The Comparative Energetics of Neotropical Marsupials

Brian K. McNab
Department of Zoology, University of Florida, Gainesville, Florida 32611, USA
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Summary. 1) The rates of metabolism and body temperatures of neotropical marsupials were measured and compared to those of Australian species.

2) Neotropical marsupials have somewhat higher basal rates of metabolism and higher thermal conductances than Australian species. The higher basal rates of neotropical species are correlated with food habits that exclude folivore specialists and to some extent with life in a mesic climate. The high conductances of neotropical marsupials relate to high, stable environmental temperatures.

3) Many small marsupials, even in a tropical rainforest, enter torpor, store fat in their tails, and maintain unusually small temperature differentials, all apparently in response to the high cost of thermoregulation at small masses.

4) Mammals with low basal rates can compensate for a small size by decreasing thermal conductance, thereby maintaining a larger temperature differential with the environment than would otherwise be expected.

5) An appreciable difference in basal rate of metabolism exists between marsupials and placentals in terrestrial carnivores and grazer-browsers, but no such difference is present in arboreal folivores, arboreal frugivore-omnivores, terrestrial omnivore-insectivores, and ant-and termite-eaters.

6) High basal rates of placentals may insure as short a gestation period as is compatible with extended intrauterine development.

7) It is suggested that marsupials have a form of reproduction that may be energetically more expensive than that found in placentals, which may require marsupials to maintain a low basal rate of metabolism.

Introduction

Marsupials are among the most interesting of mammals in terms of distribution, phylogeny, and ecological adaptation. They are found in the New World from southern Patagonia to southern Canada and in Australia from Tasmania to New Guinea and from the Solomon Islands to the Celebes. Until recently little was known of the phylogeny of marsupials, but Kirsch (1968) and Hayman et al. (1971) have shown that they fall into three equally distinct serological groups: caenolestoids, didelphoids, and Australian marsupials. Two of these groups are limited to the New World: the caenolestoids are represented by three genera belonging to the family Caenolestidae and the anatomical studies of Reig (1955) and the serological work of Kirsch (1970, and pers. comm.) suggest that living didelphoids can be grouped into two families: Microbiotheriidae and Didelphidae. Microbiotheriidae includes Dromiciops and Didelphidae has two extant subfamilies, Caluromyinae, which includes Caluromys, and most likely Caluromysiops and Glironia, while all other living didelphids apparently belong to Didelphinae.

In recent years there has been extensive interest in the energetics of marsupials, most measurements having been made on Australian species. Martin (1903) was the first person to note that Australian marsupials have low basal rates of metabolism (although some of his measurements were only 1/2 of recent values). Recently, MacMillen and Nelson (1969) and Dawson and Hulbert (1970) have shown that Australian species (although some of his measurements were only 1/2 of recent values). Recently, MacMillen and Nelson (1969) and Dawson and Hulbert (1970) have shown that Australian species (mainly dasyurids) have basal rates of metabolism equal to about 70% of the rates of placentals of the same size. Baudinette et al. (1976) have shown that dasyurids expend less energy for locomotion than placentals of the same mass.

Few biologists have addressed themselves to the significance of these low rates of metabolism. Martin (1903) suggested that it represents a phylogenetic intermediacy for marsupials between monotremes and eutherians. Eisentraut (1960) maintained "... that the lower warm-blooded animals are characterized by a very labile heat economy and a primitive regulatory mechanism." Dawson (1973) argued that the "... lower
body temperatures and lower levels of metabolism appear characteristic in the less advanced mammals and this probably reflects the early mammalian condition." Hulbert and Dawson (1974) concluded that the unusually low basal rate in a desert bandicoot results from "... a reduced output of thyroid hormone (ecological adaptation) superimposed upon a low level of cellular metabolism indicative of all marsupials (phylogenetic difference)." These authors apparently agree that the basal rate of metabolism is a conservative character, reflecting in this case a phylogenetic dichotomy between marsupials and placentals.

There is some doubt, however, that the basal rate of metabolism is evolutionarily conservative. In fact, McNab (1966, 1969, 1974, 1978) has claimed that the energetics of endotherms, including the basal rate, is sensitive to food habits and climate. Waring et al. (1966) and Kinney and Shield (1975) have specifically applied this concept to the energetics of marsupials. It therefore is of considerable interest whether New World marsupials also have low basal rates of metabolism, especially since two of the three serologically (phylogenetically?) distinct groups of marsupials occur in South America. Furthermore, the neotropical family Didelphidae includes as fossils genera that are presently believed to be similar to those from which all later marsupials were derived (see McKenna, 1969).

