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Metabolic physiology of the north-western marsupial mole, *Notoryctes caurinus* (Marsupialia : Notoryctidae)

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Abstract

We studied the thermal and metabolic physiology of a single specimen of the north-western marsupial mole, *Notoryctes caurinus*, an almost completely fossorial Australian marsupial, and compared it with the morphologically convergent Namib desert golden mole, *Eremitalpa granti namibensis*. This was the first study of any aspect of the physiology of this rare marsupial.

Mean body mass of the marsupial mole was 34 g. Body temperature (T_b) was low and labile, ranging from 22.7 to 30.8°C over a range of ambient temperature (T_a) from 15 to 30°C. The highest T_b of 30.8°C was significantly lower than expected for a marsupial of this body mass. Metabolic rate varied with T_a in an attenuated fashion for an endotherm, because of the labile T_b . Basal metabolic rate (BMR) was 0.63 mL O₂ g⁻¹ h⁻¹, at a T_a of 30°C. This was lower than expected for a 34-g marsupial, but was not different from expected for a marsupial when corrected to a T_b of 35°C (0.94 mL O₂ g⁻¹ h⁻¹). Evaporative water loss increased from 0.8 mg g⁻¹ h⁻¹ at 15°C to 3.7 at 30°C. Wet thermal conductance was 0.2 mL O₂ g⁻¹ h⁻¹ °C⁻¹ at 15°C and 0.6 at 25°C; these values were higher than expected for a marsupial. The net metabolic cost of transport (NCOT) for running (0.0022 mL O₂ g⁻¹ m⁻¹ at a mean velocity of 484 m h⁻¹) was similar to expected values for walking and running mammals. The NCOT for sand-swimming (0.124 mL O₂ g⁻¹ m⁻¹ at a mean velocity of 7.6 m h⁻¹) was substantially higher, and at a much lower velocity than for running, but was similar to NCOT for sand-swimming by the Namib golden mole. We conclude that the marsupial mole differs in some aspects of thermal and metabolic physiology from other marsupials, most likely reflecting its almost completely fossorial existence.

Introduction

Marsupial moles (*Notoryctes*) are the most unusual of all Australian marsupials, living almost entirely underground in the sand-ridged areas of central and western Australia (Johnson and Walton 1989). They are the most highly specialised of all marsupials for living underground, being accomplished burrowers that virtually 'swim' through sandy soil. The north-western marsupial mole, *N. caurinus*, is very similar to the more widespread *N. typhlops*, but is generally smaller and can be distinguished by minor external morphological and dental differences (Thomas 1920). These two species of marsupial mole are the only living representatives of the marsupial family Notoryctidae, but there is a single fossil representative from the Riversleigh Formation (Archer *et al.* 1991).

Marsupial moles resemble in general body characteristics many other fossorial mammals, e.g. talpid moles, golden moles, gophers and mole-rats (Stirling 1888a, 1888b, 1891; Johnson and Walton 1989; Johnson 1995). They are small (about 100–140 mm long, 20–60 g), with a compact body and short limbs; their dense fur is a rich cream or golden colour; the rostrum is a pad of thickened skin; the forelimbs have well developed claws for digging; and the tail is short and cylindrical. There are no external eyes or ear pinnae, but an external ear opening is apparent. Marsupial moles have a striking resemblance to placental golden moles (family Chrysochloridae), particularly *Eremitalpa granti namibensis*, which occurs in the sand dunes of the Namib Desert (Meester 1964).

The striking morphological and ecological convergence of marsupial moles with other fossorial mammals (especially the Namib golden mole) suggests a convergent physiology specialised for fossoriality. On the basis of the adaptive physiology of the Namib golden mole (Seymour *et al.* 1998) and other fossorial mammals (e.g. McNab 1966, 1979; Gettinger 1975; Vleck 1979; Withers and Jarvis 1980; Lovegrove 1986; Buffenstein and Yahav 1991; Lovegrove and Heldmaier 1994), we expected marsupial moles to have a low and labile body temperature, a low metabolic rate because of both a low body temperature and intrinsic metabolic depression, a high thermal conductance, and a high rate of evaporative water loss. We also expected marsupial moles to have a similar metabolic cost of sand-swimming as the Namib golden mole (Seymour *et al.* 1998), which is a much lower cost than the metabolic cost of construction of tunnels in hard soils (Vleck 1979; Du Toit *et al.* 1985; Lovegrove 1989).

Marsupial moles are extremely rare and it is almost impossible to capture specimens alive. After considerable effort (Thompson *et al.* 2000) we eventually obtained a live north-western marsupial mole. We examined its basic thermal and metabolic physiology, and determine its metabolic cost of transport by sand-swimming and running. We report here our results for this single specimen, recognising that we may never have the opportunity for further studies.

Methods

The north-western marsupial mole (*Notoryctes caurinus*) was obtained from Punmu, in the Great Sandy Desert of Western Australia (22°03'S, 122°10'E). The mole was taken to Perth the day after it was located, and was maintained in an aquarium containing about 15 cm of loose soil, taken from the collection site. Surprisingly, the mole was unable to burrow into air-dry sand, so the sand was kept slightly moistened to allow it to burrow. A heating pad under one end of the aquarium provided a thermal gradient from about 22 to 32°C. The mole initially weighed 38.5 g, but lost mass until a suitable diet of large insect larvae (particularly large larvae collected from dead grass trees, *Xanthorrhoea* spp) was provided; body mass then stabilised at about 34 g. Unfortunately, the mole inexplicably stopped eating and died about 5 weeks after capture. The physiology of the mole was investigated during the first three weeks of captivity, when its body mass was about 34 g but its health apparently good.

Respirometry

We used open-circuit respirometry to measure the rates of oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}), and evaporative water loss (EWL) at controlled temperatures of 15–30°C. The mole was removed from its aquarium, weighed to ± 0.01 g, and placed in a small glass jar (1000 mL volume) about half-filled with either moist or dry sand. Dry sand allowed us to measure evaporative water loss, but the mole was unable to burrow and usually went to sleep on the surface. Moist sand allowed the mole to burrow under the surface, its natural habit, but precluded measurement of EWL. Dry ambient air was passed through the sand at a constant flow-rate of 200–260 mL min⁻¹ (controlled by a Brooks model 5871-A mass flow controller). Excurrent air was passed over a Vaisala HMI 33 relative humidity/temperature probe (model HMP 31UT) then through a column of Drierite® to remove water, then through a Hereus-Leybold infrared CO₂ analyser (model Binos C) and one channel of a Servomex dual-channel paramagnetic O₂ analyser (model OA184). The mole was left in the respirometry chamber until stable metabolic and EWL traces were obtained. Body temperature was measured using a Schultheis fast-recording thermometer, immediately after the mole was removed from the respirometry chamber. Ambient temperature was monitored for excurrent chamber air by the Vaisala HMP 31UT probe.

