Bioenergetics and body size in dasyurid marsupials

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CONSIDERABLE ATTENTION has been directed to the relationships between thermoregulatory and metabolic performances and body size in homeotherms (4, 7, 8, 10, 11, 13, 16, 21). This attention has yielded adequate information for demonstrating and predicting such relationships in passerine and nonpasserine birds and in placental mammals, but few comprehensive data are available for marsupials.

While the phylogenetic dichotomy between placental and marsupials probably occurred in late Cretaceous period, these two mammalian forms have certainly been phylogenetically distinct throughout the Cenozoic era (6). With more than 100 g, but appeared to be somewhat lower in smaller forms. The few comparative data for other marsupials, together with ours, suggest a lowered BMR may be characteristic of marsupials in general.

Basal metabolism; weight-specific conductance; body temperature

Experimental animals. The 12 species of dasyurid marsupials employed in this study came from a variety of geographic locations and habitats in Australia, and ranged in size from a 7.2-g Antechinus maculatus to a 5,050-g Sarcothra harrisii (Table 1). Although some of the species were collected by the authors, most were lent or donated by several agencies and individuals (see acknowledgments). All specimens appeared to be in vigorous health and were maintained throughout the experimental period on diets including ground beef and raw egg, mice, baby chicks, and mealworms; they were housed under conditions of natural photoperiod.

Where possible, at least two specimens (a male and a female) of each species were measured; for four species only single specimens or only two of the same sex could be obtained (Table 1). The scientific names of the animals as used herein are after Marlow (12).

Basal metabolic rate (BMR). The term basal metabolism as here employed adheres to the definition of Bartholomew (1): “an approximation of the rate of fasting metabolism of the animal at rest and under no thermal stress.” Morrison (15), in a study of body temperatures of seven dasyurid species, has shown that members of this family have pronounced circadian body temperature (T_b) fluctuations, with highest T_b corresponding to the usual period of activity and lowest T_b corresponding to the period of inactivity. Using this as a guide we have made all of our measurements of BMR on quiescent postabsorptive animals within 2 hr of the midpoint of their usual daily periods of inactivity.

Metabolic measurements were in terms of oxygen consumption using a Beckman model E-2 oxygen analyzer in an open airflow system. During measurements, animals were placed individually in respirometer chambers equipped with ports for the introduction and removal of dry air and for a...
thermocouple, attached to a recording potentiometer, for measurement of ambient temperature. Depending on the size of the animal to be measured, the respirometer chambers varied in volume between 1.1 and 166.5 liters and airflow rates varied between 18 and 192 liters/hr; these combinations appeared to result in optimal air mixing within the chamber.

Ambient temperature (TA) was controlled by placing the respirometer chambers in a constant-temperature cabinet equipped with chilling and heating units, fans, and lights. In the smaller respirometer chambers TA could be controlled within±0.2 C, TA in the larger chambers was controlled within ±0.5 C. Measurements of oxygen consumption were made over 1-hr periods at TA = 10, 20, 30, 32.5, and 35 C; at least five measurements were made during each 1-hr period. Prior to measurements at a given TA, each animal was allowed a 1-hr period of adjustment to that TA. Animals were weighed just before and just after each series of oxygen-consumption measurements at each TA.

Measurements of oxygen consumption over the above range of TA provided an approximate delimitation of thermal neutrality for each animal. The basal metabolic rate for each animal was represented by the mean of the two lowest measurements of oxygen consumption in thermal neutrality.

**Weight-specific conductance.** Weight-specific conductance (C) was calculated from the relationship

$$C = \frac{M}{T_B - T_A}$$

where M is metabolic rate in milliliters O₂ per gram per hour, T_B is body temperature and T_A is ambient temperature. Weight-specific conductance was used as a measure of heat loss rather than thermal (surface-specific) conductance (e.g., ref. 22) because the former could be calculated directly from the measurements made, and also was more directly comparable with weight-specific conductance data reported for placental mammals of a wide size range (e.g., ref. 7 and 17). For all but two species (Satanellus hallucatus and Dasyurus viverrinus) conductance was calculated from measurements made between TA = 9.4 and 12.0 C. Calculations of conductance for Satanellus hallucatus were made from measurements at TA = 20.2 – 20.6 C; no calculations of conductance were obtained for Dasyurus viverrinus.