The objects of this paper are 1) to report data on the body temperature and rates of metabolism in neotropical marsupials and 2) to put these data into an evolutionary and ecological context with data from Australian species.

Materials and Methods

Data are presented in this paper on the temperature regulation and metabolism of nine species of marsupials and on the body temperature of an additional species. Monodelphis breviceps (number studied = 2) was trapped at Rancho Grande, Venezuela; Marmosa robinsoni (5) in the Panama Canal Zone; Caluromys derbianus in Panama (1), and (3) obtained on loan from the Lincoln Park Zoo (Chicago); Metachirus nudicaudatus (3) was caught near Portobelo, Panama; Philander opossum (3) trapped on Barro Colorado Island, P.C.Z., and (2) obtained on loan from the Lincoln Park Zoo; Lutreolina crassicaudata (4) from Argentina was purchased from an animal dealer; Chironectes minimus from Panama (1) obtained from commercial sources and (2) from the Lincoln Park Zoo; Didelphis marsupialis (2) trapped at B.C.I., P.C.Z.; D. virginiana (3) collected near Gainesville, Florida; and Caenolestes obscurus (2) collected at 3000 m, paramo de Puracé, Colombia.

Measurements of the rate of oxygen consumption were made in an open system employing a Beckman paramagnetic oxygen analyzer. Carbon dioxide and water were removed from the airstream after its exit from the chamber containing the animal and before measuring the flow rate. The rate of metabolism was calculated from the formula

\[ \frac{M}{W} (\text{ml}O_2/g \cdot h) = 27.257 \cdot \frac{(\Delta P_{O_2} \cdot F_i \cdot P_i)}{T \cdot W_i} \]

where \( \Delta P_{O_2} \) is the fractional change in oxygen content in the gas stream between entrance into and exit from the chamber, \( F_i \) flow rate (ml/min), \( P_i \) barometric pressure (mm Hg), \( T \) temperature of the gas stream at the site of flow rate measurement (°K), and \( W \) body mass (g). The animals were confined in a chamber that was submerged in a thermoregulated water bath for the maintenance of a constant environmental temperature. Rectal body temperature was measured immediately after each experiment at a given temperature with a Schulteiss thermometer or with a YSI telethermometer. An experiment was terminated normally after two hours and when an animal was quiescent. The rates of metabolism that were used were those that corresponded to the measurement of body temperature. If in the middle of an experiment an unusually low rate of metabolism occurred, especially if it occurred at low environmental temperatures, the rate was not used because there was no way of knowing whether it represented inactivity at a normal body temperature or a lowered body temperature, unless of course the rate was later repeated and a body temperature corresponding to the rate was measured. All rates were measured during the daylight hours, as is appropriate for nocturnal animals, and were corrected to STP.

Minimal thermal conductance was estimated from graphs of the rate of metabolism on ambient temperature by placing one or more linear curves on the data at temperatures below thermoneutrality in such a manner that the curves intersect the base line \( (M/W = 0) \) at the mean body temperature corresponding to the measurements of metabolism. Since evaporative water loss was not measured, these estimates are of "wet" conductances.

It shall be of value at several points to compare the basal rates and minimal thermal conductances of the marsupials relative to a mass-dependent standard. The choice of the standards that are used is arbitrary, except that the same standards should be used throughout. Because one of the objectives will be to compare marsupials with placentals, Kleiber's mouse-to-elephant (placental) standard is used. Kleiber's relation also has the advantage of being the most familiar standard for basal rate, although one could as well have used the marsupial curves of MacMillen and Nelson (1969) or Dawson and Hulbert (1970). The standard for minimal thermal conductance is derived from McNab and Morrison (1963) and Herreid and Kessel (1967).

Results

Measurements of body temperature and oxygen consumption as a function of ambient temperature or time in marsupials are given in Fig. 1 through 9; the parameters of energetics for both Australian and American species are given in Table 1. These data are analyzed for general patterns in the Discussion, but the opportunity is taken here to make a few detailed comments on the responses of selected species.

Gardner (1973) showed that there are two species of Didelphis living in North America, one exclusively tropical and the other mainly temperate. These species have essentially the same basal rates of metabolism (Fig. 1), although temperate D. virginiana, as might be expected, has a much lower thermal conductance than tropical D. marsupialis. There is excellent agreement between the basal rates reported for D. marsupialis by Enger (1957) and those reported for both species in this study, but these values are twice those reported for D. virginiana by Brocke (1970) and...