The analog voltage outputs of the instruments were monitored using Autoplex Unimeter digital panel meters (model XQ), programmed for the appropriate voltage range and time-averaged to minimise noise, then the RS485 outputs of the panel meters were monitored using a PC with an Autoplex AS4000 RS485/RS232 serial adapter via a COM port. The voltage inputs were recorded using a custom Visual Basic® program, which displayed data to screen and stored the raw voltage data to disk. These voltage data were analysed using a custom Excel® spreadsheet, which corrected for any baseline drift during the course of the experiment (an ambient air baseline was recorded before the mole was placed in the respirometry chamber, and after it was removed), corrected for the washout characteristics of the chamber (Bartholomew *et al.* 1981; Seymour *et al.* 1998) and calculated the STPD \dot{V}_{O_2} , \dot{V}_{CO_2} (mL g⁻¹ h⁻¹) and EWL (mg g⁻¹ h⁻¹) using equations modified from Withers (1977). Wet thermal conductance (C_{wet} : J g⁻¹ h⁻¹ °C⁻¹) was calculated as $\dot{V}_{O_2}/(T_b - T_a)$, with T_b determined at the end of the experiment and assuming 1 mL O₂ \equiv 20.1 J.

Body temperature was occasionally measured for the mole after it was left undisturbed in its aquarium. The mole was quickly located, removed from the aquarium, and its body temperature and nearby soil temperature determined using a Schultheis thermometer.

Metabolic cost of running and sand-swimming

We used a circular, rotating respirometry system (see Seymour *et al.* 1998) to measure the metabolic cost of running and sand-swimming in loose dry sand (it was not possible to measure the metabolic cost of burrowing in moist sand). For running, the outer surface of the rotating respirometer was covered with a rough paper surface to provide traction, and the mole was allowed to run along the bottom of the respirometer as it was rotated by hand. Speed of running was determined by the mole, and was measured from the rate of rotation of the respirometer and its circumference. Ambient air was drawn through the respirometer at 260 mL min⁻¹ (controlled by a Brooks model 5871-A mass flow controller) then analysed as above. For sand-swimming, the respirometer was partly filled with about 2500 mL of clean, dry sand, and the chamber was rotated by hand to keep the mole sand-swimming near the surface. The mole could burrow into the inclined edge of the dry sand, and could readily burrow once submerged in dry sand. Speed of sand-swimming was determined by the mole, and was measured from the rate of rotation of the respirometer and the approximate circumference where the mole was sand-swimming in the respirometer.

Statistics

Values are mean \pm standard errors, with sample size (n). Analysis of variance, with Student–Newman–Keuls multiple-comparison test, and regression analysis were calculated after Zar (1984). For comparison of data for the marsupial mole with other marsupials, a linear regression was calculated for all non-fossorial marsupial data and then the 95% confidence limits for the regression, and 95% confidence limits for prediction of a further datum, were calculated after Zar (1984).

Results

Body temperature

The T_b of the marsupial mole, when undisturbed in its aquarium of sand, ranged widely from 21°C to 33.2°C; the mean was $29.6 \pm 1.0^\circ\text{C}$ and the median was 30.8°C ($n = 13$).

In respirometry experiments between T_a s of 15 and 30°C, T_b was quite labile, varying from 22.7 to 30.8°C (Fig. 1). At the highest T_a of 30°C, T_b was similar for the mole on the dry sand surface sand (30.6°C) and under moist sand (30.8°C). At lower T_a s, T_b was slightly lower for the mole under moist sand than on dry sand.

Metabolic rate

When in moist sand at 25 or 30°C, the mole quickly burrowed under the surface and its metabolic rate (both \dot{V}_{O_2} and \dot{V}_{CO_2}) remained relatively constant throughout the experiment (typically 2 h duration; e.g. Fig. 2). However, at 15–20°C, the metabolic trace oscillated between about 2 and 2.5 mL O₂ g⁻¹ h⁻¹. Similarly, when on the surface of dry sand, metabolic rate (both \dot{V}_{O_2} and \dot{V}_{CO_2}) was quite constant at 30°C but was erratic at lower T_a s. Metabolic rate was usually not minimal at the end of each experiment for the mole on dry sand, so the resting value was determined for the lowest period during the experiment.

The \dot{V}_{O_2} of the mole was lowest at a T_a of 30°C, being similar in moist and on dry sand (Fig. 1). The \dot{V}_{O_2} of 0.63 mL O₂ g⁻¹ h⁻¹ at 30°C in moist sand is the best estimate of basal metabolic rate (BMR). However, because measurements were not made at higher T_a s, actual BMR could be lower.

The \dot{V}_{CO_2} data are similar to the \dot{V}_{O_2} data, and so are not shown separately. The respiratory exchange ratio ($RER = \dot{V}_{CO_2}/\dot{V}_{O_2}$) for the mole in moist soil was 0.93 ± 0.006 ($n = 4$) compared with 0.78 ± 0.044 ($n = 4$; minimum \dot{V}_{O_2}) and 0.76 ± 0.063 ($n = 4$; end of experiment) on dry sand. These values were significantly different by ANOVA ($F_{2,9} = 4.395$; $P = 0.047$) but not by a Student–Newman–Keuls multiple-comparison test ($P = 0.054$).

Evaporative water loss

The resting rate of EWL determined for the mole on dry sand increased with T_a , from 0.78 at 15°C, to 1.1 at 20°C, 1.8 at 25°C, and 3.7 mg g⁻¹ h⁻¹ at 30°C (Fig. 1). The excurrent air varied

