Water and energy metabolism in free-living multi-mammate mice, Praomys natalensis, during summer

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Received 28 June 1985; accepted 18 July 1986

A population of Praomys natalensis in a grassland area of Natal, South Africa, was studied to establish water and energy metabolism using isotope turnover techniques. Mean rate of water influx was 215.3 ml/kg day and efflux was 212.9 ± 64.3 ml/kg day. Mean CO₂ production was 3.0 ml/g h i.e. an energy expenditure of 1512 kJ/kg day. It is estimated that each P. natalensis ingests about 100 g of dry matter/kg day. The high water flux rates in P. natalensis are discussed in relation to diet and climate. Water turnover and CO₂ production are compared with those of other small free-living mammals.

The multi-mammate mouse Praomys (Mastomys) natalensis is one of the commonest and most widespread rodents in southern Africa, occurring throughout the Southern Savanna Woodland and Grassland biotic zones, as well as in the moister parts (within the 250-mm isohyet) of the South West Arid (Davis 1974). Meester, Lloyd & Rowe-Rowe (1979) regarded P. natalensis as a species with wide habitat tolerances, which within its distributional range, is generally the first small mammal species to become established in an area that is recovering from some form of disturbance.

Population eruptions of P. natalensis occur regularly (Smithers 1971; van der Merwe & Keogh 1970; Wilson 1970). In agricultural areas they are responsible for significant damage to crops (de Graaff 1981), and as the species is semi-commensal with humans and is also a vector of bubonic plague and Lassa fever (Coetzee 1975), P. natalensis is an important species to man.

The water and energy requirements of free-living animals can be determined by the doubly-labelled water turnover technique (Lifson & McClintock 1966; Nagy 1980). This technique was employed in the present study to measure the water influx and metabolic rates of P. natalensis in the field, and the subsequent estimation of food consumption rates (Nagy 1975). These eco-physiological aspects have not been recorded before for this species.

Material and methods

The study was carried out during late December (early summer) 1983 in grassland adjacent to a Eucalyptus plantation 820 m above sea level near Pietermaritzburg, Natal. The study area was within the Coastal Hinterland bioclimatic region (Phillips 1973). Mean annual rainfall is 1200 mm and falls mainly between September and March. Mean annual minimum and maximum temperatures are 14°C and 22°C respectively. Mean temperatures for December 1983, recorded at a nearby weather station, were 16°C (minimum) and 25°C (maximum).

The grassland is dominated by the grasses Aristida juncti-

formis, Paspalum commersoni, Digitaria eriantha, and Eragrostis spp. Forbs comprised 5% by occurrence.

Above-ground standing crop of the vegetation was sampled by clipping all herbage down to ground level in six 1-m² quadrats. Moist weight of each sample was determined immediately after collection, then herbage was oven dried at 60°C until no further loss of weight was recorded. Mean above-ground standing crop was 365 g/m² ± 117 (dry weight). The mean moisture content of the six samples was 65.8% ± 8.

The animals were caught in Elliott and Sherman live traps using a bait of rolled oats and peanut butter. Traps were set in the evening and checked in the early morning. The animals were removed from the traps, weighed, injected intraperitoneally with isotopes and returned to the traps for 3 h to allow equilibration of isotopes. Each animal was injected with 100 µl of 95% atoms excess H₂¹⁸O and 100 µl of tritiated water containing 20 MBq. Some animals were injected with tritiated water only.

After isotope equilibration the animals were bled from the infra-orbital sinus with micro-haematocrit tubes and then individually marked by toe-clipping prior to release at the points of capture.

The traps were set every two or three days for recaptures and for three days at the end of the study. At recapture animals were reweighed, re-bled and then released.

All blood samples were flame-sealed and then refrigerated until extraction. Extraction of water from whole blood samples was achieved by heat distillation in sealed pasture pipettes that were under partial vacuum. When the blood was apparently dry, the water condensate was isolated by flame sealing and stored at room temperature until analysed.

The activities of tritiated water in extracted water samples and standard dilutions of the injectate were determined on 5 µl sub-samples in 3 ml of PCS scintillation cocktail. Counting was done in a Beckman 4 000 LSC.

¹⁸O concentrations in extracted water samples were determined by placing 20 µl subsamples in Urey tubes with a
standard CO₂ gas charge. The tubes were incubated at 80°C for 15 h, during which an equilibrium was established between oxygen atoms in the water and CO₂. After this was achieved the ¹⁸O levels in the CO₂ samples were determined in an isotope ratio mass spectrometer (VG Micromass, model 903).

Total body water was determined by the degree of dilution of the injected isotopes relative to standard dilutions. Water influx, efflux, and CO₂ production rates were determined from the changes in isotope levels during the release periods, using standard equations (Nagy 1980; Lison & McClintock 1966). It was assumed that the mass-specific pool sizes for individuals did not change during the measurement periods and that any changes in body mass and absolute water pools were linear. Water turnover and CO₂ production rates were calculated for all intervals between captures for each animal.

CO₂ production rates were converted to energy expenditure rates assuming an energy equivalent of 21 J/ml CO₂. All mean values are given with SD.