**Body temperatures.** Except for Sarcoptes, body temperatures were measured manually at each TA at the end of each 1-hr period of oxygen consumption measurements. Body temperature was measured to the nearest 0.1°C by inserting a polyethylene ensheathed thermocouple into the cloaca and well up into the large intestine; all measurements were made within 30 sec after the animals were removed from their respirometer chambers. Body temperatures in Sarcoptes were measured continuously during measurements of oxygen consumption by means of a radio-telemetering device, as it coursed through the gastrointestinal tract.

**Computations.** All computations of the relationships between basal metabolic rate and body weight, and thermal conductance and body weight were made with an IBM disc operating system 360 computer, model 40.

**Results**

**Basal metabolic rate.** The relationship between basal metabolic rate and body size in dasyurid marsupials is described in Fig. 1 and summarized in Table 2. This relationship appears to be linear on a log/log plot (Fig. 1) and the curve, fitted by the method of least squares, is described by the equation:

$$\log M = 0.389 - 0.261 \log W$$

where M is oxygen consumption in milliliters per gram per hour and W is body weight in grams. The standard deviation in this logarithmic relationship of the Y intercept is 0.058 and of slope is 0.028.

As seen in Table 2, all of the measurements of basal metabolism for all species were made between TA = 30 and 35.5 C. Although the experimental technique did not lend itself to precise delimitations of thermal neutrality, the thermal neutral zones for all but Dasyurus and Sarcoptes appeared to extend between TA = 30 and 35 C; for the latter two, thermal neutrality was shifted downward and seemed to extend between TA = 20 and 32 C.

**Weight-specific conductance.** The relationship between

<table>
<thead>
<tr>
<th>Code No.</th>
<th>Species</th>
<th>Weight, g</th>
<th>Number</th>
<th>Collecting Locality</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Antechinus maculatus</td>
<td>7-10</td>
<td>1</td>
<td>NE Queensland</td>
<td>Tropical rainforest</td>
</tr>
<tr>
<td>2</td>
<td>Sminthopsis crassicaudata</td>
<td>14-15</td>
<td>1</td>
<td>E South Australia</td>
<td>Desert</td>
</tr>
<tr>
<td>3</td>
<td>Antechinus stuartii</td>
<td>21-23</td>
<td>1</td>
<td>E Victoria</td>
<td>Wet sclerophyll forest</td>
</tr>
<tr>
<td>4</td>
<td>Antechinus pygmaeus</td>
<td>22-25</td>
<td>1</td>
<td>SW Queensland</td>
<td>Desert</td>
</tr>
<tr>
<td>5</td>
<td>Pseudocheirus macdonnellensis</td>
<td>38-48</td>
<td>1</td>
<td>SW Northern Territory</td>
<td>Desert</td>
</tr>
<tr>
<td>6</td>
<td>Dasyurus viverrinus</td>
<td>33-36</td>
<td>2</td>
<td>SW Queensland</td>
<td>Desert</td>
</tr>
<tr>
<td>7</td>
<td>Dasyurus viverrinus</td>
<td>120-175</td>
<td>1</td>
<td>E Victoria</td>
<td>Wet sclerophyll forest</td>
</tr>
<tr>
<td>8</td>
<td>Phascolarctos cinereus</td>
<td>350-648</td>
<td>1</td>
<td>NE Tasmania</td>
<td>Dry sclerophyll forest</td>
</tr>
<tr>
<td>9</td>
<td>Dasyurus viverrinus</td>
<td>500-597</td>
<td>1</td>
<td>S Victoria</td>
<td>Dry sclerophyll forest</td>
</tr>
<tr>
<td>10</td>
<td>Dasyurus viverrinus</td>
<td>1752</td>
<td>1</td>
<td>NE Tasmania</td>
<td>Dry sclerophyll forest</td>
</tr>
<tr>
<td>11</td>
<td>Dasyurus viverrinus</td>
<td>5000</td>
<td>1</td>
<td>NE Tasmania</td>
<td>Dry sclerophyll forest</td>
</tr>
</tbody>
</table>