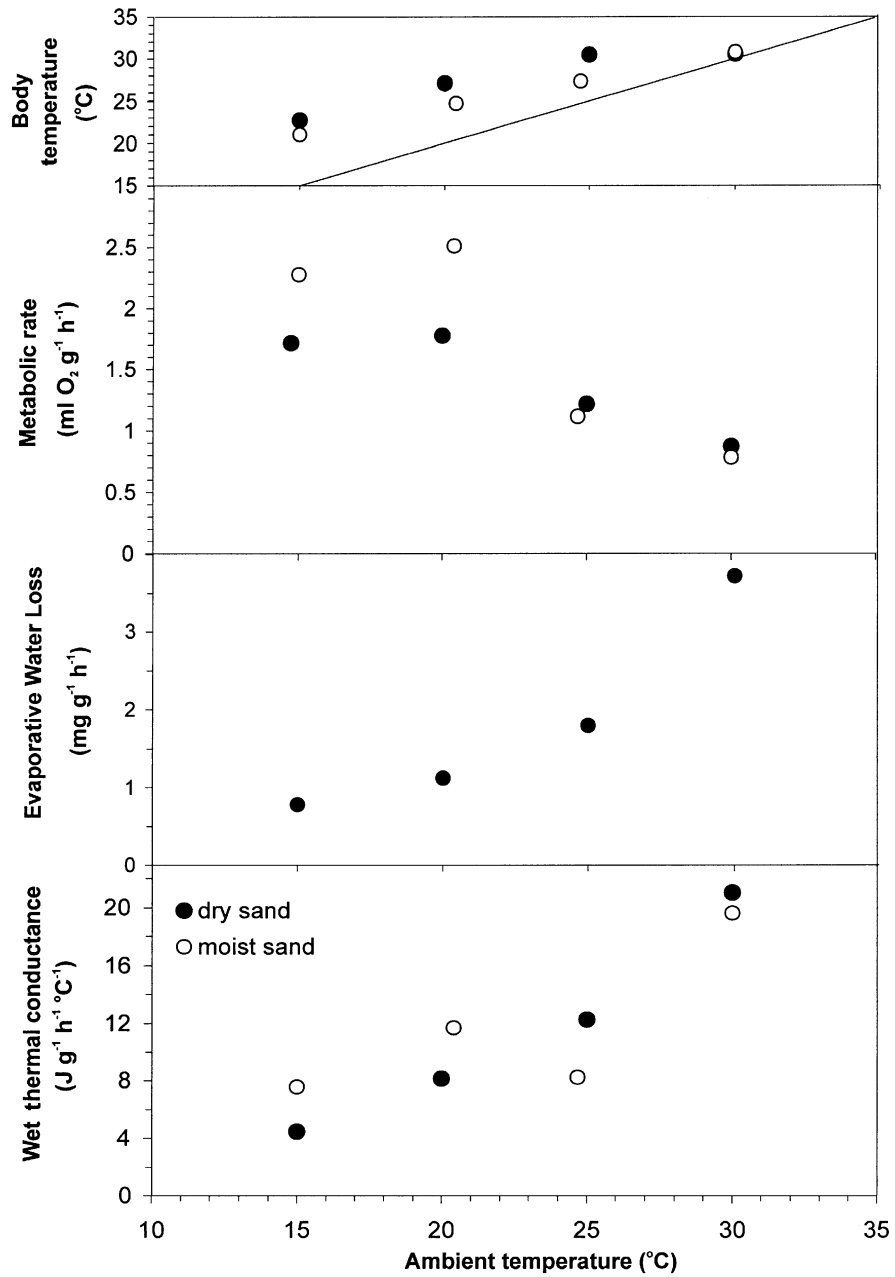


Fig. 1. Effect of ambient temperature on body temperature, oxygen consumption rate, rate of evaporative water loss, and wet thermal conductance, for a north-western marsupial mole, *Notoryctes caurinus*, on dry sand and burrowed under moist sand. The isothermal line for T_b is shown.

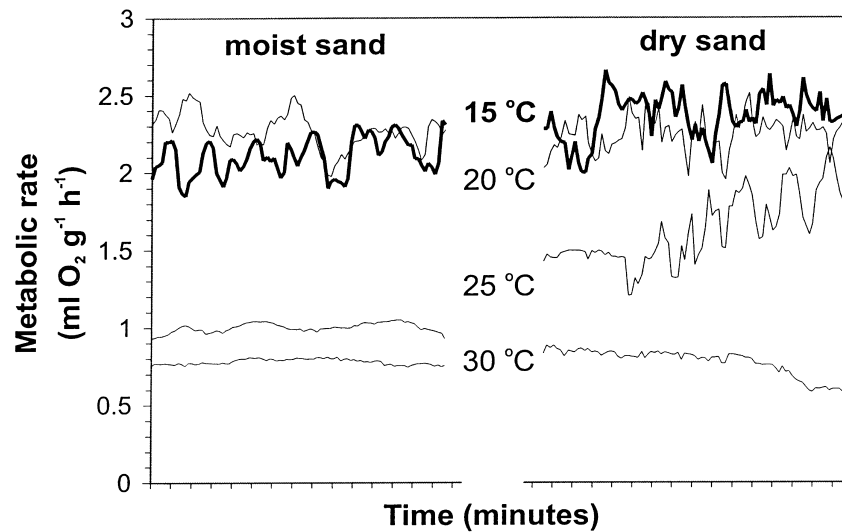


Fig. 2. Sections of respirometry traces for oxygen consumption rate of a north-western marsupial mole, *Notoryctes caurinus*, burrowed under moist sand and on the surface of dry sand, at ambient temperatures of 15, 20, 25 and 30°C.

in relative humidity from 5 to 7 torr at 15–25°C to 12 torr at 30°C. The ratio of EWL to metabolic rate increased from 0.45 mg (mL O₂)⁻¹ at 15°C, to 0.63 at 20°C, 1.48 at 25°C, and 4.25 at 30°C. The EWL/ \dot{V}_{O_2} is calculated to be 1 mg (mL O₂)⁻¹ at a T_a of 21.5°C, from an exponential fit to these data.

Thermal conductance

Wet thermal conductance (C_{wet}) was lowest at T_a = 15°, similar at 20 and 25°, and highest at 30°C (Fig. 1), but we consider the 30°C datum to be unreliable because of the small T_b-T_a difference. Dry thermal conductance (C_{dry}: J g⁻¹ h⁻¹ °C⁻¹; assuming a latent heat of evaporation of 2400 J g⁻¹) was slightly less than C_{wet} for the mole on dry sand, being 7.3 J g⁻¹ h⁻¹ °C⁻¹ for T_as of 15, 20 and 25°C.

Metabolic cost of running and sand-swimming

Sand-swimming was maintained fairly continuously for over 40 min, but at a variable speed of 2–18 m h⁻¹ (average 7.6 ± 2.4 m h⁻¹; n = 8 one-half revolutions of the respirometer). The metabolic rate stabilised at 2.06 mL O₂ g⁻¹ h⁻¹. These values correspond to a total gross metabolic cost of transport (GCOT) by sand-swimming of 0.271 mL O₂ g⁻¹ m⁻¹ (2.06 mL O₂ g⁻¹ h⁻¹ ÷ 7.6 m h⁻¹). The net cost of transport (NCOT) by sand-swimming can be calculated from these data and the resting metabolic rate at 25°C of 1.12 mL O₂ g⁻¹ h⁻¹, to be 0.124 mL O₂ g⁻¹ m⁻¹ [(2.06–1.12) mL O₂ g⁻¹ h⁻¹ ÷ 7.6 m h⁻¹].

The mole ran in the respiratory chamber with a slow and seemingly laborious ‘shuffling’ action. Nevertheless, running was maintained for over 60 min at a remarkably constant speed of 484 ± 7 m h⁻¹ (n = 104 revolutions of the respirometer), with a range of 319–688 m h⁻¹, and metabolic rate stabilised at 2.18 mL O₂ g⁻¹ h⁻¹. These data correspond to a GCOT by running of 0.0045 mL O₂ g⁻¹ m⁻¹ (=2.18 mL O₂ g⁻¹ h⁻¹ ÷ 484 m h⁻¹) and a NCOT by running of 0.0022 mL O₂ g⁻¹ m⁻¹ [(2.18–1.12) mL O₂ g⁻¹ h⁻¹ ÷ 484 m h⁻¹].

Discussion

Marsupial moles are the most specialised extant marsupials with respect to morphology and ecology. They are extremely convergent with golden moles (Chrysochloridae) and early descriptions of marsupial moles even suggested that they were chrysochlorids (see Johnson and Walton 1989; Johnson 1995; Thompson *et al.* 2000). Whether the marsupial mole was convergent physiologically with the Namib Desert golden mole (see Fielden *et al.* 1990a, 1990b; Seymour *et al.* 1998) was the impetus for our search for a live marsupial mole and this study. We expected marsupial moles to be physiologically specialised for fossoriality with respect to T_b and thermoregulation, BMR, EWL and thermal conductance, but not unusual in the cost of transport by sand-swimming or running.

