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FIELD METABOLIC RATE OF A SMALL MARSUPIAL MAMMAL, THE HONEY POSSUM (*TARSIPES ROSTRATUS*)

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Doubly-labeled-water measurements of field metabolic rates and water influx rates in free-ranging honey possums (mean mass = 9.9 g) during late winter in Western Australia indicated that these nectarivores had lower daily energy expenditures than did insectivorous, dasyurid marsupials of similar body mass. Honey possums are capable of using torpor, and some individuals apparently did so during this study. Honey possums have an unusually high basal metabolic rate, and their field metabolic rate is ca. 2.7 times the basal rate, which is much lower than the 4.6–6.9 times the basal rate in small insectivorous marsupials. Nevertheless, the daily cost of living we measured for honey possums is 75% greater than for eutherian mammals of similar body mass. Small marsupials in general have much higher energy and food requirements in the field than do small eutherian mammals.

Key words: daily energy expenditure, diet effect, doubly labeled water, foraging mode, field metabolic rate, torpor, water influx rate

The honey possum (family Tarsipedidae) is one of the smallest of marsupials, weighing only 5–18 g. They are only slightly larger than the smallest marsupials, the 2–13 g ningauis (three species in the family Dasyuridae), and are of similar size to the planigales (5–15 g; Dasyuridae) and the pygmy possums *Cercartetus* and *Acrobates* (12–25 g; Burramidae—Nowak, 1991). Maintenance of a high, constant body temperature (endothermy) is energetically expensive in small mammals, due to their high surface-to-volume ratio, and consequent high rate of heat loss to the environment (Bartholomew, 1982). Thus, the field energetics of a small mammal are of considerable physiological, ecological, and evolutionary interest.

The honey possum is common on the coastal-sand plain in the southern part of Western Australia and eats only nectar and pollen, which are available throughout the year from a variety of plant species, es-

pecially *Banksia* growing in the area. *Tarsipes rostratus* has a high basal metabolic rate (2.9 ml O₂ g⁻¹ h⁻¹ or 440 kJ kg^{-0.75} d⁻¹—Withers et al., 1990) compared with that expected for a marsupial of its body mass (1.3 ml O₂ g⁻¹ h⁻¹ or 220 kJ kg^{-0.75} d⁻¹—Dawson and Hulbert, 1970), and it has a higher body temperature than most marsupials (37°C instead of 34°C). The relatively high basal metabolic rate may reflect the specialized nectar diet (McNab, 1980) as well as the higher body temperature (Blaxter, 1989). Honey possums may become torpid on cold days, going through a deep but short-term drop in body temperature (minimum body temperature = 5°C—Collins et al., 1988; Renfree and Wooller, 1983; Withers et al., 1990).

The present study was conducted to test several predictions about field metabolic rate (the energetic cost of living in the wild) of honey possums. Four questions were addressed. Do these nectarivores, which for-

age in an unhurried manner, have lower field metabolic rates than do active, predatory insectivores, such as dasyurid marsupials? Do honey possums have field metabolic rates that are high relative to similar-sized eutherian mammals, as do the dasyurids studied to date (Nagy, 1987)? Do honey possums exhibit unusually high field metabolic rates in accord with their high basal metabolic rates, implying a predictable relationship between field and basal metabolic rate between species (Koteja, 1991)? Do honey possums have highly variable field metabolic rates, especially on the low side, reflecting use of torpor under natural conditions, and how much energy is saved by using torpor?

MATERIALS AND METHODS

Field metabolic rates and water influx rates were measured with the doubly-labeled-water method (Nagy, 1983). This technique involves labeling an animal's body water with two isotopes, tritium (^3H) and heavy oxygen (^{18}O), and determining the washout rates of both isotopes from the animal while it is living undisturbed in its natural habitat. The tritium remains on water molecules and traces water flux through the animal. The ^{18}O equilibrates rapidly between water and CO_2 dissolved in body water (due to the action of carbonic anhydrase in red blood cells and elsewhere), so ^{18}O washes out faster than tritium, because it leaves the animal as C^{18}O_2 as well as H_2^{18}O . Thus, the difference between washout rates of tritium and ^{18}O represents CO_2 production alone and is a measure of metabolic rate.