**Table 1.** Code numbers, body weights, numbers and sex, and collecting localities and habitats of dasyurid marsupials employed in this study.
FIG. 1. Relationships between basal metabolic rate and body size of dasyurid marsupials and placental mammals. Solid line was fitted to the dasyurid data by the method of least squares. Dashed line was fitted to Brody's (4) least-squares equation for placental mammals. In these equations $M$ represents basal metabolism in milliliters O$_2$ per gram per hour, and $W$ represents body weight in grams. Numbers 1-12 identify measurements from individual animals and species as indicated by code numbers in Table 1.

FIG. 2. Relationships between weight-specific conductance and body size of dasyurid marsupials and placental mammals. Solid line was fitted to dasyurid data by method of least squares, Dashed line was fitted to Herreid and Kessel's (7) least-squares equation for placental mammals. In these equations $C$ represents weight-specific conductance in milliliters O$_2$ per gram per hour per degree C, and $W$ represents body weight in grams. Other symbols as in Fig. 1.

TABLE 2. Mean body weights, basal metabolic rates, ambient and body temperatures in thermal neutral zone (TNZ), and body temperatures below TNZ

<table>
<thead>
<tr>
<th>Species</th>
<th>$\bar{X}$ Body Weight, g</th>
<th>$\bar{X}$ BMR, ml O$_2$/g per hr</th>
<th>$\bar{T}_B$ at BMR, °C</th>
<th>$\bar{X}$ $T_b$ at below TNZ, °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antechinus maculatus</td>
<td>8.5</td>
<td>1.26</td>
<td>31.3</td>
<td>34.8</td>
</tr>
<tr>
<td>Sminthopsis crassicaudata</td>
<td>14.5</td>
<td>1.67</td>
<td>33.8-35.5</td>
<td>38.6</td>
</tr>
<tr>
<td>Antechinus stuartii</td>
<td>22.1</td>
<td>1.53</td>
<td>31.2-32.7</td>
<td>36.7</td>
</tr>
<tr>
<td>Antechinomys spenceri</td>
<td>24.2</td>
<td>0.98</td>
<td>31.2-34.0</td>
<td>36.6</td>
</tr>
<tr>
<td>Pseudantechinus macdonnellii</td>
<td>43.1</td>
<td>0.63</td>
<td>30.1-30.4</td>
<td>31.3</td>
</tr>
<tr>
<td>Dasycercus cristicola</td>
<td>88.8</td>
<td>0.52</td>
<td>34.9-35.1</td>
<td>37.7</td>
</tr>
<tr>
<td>Dasyuroides byrnei</td>
<td>89.0</td>
<td>0.97</td>
<td>31.1-31.4</td>
<td>36.2</td>
</tr>
<tr>
<td>Phascogale tapoatefa</td>
<td>137.2</td>
<td>0.38</td>
<td>33.7-34.0</td>
<td>37.4</td>
</tr>
<tr>
<td>Satelulus hallucatus, juvenile</td>
<td>137.2</td>
<td>0.62</td>
<td>32.5-32.6</td>
<td>37.0</td>
</tr>
<tr>
<td>Satelulus hallucatus, adult</td>
<td>394.4</td>
<td>0.31</td>
<td>33.1-35.3</td>
<td>33.7</td>
</tr>
<tr>
<td>Dasyurus viverrinus</td>
<td>909.9</td>
<td>0.45</td>
<td>30.0</td>
<td>36.7</td>
</tr>
<tr>
<td>Dasyurus maculosus</td>
<td>1782.0</td>
<td>0.30</td>
<td>30.8</td>
<td>36.9</td>
</tr>
<tr>
<td>Sarcophilus harrisii</td>
<td>5000.0</td>
<td>0.28</td>
<td>31.0</td>
<td>36.8</td>
</tr>
</tbody>
</table>

The standard deviation of the $Y$ intercept is 0.049, and of the slope is 0.025.