To put our data for *Notoryctes caurinus* in perspective with other marsupials, we use predictive linear regression analysis (Zar 1984) of data for all non-fossorial marsupials with the marsupial mole datum analysed as a further single point. We summarised T_b , T_a , and \dot{V}_{O_2} data for marsupials (see Appendix), and analysed by linear regression these data, excluding the data for *N. caurinus* and the semi-fossorial bilby and wombat. Where there were two or more values for a single species, we averaged the data (T_b) or $\log_{10}(\text{data})$ (mass, \dot{V}_{O_2} , C). A formal phylogenetic analysis of our results, although desirable, is not necessary or possible at present. The phylogenetic status of marsupial moles is uncertain (Springer *et al.* 1994; Retief *et al.* 1995) and they may be as distinct from all other Australian marsupials as the South American microbiotheriids and American didelphids (Colgan 1999). We presume that the unusual aspects of the physiology of the marsupial mole are specialised and adaptive, but this remains to be demonstrated by a formal phylogenetic analysis when this becomes possible.

Body temperature and thermoregulation

The marsupial mole is thermolabile with a low and variable T_b . The highest T_b that we recorded during metabolic experiments was 30.8°C for the mole in moist sand at 30°C T_a . The highest T_b recorded for the mole when active on the sand surface in the aquarium was 33.3°C, and the median T_b was 30.8°C.

Body temperature measured for a variety of non-fossorial marsupials when thermoneutral (Fig. 3; see Appendix) ranges from about 32 to 39°C, with an average of 35.3 ± 0.13 ($n = 59$).

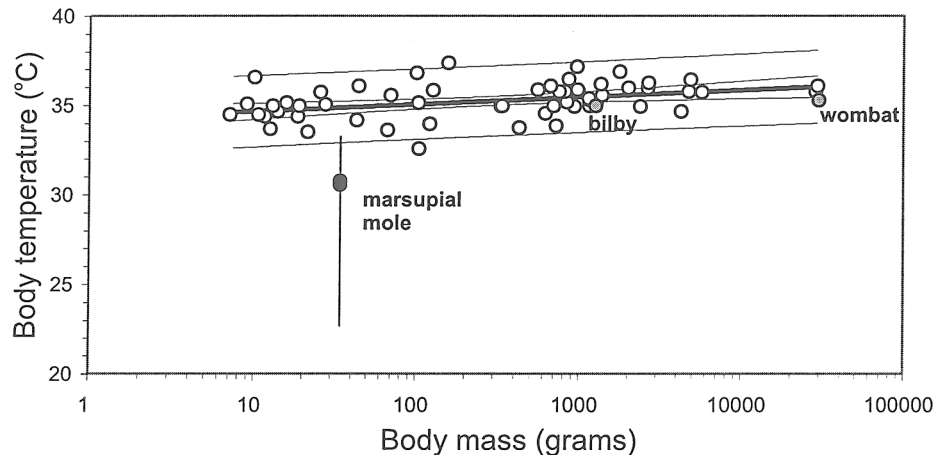


Fig. 3. Relationship between body mass and body temperature for the north-western marsupial mole, *Notoryctes caurinus* (black circles), the semi-fossorial bilby and hairy-nosed wombat (grey filled circles) and non-fossorial marsupials (open circles). Vertical line for the marsupial mole indicates the range of measured T_b s. The regression line for non-fossorial marsupials is shown with the 95% confidence bands for the regression (inner band) and 95% confidence bands for prediction of a further datum (outer band). See Appendix for data.

There is a slight but highly significant effect of body mass on T_b : $T_b = 34.3 (\pm 0.35) + 0.40 (\pm 0.13) \log_{10}(\text{mass})$ ($r^2 = 0.140$, slope significantly different from 0 at $P = 0.004$). The T_b values measured in experiments for the marsupial mole at a T_a of about 30°C and the median T_b of 30.8 were lower than the T_b of other marsupials in their thermoneutral zone and fell below the 95% confidence band for a further predicted datum (Fig. 3). However, we cannot determine the thermoneutral zone for the marsupial mole from our data (see below), but it is possible that T_b would increase at higher T_a . The highest T_b of the mole measured during spontaneous activity (33.3°C) falls within the lower 95% predicted band for other small marsupials. The hairy-nosed wombat, a semi-fossorial but considerably larger marsupial, is also quite thermolabile, with T_b varying from about 30° to over 38°C (Wells 1978) but it and the bilby generally have a typical marsupial T_b in the thermoneutral zone (Fig. 3).

The marsupial mole, like some fossorial mammals (Namib golden mole and naked mole-rat) is thermolabile with a low and variable T_b , but not all fossorial mammals are similarly thermolabile with a low T_b (McNab 1966, 1979). The thermolability of the marsupial mole, golden mole and naked mole-rat may be an adaptation for energy conservation by these mammals in their arid environment rather than being a thermal adaptation to fossoriality *per se*.

Metabolic rate

The metabolic rate of the marsupial mole increased at lower T_a , except when T_b became considerably reduced at the lowest T_a s. If the metabolic rate of the marsupial mole is basal when measured at a T_a of 30°C, then its BMR is 0.63 mL O₂ g⁻¹ h⁻¹; if not, then BMR is lower than 0.63 mL O₂ g⁻¹ h⁻¹. A BMR of 0.63 mL O₂ g⁻¹ h⁻¹ is lower than expected for a non-fossorial marsupial of equivalent body mass (see below). The semi-fossorial hairy-nosed wombat also has a lower-than-predicted BMR, of only 56% of predicted (Wells 1978) and the semi-fossorial bilby has a BMR 86–95% of predicted (Hulbert and Dawson 1974; Kinnear and Shield 1975). Fossorial mammals from arid environments generally have a lower-than-predicted metabolic rate (McNab 1966, 1979). This is presumably a specialised trait for energy conservation in low-productivity environments such as underground or deserts, and avoiding overheating in a warm and humid fossorial environment.

However, there is a confounding effect of T_b on \dot{V}_{O_2} (Q_{10} effect; see Dawson and Hulbert 1970; Geiser 1988) so we have corrected the \dot{V}_{O_2} data for marsupials from their measured T_b to a standardised value of 35°C, using a Q_{10} of 2.5 (Guppy and Withers 1999). We are unable to determine a Q_{10} for the marsupial mole from our data because there was always a thermoregulatory increment in \dot{V}_{O_2} . The allometric summary of T_b -corrected basal metabolic data for non-fossorial marsupials is

$$\log_{10} \dot{V}_{O_2} = 0.427 (\pm 0.028) + 0.725 (\pm 0.011) \log_{10}(\text{mass}) \quad (n = 59; r^2 = 0.988).$$

The un-transformed relationship is $2.67g^{0.725}$. This relationship is very similar to that first determined for marsupials of $2.60g^{0.74}$ by Dawson and Hulbert (1969).

The T_b -corrected BMR of the marsupial mole (31.8 mL O₂ h⁻¹ by T_b adjustment from 30.6 to 35°C) conforms very closely with data for other marsupials (Fig. 4). This indicates that the low BMR of the marsupial mole is fully accounted for by its low T_b without there being any intrinsic metabolic depression, as is also the case for the bilby. In contrast, T_b -adjusted BMR of the hairy-nosed wombat is lower than predicted, as is BMR of the Namib golden mole (Seymour *et al.* 1998; Fig. 4), which, as a placental mammal, should have a BMR about 40% higher than a marsupial (Dawson and Hulbert 1969). That the marsupial mole lacks any intrinsic metabolic depression suggests that it is not so physiologically specialised as some other fossorial or arid-adapted mammals, such as the hairy-nosed wombat and the Namib golden mole.