The fieldwork was done 27–29 August 1986 at the Fitzgerald River Reserve (latitude $30^\circ 10' \text{S}$, longitude $119^\circ 31' \text{E}$) in Western Australia. Honey possums were captured and recaptured using pitfall traps set in a grid design. Traps were unbaited, and honey possums were caught when they descended to the ground and fell into the pits. The traps were cleared at first light, reducing to a minimum the time any animal could have spent without food in the trap. Some individuals were torpid when traps were cleared, but most were alert upon capture. Temperatures were low and characteristic of winter ($5\text{--}12^\circ\text{C}$), and rainfall was common during the

study period. Animals were weighed, their ears were punched for identification, and they were injected with $125\ \mu\text{l}$ of sterile water containing 95 atoms % oxygen-18 and 1.5 MBq of tritium. A small ($20\ \mu\text{l}$) blood sample was taken from a postorbital eye sinus; then, the animal was released at its point of capture. Laboratory methods regarding use of doubly labeled water were as described in detail elsewhere (Nagy et al., 1988). Briefly, pure water was distilled from the blood samples and used to measure tritium concentration by liquid scintillation counting and ^{18}O concentration by proton activation analysis (Wood et al., 1975). The intervals for measurement of doubly labelled water averaged 0.94 ± 0.06 days. Differences in physiological variables due to differences in body mass between individuals were accounted for before comparisons were made by converting measured values of field metabolic rate (in kJ d^{-1}) and water influx rate (in ml d^{-1}) to ratios of measured to predicted values for the individual's body mass (Table 1).

Field metabolic rates were converted from units of CO_2 production to heat equivalents (kJ) on the basis of presumed nutrients (carbohydrate, fat, and protein) being catabolized by honey possums. Their diet probably was mostly carbohydrate, with some protein from pollen; both have similar conversion factors, being 20.8 and 23.1 kilojoule/liter of CO_2 , respectively, and we used the intermediate value of 21 kilojoule/liter of CO_2 . Some study animals lost appreciable amounts of body mass during our measurements, and these may have metabolized some body fat, which has a higher conversion factor (27.7 kilojoule/liter of CO_2). However, we did not measure body-water contents at the end of the measurement periods; so, we do not know if these mass losses were due mainly to fat catabolism (animal not eating enough) or to water imbalance. In the unlikely event that the animals which lost mass used fat exclusively for their energy metabolism over the entire measurement interval, our estimates of their field metabolic rates could be $\leq 24\%$ too low. However, there is a way to evaluate whether the animal was eating enough to achieve energy balance. The feeding rate of a nondrinking animal should be correlated with its rate of water intake, if dietary water content is constant (Nagy, 1975). Making this assumption, the rate of body mass change should correlate positively with the relative water flux

TABLE 1.—Summary of field metabolic rate and water influx rate in honey possums in Western Australia in late August 1986.

Animal no ^a	Mean mass (g)	Δ mass, (% d ⁻¹)	Field metabolic rate			Water influx rate	
			kJ d ⁻¹	Relative to predicted ^b	Relative to BMR ^c	ml d ⁻¹	Relative to predicted ^d
M1(1)	5.25	-2.05	21.8	0.71	2.54	5.49	0.81
M1(2)	5.30	3.85	29.7	0.96	3.44	6.15	0.91
F1	10.50	-7.27	30.4	0.66	2.11	6.79	0.66
F2	17.75	-5.96	31.2	0.50	1.46	8.13	0.58
M2	6.45	-19.90	35.4	1.02	3.53	7.28	0.95
F3	14.90	-1.33	41.4	0.74	2.21	12.32	0.97
F4	12.70	5.69	51.6	1.01	3.10	39.10	3.40
F5(1)	10.80	-2.06	31.0	0.67	2.10	5.67	0.54
F5(2)	10.45	-4.67	14.2	0.34	0.98	1.40	0.14
F6	9.50	-13.35	38.6	0.89	2.89	2.38	0.25
M3(1)	10.40	-9.97	43.0	0.96	2.99	4.71	0.46
M3(2)	9.70	-3.96	25.5	0.59	1.91	3.31	0.34
M4	8.05	1.25	46.6	1.19	3.94	17.65	2.02
M5	9.90	2.27	51.8	1.17	3.75	8.81	0.89
M6	7.35	-1.52	41.2	1.11	3.73	6.97	0.84
$\bar{X} \pm 1 SD$	9.9 \pm 3.4	-3.9 \pm 6.7	34.4 \pm 11.1	0.83 \pm 0.26	2.71 \pm 0.90	9.1 \pm 9.2	0.92 \pm 0.82

^a m = male; F = female. Day in parentheses.

^b Field metabolic rate was predicted using $\text{kJ d}^{-1} = 11.8\text{BM}^{0.576}$, where BM is body mass in grams (Nagy, 1987).

^c Basal metabolic rate was predicted using $\text{kJ d}^{-1} = 440\text{BM}^{0.75}$, with BM in kilograms (Withers et al., 1990).

^d Water influx rate was predicted using $\text{ml d}^{-1} = 2.49\text{BM}^{0.602}$, with BM in grams (Nagy and Peterson, 1988).

rate. The actual correlation, using the values in Table 1, is described by the equation: $Y = 0.0616X + 1.15$ ($n = 15$, $r^2 = 0.259$, $P = 0.05$), where X = rate of body mass change in % d⁻¹ and Y = ratio of measured to predicted water influx rate. This correlation indicates that, over some measurement intervals, honey possums were eating, but not enough to maintain energy balance and were using stored body fat to supply part of their energy requirements. Thus, for those four animals having a water influx ratio (measured to predicted) <0.5 (Table 1), we used an intermediate conversion factor of 25 kilojoule/liter of CO₂.