Body temperatures. Measurements of body temperatures in thermal neutrality and as a function of body size are indicated in Fig. 3, and summarized in Table 2. Due to the absence of a clearly defined relationship in body temperature data, a least-squares analysis was omitted. However, the data as plotted in Fig. 3 merit the qualitative discussion that follows.

Representative body temperatures of animals below thermal neutrality (and those used in calculations of weight-specific conductance) are indicated in Table 2.

DISCUSSION

One of the most commonly used equations for relating basal metabolism to body size in placental mammals is that by Brody (4):

$$M (\text{kcal/kg per 24 hr}) = 70.5 W^{-0.66}$$

This has been converted by Morrison, Ryser, and Dawe (19) to:

$$M (\text{ml O}_2/\text{g per hr}) = 3.8 W^{-0.37}$$

These values are statistically indistinguishable from those preferred by Kleiber (10):

$$M (\text{kcal/kg per 24 hr}) = 70 W^{-1/4}$$

or

$$M (\text{ml O}_2/\text{g per hr}) = 3.5 W^{-1/4}$$
In the manner of Morrison, Ryser, and Dawe (19), we have assigned oxygen consumption values (the production of 4.8 cal requires the consumption of 1.0 ml O₂) to Brody's (4) raw data for placental mammals (which, incidentally, seem to include data for a number of chickens and some doves), converting his data into milliliters O₂ per gram per hour. A regression analysis was then conducted on these converted data to enable statistical comparison with our data for dasyurid marsupials. The equation derived from Brody's (4) data is:

\[ \log M = 0.395 - 0.261 \log W, \quad M = 2.40 W^{-0.261} \]

The standard deviation in this logarithmic relationship for \( Y \) intercept is .020, and for slope is .005. This is in substantial agreement with Morrison, Ryser, and Dawe (19).

The relationship between basal metabolism in milliliters O₂ per gram per hour and body weight in dasyurid marsupials (Fig. 1) is described by the equation:

\[ \log M = 0.389 - 0.261 \log W, \quad M = 2.40 W^{-0.261} \]

The lines fitted to Brody's (4) data for placental mammals and to ours for dasyurid marsupials are indicated in Fig. 1, and are virtually parallel as predicted by the close agreement of the exponents. A t test was performed and no statistically significant difference between slopes was detected. Thus the rate increase of metabolism with decreasing weight is virtually the same for both dasyurid marsupials and placental mammals. However, basal metabolic intensity in dasyurid marsupials is considerably below that for placentals, a reduction averaging 32. 1 \( \pm \) so 15.3 % of that predicted by Brody's (4) equation for placental mammals of the same sizes. The \( Y \) intercept of the dasyurid fitted line is significantly \( (P > .05) \) below that of the parallel placental line. (Because of the relatively great variability of the dasyurid data and the near absence of variability in the placental data, elements of the Behrens-Fisher problem were present (see Bennett and Franklin (3), p. 177). In this analysis a conservative estimate of degrees of freedom (27) was used (dasyurid \( N = 29 \), placental \( N = 57 \)) requiring for significant difference \( (P > .05) \) between \( Y \) intercepts a difference of .1909. The observed intercept difference was .1913.) Thus both dasyurid marsupials and placental mammals conform in basal metabolism to the general mammalian equation \( C = 1.0 W^{-2.25} \), as implied by Morrison and Ryser (17), and as proposed by McNab and Morrison (14) and Herreid and Kessel (7).