Evaporative water loss

The EWL values of less than 1.0 to over 3.5 mg g⁻¹ h⁻¹ measured for the marsupial mole, asleep on the surface of dry sand, encompass the predicted EWL for a 34-g dasyurid marsupial

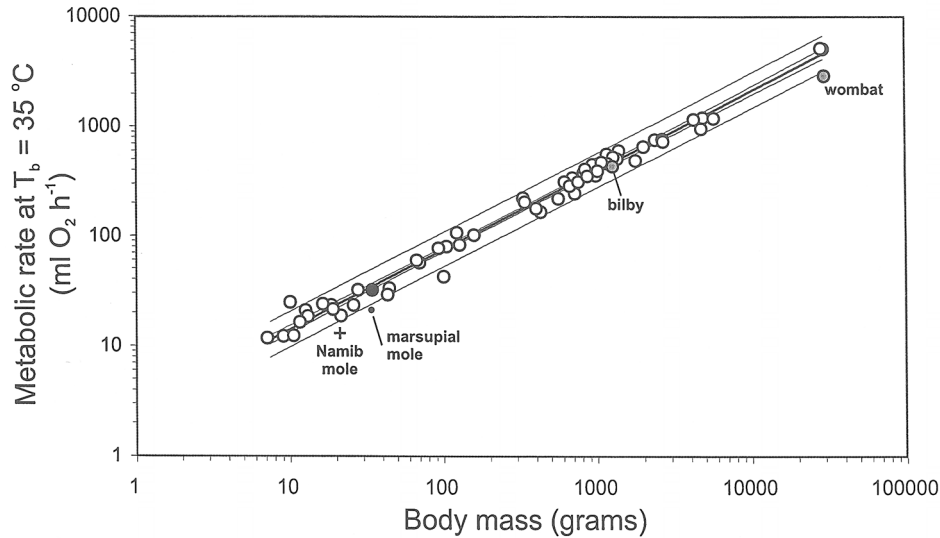


Fig. 4. Relationship between body mass and metabolic rate for the north-western marsupial mole, *Notoryctes caurinus* (black circles), the semi-fossorial bilby and hairy-nosed wombat (grey filled circles), and non-fossorial marsupials (open circles), corrected to a body temperature of 35°C. The uncorrected metabolic rate of the marsupial mole (smaller solid circle) is also shown for comparison. The regression line for non-fossorial marsupials is given, with the 95% confidence bands for the regression (inner band) and 95% confidence bands for prediction of a further datum (outer band). Value for the Namib golden mole, *Eremitalpa granti namibensis* (+), is also shown. See Appendix for uncorrected marsupial data.

of $3.1 \text{ g}^{-1} \text{ h}^{-1}$ at T_a of 10–30°C (Hinds and MacMillen 1986). The ratio of $\text{EWL}/\dot{V}_{\text{O}_2}$, which increased from 0.45 at 15°C to 4.25 $\text{mg g}^{-1} \text{ h}^{-1}$ at 30°C, is calculated to be 1.0 at a T_a of 21.5°C. The predicted T_a at which $\text{EWL} = \dot{V}_{\text{O}_2}$ is very similar, at about 21.3°C (Hinds and MacMillen 1986). Thus, the interrelationships between metabolism, T_a and EWL are similar to expected for a dasyurid marsupial, despite differences in T_b and metabolic rate from expected values.

Thermal conductance

The wet thermal conductance of the marsupial mole varied from 5.2 to 11.7 $\text{J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$, at T_a s from 15 to 25°C. The lower C_{wet} for the marsupial mole at low T_a may reflect the low T_b , decreased peripheral circulation, and possibly piloerection. These conductance values for the marsupial mole are considerably higher (125–282%) than would be expected for a marsupial of the same body mass ($14 \text{ J g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}$; Fig. 5): $\log_{10} C_{\text{wet}} (\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1} \text{ }^\circ\text{C}^{-1}) = -0.044 (\pm 0.058) - 0.399 (\pm 0.022) \log_{10}(\text{mass})$ ($n = 58$; $r^2 = 0.852$) or $C_{\text{wet}} = 0.90 \text{ g}^{-0.399}$. The C_{wet} of the marsupial mole would also seem to be higher than expected for a placental mammal of equivalent mass. A high C_{wet} is common for large fossorial mammals and small fossorial mammals from arid environments, and would promote heat dissipation underground (McNab 1979). However, the wet thermal conductance of the semi-fossorial bilby (Hulbert and Dawson 1974) and hairy-nosed wombat (Wells 1978) are not substantially higher than expected (Fig. 5).

Energy cost of burrowing and running

The marsupial mole is morphologically specialised for burrowing, with a compact body form, spade-like feet, and short, muscular limbs, like the Namib golden mole. The metabolic rate of the marsupial mole when sand-swimming was remarkably similar to that for the Namib golden mole at an equivalent velocity, although the Namib golden mole sand-swims at a considerably

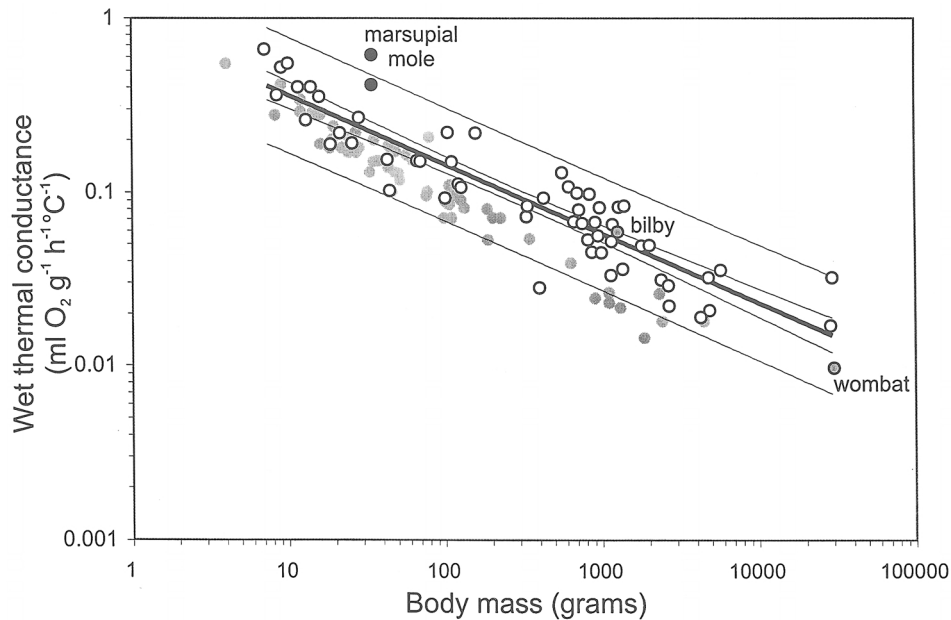


Fig. 5. Relationship between body mass and wet thermal conductance at $T_a = 25^\circ\text{C}$ for the north-western marsupial mole, *Notoryctes caurinus* (black circles), and for the semi-fossorial bilby and hairy-nosed wombat (grey filled circles) and non-fossorial marsupials (open circles) within their thermoneutral zone. Regression line for non-fossorial marsupials is shown, with 95% confidence bands for the regression and 95% confidence bands for prediction of a further datum. Values for placental mammals (light grey symbols) are also shown. See Appendix for marsupial data; placental data are from Aschoff (1981).

higher velocity (Fig. 6). The metabolic rate of the marsupial mole was similar when running as when sand-swimming, but running velocity was considerably higher. Again, the metabolic rate of the running marsupial mole was consistent with that of the Namib golden mole at equivalent velocity.

