor and hibernation in birds and mammals: importance of body size. Clin Exp Pharmacol Physiol 25: 736–740

Geiser F, Coburn DK, Körtner G, Law BS (1996) Thermoregulation, energy metabolism, and torpor in blossom-bats, *Syconycteris australis* (Megachiroptera). J Zool (Lond) 239: 583–590

Hume ID (1982) Digestive physiology and nutrition of marsupials. Cambridge University Press, Cambridge

Koteja P (1991) On the relation between basal and field metabolic rate in birds and mammals. Funct Ecol 5: 56–64

Kulzer E, Storf R (1980) Schlaf-Lethargie bei dem afrikanischen Langzungenflughund *Megaloglossus woermanni* Pagenstecher, 1885. Z Säugetierkd 45: 23–29

Law BS (1992) The maintenance nitrogen requirements of the Queensland blossom-bat (*Syconycteris australis*) on a sugar/pollen diet: is nitrogen a limiting resource? Physiol Zool 65: 634–648

Law BS (1993) Roosting and foraging ecology of the Queensland blossom-bat (*Syconycteris australis*) in north-eastern New South Wales: flexibility in response to seasonal variation. Wildl Res 20: 419–431

Law BS (1994) *Banksia* nectar and pollen: dietary items affecting the abundance of the common blossom-bat, *Syconycteris australis* in south eastern Australia. Aust J Ecol 19: 425–434

Law BS (1995) The effect of energy supplementation on the local abundance of the common blossom-bat *Syconycteris australis* in south-east Australia. Oikos 72: 42–50

Lovegrove BG (1996) The low basal metablic rates of marsupials: the influence of torpor and zoogeography. In: Geiser F, Hulbert AJ, Nicol SC (eds) Adaptations to the cold: Tenth International Hibernation Symposium. University of New England Press, Armidale, 141–151

McNab BK (1983) Energetics, body size and the limits of endothermy. J Zool (Lond) 199: 1–29

Nagy KA (1980) CO_2 production in animals: analysis of potental errors in the doubly labeled water method. Am J Physiol 238: R466–R473

Nagy KA (1983) The doubly labelled water ($^3HH^{18}O$) method: a guide to its use. Publication no. 12-1417. University of California, Los Angeles

Nagy KA (1987) Field metabolic rate and food requirement scaling in mammals and birds. Ecol Monogr 57: 111–128

Nagy KA, Gruchacz MJ (1994) Seasonal water and energy metabolism of the desert-dwelling kangaroo rat (*Dipodomys merriami*). Physiol Zool 67: 1461–1478

Richards AJ (1997) Plant breeding systems. Chapman and Hall, London

Speakman JR (1997) Doubly labelled water, theory and practice. Chapman and Hall, London

Speakman JR, Racey PA (1991) No cost of echolocation for bats in flight. Nature 350: 421–423

Winter Y, Helversen O von (1998) The energy cost of flight: do small bats fly more cheaply than birds? J Comp Physiol B 168: 105–111

Wood RA, Nagy KA, MacDonald NS, Wakakuwa ST, Beckman RJ, Kaaz H (1975) Determination of oxygen-18 in water contained in biological samples by charged particle activation. Anal Chem 47: 646–650

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