The body temperatures of dasyurid marsupials in thermal neutrality were not treated statistically, but suggest some trends based purely on inspection (Fig. 3 and Table 2). Above a body weight of about 100 g, dasyurid TB varied closely around 37 C with a mean of 37.2 \( \pm \) 0.6 C (\( N = 10 \)). Below a body weight of 100 g there is the suggestion of an inverse relationship between TB and body size. This has to be regarded only as a suggestion, however, since both the lowest and highest body temperatures were recorded within this weight class, and the highest body temperatures (38.3 and 38.7 C) were those of Smimthis crassicaudata, the next to smallest species measured (body weights 14.1 and 14.8 g). The smallest species we measured (Antechinus maculatus, body weights 7.2 and 9.7 g) had low body temperatures of 34.5 and 35.0 C. It is unfortunate that we were unable to obtain specimens of the smallest Australian marsupial, the dasyurid Planigale spp. (ca. 3-6 g), which would have further clarified any trends. In his study of body temperatures of dasyurids, Morrison (15) makes no mention of apparent relationships between \( T_B \) and body size, and concludes that dasyurids are fully the equal of higher (placental) mammals in \( T_B \) level if measured under the same conditions.

Since our measurements were confined to the usual period of inactivity and low \( T_B \), we are unable to state unequivocally whether oxygen consumption of dasyurids remains reduced below that of placentals during the usual period of activity and high \( T_B \). However, it is interesting to note that in birds, which experience circadian \( T_B \) cycles equal in magnitude to those of dasyurids, no clear differences
exist between diurnal and nocturnal resting metabolic values (11). We suspect that dasyurid marsupials operate at metabolic levels reduced below those of placentals regardless of state of activity or \( T_b \), and that “normal” mammalian body temperatures are maintained at ambient temperatures below thermal neutrality (Table 2) by physical and physiological control of heat loss (weight-specific conductance) at least equal in magnitude to that of placentals (Fig. 2).

In addition, we feel that this reduction in metabolism is not restricted solely to dasyurid marsupials, but very likely is characteristic of the order Marsupialia in general. Bartholomew and Hudson (2) report a reduction in basal metabolism of 30% below the predicted placental level for *Cercartetus* (*Cercartetus*) namus, an Australian phalangerid marsupial; they attribute this reduction to the abundant subcutaneous fat deposits in their experimental animals, but the reduction also agrees very closely with the average for dasyurids (32%). Brown and Main (5) have observed that the nitrogen requirements and urinary nitrogen excretion of the Australian macropodid marsupial, *Macropus robustus*, are markedly less than in placentals of similar size, suggesting a corresponding reduction in energy metabolism; they also state that the level of energy intake, heart beat rate, and other indirect indicators of the rate of energy metabolism suggest that basal metabolism of a number of macropodid species may be reduced. In addition, Kinnear, Purohit, and Main (9) report that preliminary measurements of energy metabolism in two macropodids (*Macropus eugeni* and *Setonix brachyurus*) reveal reductions between 30 and 40% below the predicted placental level. And lastly, Morrison and McNab (16) report, in a study of a South American didelphid marsupial (*Marmosa microtarsus*), two levels of basal metabolism with the lowest representing approximately a 40% reduction from the predicted placental rate. Clearly, additional studies of basal metabolism in a variety of marsupials are needed before a more definitive statement can be made about the energy metabolism of marsupials in general, but a reduced rate certainly seems likely.

It is also interesting to note that in these dasyurids, which originate from latitudes ranging from about 16° to 40° south and from habitats ranging from tropical rain forests to deserts (see Table 1), there is a much greater conformity of bioenergetics to body size than to any environmentally related influences. The only probable environmentally related phenomenon noted was the apparently greater length of thermal neutrality in the higher latitude Victorian *Dasyurus maculatus* and Tasmanian *Sarcophilus harrisii*.

Thus it would appear that dasyurid marsupials parallel placentals very closely in their bioenergetics, differing primarily in a reduction in basal metabolism and, presumably, in an overall reduction in energy metabolism whether in or out of thermal neutrality and active or quiescent. There can be no question that marsupials are just as “good” homeotherms as placentals and birds; they have merely solved their problem of homeothermy in slightly different ways.

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