The energy costs of running might be expected to be higher than for other mammals that are not specialised for digging, but the NCOT for running by the marsupial mole is only 43% higher (and for the Namib golden mole is only 23% higher) than allometric predictions (Fig. 7). These values are well within the variability of the data, and are not statistically different from predicted, so it is perhaps surprising that the energy costs of running by these specialised sand-swimmers are as low as they are.

The net energy cost of sand-swimming for the marsupial mole (81 J m^{-1}) is similar to that for the Namib mole (73 J m^{-1} ; Seymour *et al.* 1998). Unfortunately, it was not possible to measure metabolic cost for the marsupial mole burrowing through moist, compact sand. Such measurements would have been more ecologically informative, because the marsupial mole appears not to 'sand-swim' in loose sand dunes but to burrow in fairly compact soil where sand-filled excavations can be seen in soil cross-sections (Johnson and Walton 1989; J. Benshemesh, personal communication). These field observations are consistent with our observation of the inability of the captive marsupial mole to burrow into loose sand from the surface.

The energy cost of running (1.43 J m^{-1}) was only 1.8% of the cost of sand-swimming by the marsupial mole, similar to the difference observed for the Namib mole. Although it is much more economical to travel on the surface than swim through the sand, marsupial mole tracks are rarely seen on the surface and it appears that most foraging occurs underground. A relatively uniform and high density of subterranean food presumably provides an energy return that is

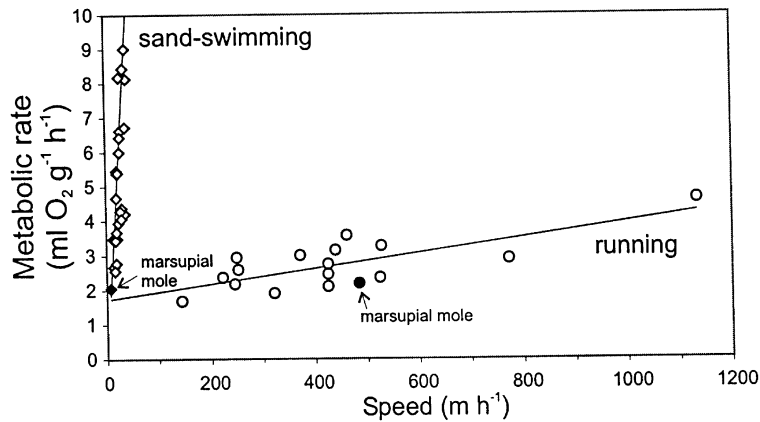


Fig. 6. Comparison of metabolic rate when running (circles) and sand-swimming (diamonds) for the north-western marsupial mole, *Notoryctes caurinus* (solid symbols), and the Namib golden mole, *Eremitalpa granti namibensis* (open symbols) (Seymour *et al.* 1998).

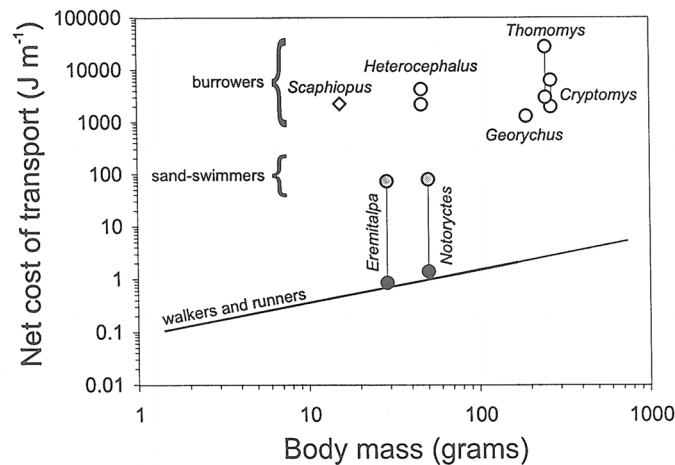


Fig. 7. Relationship between net cost of transport for running and sand-swimming by the north-western marsupial mole, *Notoryctes caurinus*, compared with the net costs of transport for the Namib golden mole, *Eremitalpa granti namibensis* (Seymour *et al.* 1998), various burrowing mammals (Vleck 1979; Du Toit *et al.* 1985; Lovegrove 1989), a toad (Seymour 1973) and mammals walking/running (Taylor 1980).

greater than the energy required to find it by burrowing. Unfortunately, little is known of the actual diet of marsupial moles (Winkel and Humphrey-Smith 1988). The opposite situation occurs in the Namib Desert, where arenicolous insects are so patchy and scarce that the Namib golden mole widely forages (up to a kilometre or so per night) by running on the surface, and 'dives' into the sand periodically to listen for and consume subterranean prey (Seymour *et al.* 1998).

The costs of sand-swimming, while considerably higher than for running, are considerably less than the costs of tunnelling by fossorial mammals (Seymour *et al.* 1998; Fig. 7). Both of these sand-swimmers have costs 1–2 orders of magnitude less than the costs of digging a tunnel in compact soil by other burrowing mammals (Vleck 1979; DuToit *et al.* 1985; Lovegrove 1989;

Fig. 7). Not only does the cost of burrowing depend on the density and adhesion of soil particles, there is the added cost of removing the soil from the tunnel system (Vleck 1979, 1981). Because the sand-swimming moles simply push through the sand that collapses behind them (Gasc *et al.* 1986), they avoid the costs of shearing, moving and lifting the soil to the surface.

Physiological convergence of the marsupial and Namib moles?

Stirling's first reports (1888a, 1888b, 1891) of a *Notoryctes typhlops* noted its striking similarity with golden moles but speculated that it might be a monotreme because there was no trace of a separate urogenital orifice in the poorly preserved specimen. Cope (1892) questioned whether *Notoryctes* was a marsupial and suggested a close affinity with golden moles. That *Notoryctes* is a marsupial is now undoubted; both Ogilby (1888) and Gadow (1888) placed the marsupial mole in the Polyprotodontia with its nearest relatives being the Dasyuridae, but its current systematic status within the Marsupialia remains uncertain (Springer *et al.* 1994; Retief *et al.* 1995; Colgan 1999).