RESULTS

Field metabolic rates of honey possums (mean body mass 9.9 g) averaged 34 kJ d⁻¹, which is 2.7 times their estimated basal metabolic rate. Individual field-metabolic-rate values were highly variable, ranging from 1.0 to 3.9 times basal metabolism (Table 1). One animal had a field metabolic rate that was the same as its predicted basal rate. We presume this animal, and at least a few others, used torpor during part of the

field measurement period. Honey possums in captivity have torpor bouts ranging in length from 6.7 to 14.4 h, with an average of 10.5 h (Withers et al., 1990), which would include 28–60% of our ca. 24-h periods of measurement. Water influx rates averaged 9.1 ml d⁻¹, which is 106% of that predicted for a marsupial in the field (Table 1). Water influx rates also were quite variable, ranging from 14 to 340% of predicted.

DISCUSSION

Honey possums had field metabolic rates that averaged 83% of those expected (Nagy, 1987: equation 26) for a marsupial of their body mass (Table 1). Two small dasyurid marsupials, which are insectivores, had somewhat higher field metabolic rates: dunarts (*Sminthopsis crassicaudata*, 11.4 g) at 102% of predicted values; brown antechinus (*Antechinus stuartii*, 22.7 g) at 91% of predicted values (Nagy, 1987). However, the mean field metabolic rate of *A. stuartii* does not differ significantly from that of honey possums, judging by its inclusion

within the 95% confidence intervals for the mean of the honey possum (60–98% of predicted field metabolic rate). The larger Swainson's antechinus (*Antechinus swainsonii*, 47.5 g, mean of values reported in Nagy, 1987: table 1) had a much higher field metabolic rate, averaging 123% of that predicted from body mass. We conclude that honey possums live a life that requires a moderate to low expenditure of energy compared with small insectivorous marsupials, in accord with expectations based on differences in diet and foraging mode.

The daily cost of living for honey possums is high, however, compared with that expected for a eutherian mammal of the same body mass. Field metabolic rates of honey possums averaged 174% of those predicted for eutherians having the same body mass (Nagy, 1987: equation 18). At body masses <71 g, marsupials in general have significantly higher field metabolic rates than do eutherian mammals (Nagy, 1987); yet, marsupials have significantly lower basal metabolic rates than eutherians (at all body masses—Hayssen and Lacy, 1985), for reasons that are not understood at present.

There are reasons to suggest that field metabolic rate and the basal metabolic rate of an animal may be related to each other and, hence, also may covary between species (Koteja, 1991). This raises the possibility that field metabolic rate may be a constant multiple of basal metabolism among terrestrial vertebrates (Peterson et al., 1990). Accordingly, the unusually high basal metabolic rate of honey possums in comparison with other marsupials (Withers et al., 1990) should be accompanied by a similarly high field metabolic rate in honey possums. Our results do not support this hypothesis and indicate that basal metabolism does not serve as a reliable predictor of field metabolism. The ratio of field metabolic rate to basal metabolic rate of 2.7 in honey possums (Table 1), in fact, is lower than those of other small marsupials (6.9 in dunnarts and 4.6 in brown antechinuses—

Peterson et al., 1990). The field metabolic rates measured in the present study may not reflect the maximum values of honey possums for two reasons. First, the season in which we made measurements (winter) may not be the season of greatest energy expenditure by these animals. Some species of endothermic animals have field metabolic rates that vary considerably during the course of a year, often being high during the breeding season, but other species have relatively constant field metabolic rates through time (Nagy, 1987). Second, all the field metabolism measurements in this study could have included some periods of torpor. There was much variation in field metabolic rates between individuals and measurement periods, with the coefficient of variation in this study ($100 \text{ SD}/\text{mean} = 31\%$) being about twice those typically found in other studies on mammals. Moreover, the variation was due mostly to unusually low field metabolic rates, which is consistent with the use of torpor during at least some measurement intervals. Unfortunately, we could not determine the body-temperature patterns of our animals. They were too small to carry temperature-sensitive radiotransmitters, and the process of finding a marked animal and measuring body temperature with a rectal probe frequently during the field-measurement period would disturb the animals so much that measurements of their field metabolic rate would be of questionable relevance to the natural situation.

Torpor can be beneficial in that it can save much energy. For example, the lowest three values for field metabolism that we measured were only 38% of the highest three values, suggesting that use of torpor could reduce daily energy expenditure by nearly two-thirds. However, this is not without other kinds of cost. The penalties of using torpor include possible decreased food intake and increased vulnerability to predators. It will be interesting to examine the seasonal use of torpor by free-living honey possums in relation to variation in food sup-

ply, ambient temperature, reproductive activities, and predation pressure.

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