The extreme morphological convergence of the marsupial mole and the Namib golden mole led us to this physiological study. Comparisons of the physiology of these two highly specialised fossorial desert mammals reveal some remarkable similarities and differences. The marsupial mole and the Namib golden mole are similarly thermolabile and both have a low and variable metabolic rate. However, the BMR for the marsupial mole when corrected to a T_b of 35°C is typical of values for marsupials in general (Fig. 5) and suggests no intrinsic metabolic depression, unlike the BMR of the Namib golden mole, which is considerably lower (even though it is a placental mammal and should have a higher BMR) and indicates intrinsic metabolic depression. Both the marsupial mole and the Namib golden mole have a high C_{wet} , especially at higher T_a . The marsupial and Namib moles are remarkably similar in their running speed and metabolic cost of running, both having a similar cost of transport as more typical running mammals. The metabolic cost of sand-swimming is similar for the marsupial and Namib moles, presumably because of the similar mechanical requirements, but the Namib mole burrows through sand considerably faster (15–40 m h⁻¹) than the marsupial mole (2–18 m h⁻¹). Another notable difference is their burrowing capabilities in dry sand. Golden moles are adept at sand-swimming in completely dry, loose sand (Meester 1964; Gasc *et al.* 1986; Seymour *et al.* 1998) but the marsupial mole was unable to burrow into dry sand because its excavation simply filled with sand as fast as it was removed. Nevertheless, the marsupial mole could sand-swim through dry sand in the rotating chamber once it was completely surrounded by sand. The Namib mole and marsupial mole may have a different burrowing motion of the forelimbs and perhaps a different role of the hind limbs and tail in sand-swimming.

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Appendix. Body mass, ambient temperature (T_a), body temperature (T_b), basal metabolic rate (BMR) and wet thermal conductance (C_{wet}) [= $BMR/(T_b - T_a)$] for marsupials

Species	Mass (g)	T_a (°C)	T_b (°C)	BMR (mL g ⁻¹ h ⁻¹)	C_{wet} (mL g ⁻¹ h ⁻¹ °C ⁻¹)	Data source
<i>Planigale tenuirostris</i> and <i>P. ingrami</i>	7.1	33.1	34.5	1.59	0.663	Dawson and Wolfers (1978)
<i>Planigale gilesi</i>	8.3	31.4	32.6	1.43	0.75	Geiser and Baudinette (1988)
<i>Planigale (Antechinus?) maculatus</i>	8.5	31.3	34.8	1.26	0.36	MacMillen and Nelson (1969)
<i>Planigale gilesi</i>	9.4	33.1	35.9	1.4	0.50	Dawson and Wolfers (1978)
<i>Planigale gilesi</i>	9.5	33.4	36.8	1.28	0.38	Dawson and Dawson (1982)
<i>Tarsipes rostratus</i>	10	30	36.6	2.9	0.55	Withers <i>et al.</i> (1990)
<i>Ningau yvonnae</i>	11.6	31.5	34.4	1.35	0.40	Geiser and Baudinette (1988)
<i>Cercartetus lepidus</i>	12.6	27	33.7	1.49	0.222	Geiser (1987)
<i>Marmosa microtarsus</i>	13	28	35	1.44	0.26	Morrison and McNab (1962)
<i>Planigale maculata</i>	13.1	32	34.2	1.01		Morton and Lee (1978)
<i>Acrobates pygmaeus</i>	14	32	34.7	1.08	0.40	Fleming (1985a)
<i>Sminthopsis crassicaudata</i>	14.1	32	33.8	1.33	0.737	Dawson and Hulbert (1970)
<i>Sminthopsis crassicaudata</i>	14.5	33.8	38.6	1.67	0.35	MacMillen and Nelson (1969)
<i>Sminthopsis crassicaudata</i>	15.6	30	35	1.85	0.37	Hinds <i>et al.</i> (1993)
<i>Sminthopsis macroura</i>	16.7	30	32.7	1.26	0.47	Hinds <i>et al.</i> (1993)
<i>Sminthopsis crassicaudata</i>	17.3	28	34.1	1.22	0.20	Geiser and Baudinette (1987)
<i>Sminthopsis crassicaudata</i>	17.7	30	34.3	1.25	0.29	Geiser and Baudinette (1987)
<i>Cercartetus concinnus</i>	18.6	28	34.4	1.20	0.188	Geiser (1987)
<i>Sminthopsis crassicaudata</i>	19	25		1.88		Kennedy and MacFarlane (1971)
<i>Sminthopsis murina</i>	19		35	1.13		Geiser <i>et al.</i> (1984)
<i>Sminthopsis macroura</i>	22	31	33.9	1.07	0.20	Geiser and Baudinette (1987)
<i>Antechinus stuartii</i>	22.1	31.2	36.7	1.53	0.28	MacMillen and Nelson (1969)
<i>Antechinomys laniger</i>	24.2	31.2	36.7	0.98	0.18	MacMillen and Nelson (1969)
<i>Antechinus stuartii</i>	26.1		34.1	1.06		Geiser (1988)
<i>Sminthopsis macroura</i>	26.9	31	34.0	0.33	0.11	Geiser and Baudinette (1987)
<i>Antechinomys laniger</i>	27.4	30	34.8	0.98	0.204	Geiser (1986)
<i>Notoryctes caurinus</i>	34.2	30	30.6	0.63	-0.5	This study
<i>Antechinus stuartii</i>	36.5	30.5	34.4	1.00	0.257	Dawson and Hulbert (1970)

Appendix (continued)

Species	Mass (g)	T _a (°C)	T _b (°C)	BMR (mL g ⁻¹ h ⁻¹)	C _{wet} (mL g ⁻¹ h ⁻¹ °C ⁻¹)	Data source
<i>Monodelphis breviceaudata</i>	40	29	33.5	0.92	0.19	McNab (1978)
<i>Pseudantechinus macdonnellensis</i>	43.1	30.1	34.2	0.63	0.154	MacMillan and Nelson (1969)
<i>Burracmys parvus</i>	44.3		36.1	0.83		Fleming (1985b)
<i>Cercartetus nanus</i>	70	30.0	35.6	0.86	0.15	Bartholomew and Hudson (1962)
<i>Dasyuroides byrnei</i>	73		35.5	0.84		Geiser <i>et al.</i> (1986)
<i>Monodelphis domestica</i>	82			0.787		Thompson and Nicoll (1986)
<i>Dasyercus cristicaudata</i>	89	34.9	37.7	0.52	0.19	MacMillan and Nelson (1969)
<i>Dasyuroides byrnei</i>	89	31.1	36.2	0.87	0.17	MacMillan and Nelson (1969)
<i>Monodelphis domestica</i>	104	30	32.6	0.577	0.22	Dawson and Olson (1988)
<i>Monodelphis breviceaudata</i>	111	28	33.8	0.68	0.12	McNab (1978)
<i>Dasyuroides byrnei</i>	112	32.5		0.87		MacMillan and Dawson (1986)
<i>Dasyercus cristicaudata</i>	113	25	36	0.49	0.045	Kennedy and MacFarlane (1971)
<i>Dasyuroides byrnei</i>	115	31.1	35.6	0.65	0.144	Dawson and Dawson (1982)
<i>Dasyuroides byrnei</i>	115	30	34.2	0.78	0.186	Geiser and Baudinette (1987)
<i>Dasyuroides byrnei</i>	118	28	34.3	0.70	0.111	Geiser and Baudinette (1987)
<i>Dasyuroides byrnei</i>	120	30	35.3	0.763	0.144	Hinds <i>et al.</i> (1993)
<i>Marmosa robinsoni</i>	122	26.5	34	0.8	0.111	McNab (1978)
<i>Petaurus breviceps</i>	122	30	34.9	0.689	0.141	Hinds <i>et al.</i> (1993)
<i>Petaurus breviceps</i>	128	30	36.4	0.69	0.108	Dawson and Hulbert (1970)
<i>Petaurus breviceps</i>	132	27	36.3	0.74	0.080	Fleming (1980)
<i>Phascogale tapoatafa</i>	157	33.7	37.4	0.81	0.219	MacMillan and Nelson (1969)
<i>Caluromys derbianus</i>	305	27	36	0.80	0.083	McNab (1978)
<i>Metachirus nudicaudatus</i>	336	27.5	35	0.61	0.083	McNab (1978)
<i>Caluromys derbianus</i>	357	25	34	0.57	0.063	McNab (1978)
<i>Myrmecobius fasciatus</i>	400	20	32.5	0.356	0.028	McNab (1984)
<i>Isoodon auratus</i>	428	30	33.8	0.35	0.092	Withers (1992)
<i>Dasyurus hallucatus</i>	532	30	33.7	0.361	0.098	Hinds <i>et al.</i> (1993)
<i>Dasyurus (Satanellus) hallucatus</i>	584	35.1	38.1	0.51	0.17	MacMillan and Nelson (1969)
<i>Echymipera rufescens australis</i>	616	30	34.6	0.49	0.107	Hulbert and Dawson (1974)
<i>Perameles nasuta</i>	645	30	36.1	0.49	0.080	Hulbert and Dawson (1974)

<i>Echymipera kalabu</i>	695	30	35.0	0.49	0.099	Hulbert and Dawson (1974)
<i>Isoodon obesulus</i>	717	30	33.9	0.31	0.079	Hinds <i>et al.</i> (1993)
<i>Philander opossum</i>	751	29.5	35.8	0.45	0.066	McNab (1978)
<i>Lutreolina crassicaudata</i>	812	27	35.8	0.50	0.053	McNab (1978)
<i>Perameles gunni</i>	837	30	35.2	0.502	0.097	Hinds <i>et al.</i> (1993)
<i>Pseudocheirus occidentalis</i>	861	26	36.5	0.475	0.045	Kinnear and Shield (1975)
<i>Isoodon macrourus</i>	880	28	34.7	0.447	0.0667	Dawson and Hulbert (1970)
<i>Dasyurus viverrinus</i>	910	30	36.7	0.45	0.067	MacMillen and Nelson (1969)
<i>Chironectes minimus</i>	923	34.6	34.6	0.397		Thompson (1988)
<i>Chironectes minimus</i>	946	24.5	35.3	0.58	0.056	McNab (1978)
<i>Potorous tridactylus</i>	950	24	35.9	0.52		Wallis and Farrell (1992)
<i>Potorous tridactylus</i>	950	24	37.2	0.463	0.039	Hudson and Dawson (1975)
<i>Bettongia penicillata</i>	966	30	37.2	0.583	0.081	Hinds <i>et al.</i> (1993)
<i>Petauroides volans</i>	1000	20		0.428		Foley (1987)
<i>Didelphis marsupialis</i>	1000	25.5	35	0.52	0.054	Enger (1957)
<i>Macrotis lagotis</i>	1011	30	34.9	0.355	0.072	Hulbert and Dawson (1974)
<i>Potorous tridactylus</i>	1028	30	35.8	0.297	0.051	Hinds <i>et al.</i> (1993)
<i>Dasyurus viverrinus</i>	1054	30	35.1	0.357	0.070	Hinds <i>et al.</i> (1993)
<i>Bettongia penicillata</i>	1070	24		0.52		Wallis and Farrell (1992)
<i>Potorous tridactylus</i>	1120	25		0.452		Nicol (1976)
<i>Petauroides volans</i>	1141	20	35.4	0.503	0.033	Rübsamen <i>et al.</i> (1984)
<i>Echymipera rufescens rufescens</i>	1276	30	35.2	0.424	0.082	Hulbert and Dawson (1974)
<i>Didelphis marsupialis</i>	1329	25.5	35	0.46	0.050	McNab (1978)
<i>Dasyurus geoffroyi</i>	1354	27	36.2	0.42	0.036	Arnold and Shield (1970)
<i>Bettongia gairmardi</i>	1385	30	35.6	0.463	0.083	Hinds <i>et al.</i> (1993)
<i>Didelphis virginiana</i>	1548	21.5	34.6	0.43	0.032	McNab (1978)
<i>Isoodon macrourus</i>	1551	30	35.9	0.37	0.063	Hulbert and Dawson (1974)
<i>Macrotis lagotis</i>	1577	28	35.1	0.340	0.048	Kinnear and Shield (1975)
<i>Dasyurus maculatus</i>	1782	30.8	36.9	0.33	0.049	MacMillen and Nelson (1969)
<i>Trichosurus vulpecula</i>	1982	27	36.2	0.32	0.034	Dawson and Hulbert (1970)
<i>Trichosurus vulpecula</i>	2027	30	35.8	0.41	0.071	Hinds <i>et al.</i> (1993)
<i>Didelphis virginiana</i>	2660	29	35.5	0.243	0.0374	Lustick and Lustick (1972)
<i>Lagorchestes conspicillatus</i>	2660	25	36	0.32	0.029	Dawson and Bennett (1978)
<i>Setonix brachyurus</i>	2674	22	36.3	0.312	0.022	Kinnear and Shield (1975)

Appendix (continued)

Species	Mass (g)	T _a (°C)	T _b (°C)	BMR (mL g ⁻¹ h ⁻¹)	C _{vet} (mL g ⁻¹ h ⁻¹ °C ⁻¹)	Data source
<i>Aepyprymnus rufescens</i>	3000	24		0.42		Wallis and Farrell (1992)
<i>Didelphis virginiana</i>	3257	22	34.8	0.33	0.025	McNab (1978)
<i>Phalanger maculatus</i>	4250	21	34.7	0.269	0.019	Dawson and Degabriele (1973)
<i>Phascogaleos cinereus</i>	4765	25.3	35.8	0.217	0.032	Degabriele and Dawson (1979)
<i>Macropus eugenii</i>	4796	25	36.4	0.29	0.0253	Dawson and Hulbert (1970)
<i>Macropus eugenii</i>	4960	24	36.5	0.28	0.017	Dawson <i>et al.</i> (1969)
<i>Sarcophilus harrisi</i>	5050	31	36.8	0.28	0.048	MacMillen and Nelson (1969)
<i>Sarcophilus harrisi</i>	6500	28	34.7	0.179	0.026	Nicol and Maskrey (1980)
<i>Macropus rufa</i>	25000	22	35.7	0.215	0.016	Dawson (1973)
<i>Macropus robustus</i>	29300	30	36.1	0.194	0.032	Dawson (1973)
<i>Lasiorhinus latifrons</i>	29917	25	35.3	0.10	0.0097	Wells (1978)
<i>Macropus rufa</i>	32490	26	35.9	0.178	0.018	Dawson and Hulbert (1970)

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