Results
Twenty *P. natalensis* were captured and injected with isotopes and 14 of them (70%) were subsequently recaptured on one or more occasions. Water turnover data were obtained for 14 individuals with a total of 29 turnover periods, and 6 individuals provided 10 estimates of CO₂ production.

There were no significant differences between total body water estimates derived from tritiated water and ¹⁸O dilution, and the mean tritiated water space was 73.7 ± 2.59 ml/100 g body mass (*n* = 14).

The mean body mass of animals was 57.3 ± 9.5 g and there were no consistent or large variations in the body mass of individuals, apart from one pregnant female that weighed 73 g at initial capture and increased to 85.5 g by the final capture five days later. Since there were no major changes in the masses of the other individuals, water influx and efflux estimates were in close agreement. The mean rate of water influx based on all turnover periods was 215.3 ± 53.0 ml/kg day (*n* = 29), and for individual animals was 225.1 ± 60.4 ml/kg day.

The mean rate of CO₂ production from all turnover periods was 3.0 ± 0.37 ml/g h (*n* = 10), and for individual animals was 3.09 ± 0.40 (*n* = 6). This represents a daily CO₂ production rate of 72 ml/g, and is equivalent to an energy expenditure of 1512 kJ/kg day.

Discussion
The metabolic and water turnover rates of mammals are scaled to body mass with power indices of 0.75 and 0.82 respectively (Kleiber 1975; Macfarlane & Howard 1972). Allometric conversions facilitate comparisons among species that differ substantially in body mass, therefore both mass specific and allometric metabolic and water influx rates of *P. natalensis* as well as a range of other small mammals are shown in Table 1.

The rates of water influx in *P. natalensis* are fairly high compared with field rates that have been found in most other rodents (Table 1). Water flux rates have been studied predominantly in desert rodents, most of which are granivorous, and hence obtain little free water from their food. *P. natalensis* is also granivorous but grass, leaves and insects also form part of the diet (Hanney 1965; Taylor & Green 1976). In addition, the present study was carried out in an area which has a mesic, mild climate with seasonal rainfall, and vegetation was lush from recent rain (mean water content of grass in the area was 65.8 ± 8%). Therefore the higher rates of water influx in *P. natalensis* are understandable. These water turnover rates are similar to those found in *Rattus fuscipes* (Morris 1981), a species that is generally associated with mesic habitats in Australia, but much lower than are found in some other small mammals e.g. *Clethrionomys*, *Arvicola*, and *Sminthopsis* (Table 1).

The metabolic rates in free-living *P. natalensis* are intermediate to those that have been reported for other rodents (Table 1). The ratio of water to energy use in *P. natalensis* was 0.14, which is much higher than the values reported for desert rodents; 0.04 to 0.07 ml/kJ (Mullen 1971; Withers, Louw & Henschel 1980).

Because of the omnivorous diet of *P. natalensis* it is difficult to relate water turnover and metabolic rates directly to food consumption and assimilation. However when the water content of an animal’s diet is high there may be little or no requirements for drinking. Under these circumstances water

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### Table 1 Water influx and CO₂ production in free-living small mammals during summer

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass (g)</th>
<th>Water influx (ml/kg/day)</th>
<th>CO₂ production (ml/g/h)</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Perognathus formosus</em></td>
<td>16.0</td>
<td>70</td>
<td>33.2</td>
<td>Mullen (1970)</td>
</tr>
<tr>
<td><em>Dipodomys merriami</em></td>
<td>31.0</td>
<td>130</td>
<td>69.6</td>
<td>Mullen &amp; Chew (1973)</td>
</tr>
<tr>
<td><em>D. microps</em></td>
<td>55.0</td>
<td>110</td>
<td>65.3</td>
<td>Mullen (1971)</td>
</tr>
<tr>
<td><em>Merriones shawii</em></td>
<td>108.4</td>
<td>155</td>
<td>103.9</td>
<td>Lachiver <em>et al.</em> (1978)</td>
</tr>
<tr>
<td><em>M. libycus</em></td>
<td>85.0</td>
<td>127</td>
<td>81.5</td>
<td>Lachiver <em>et al.</em> (1978)</td>
</tr>
<tr>
<td><em>Petromyscus collinus</em></td>
<td>19.0</td>
<td>74</td>
<td>36.3</td>
<td>Withers <em>et al.</em> (1980)</td>
</tr>
<tr>
<td><em>Aethomys namaensis</em></td>
<td>46.0</td>
<td>70</td>
<td>40.2</td>
<td>Withers <em>et al.</em> (1980)</td>
</tr>
<tr>
<td><em>Petromus typicus</em></td>
<td>130.0</td>
<td>39</td>
<td>27.0</td>
<td>Withers <em>et al.</em> (1980)</td>
</tr>
<tr>
<td><em>Pseudomys albocinereus</em></td>
<td>18.6</td>
<td>174</td>
<td>84.9</td>
<td>Morris &amp; Bradshaw (1981)</td>
</tr>
<tr>
<td><em>Mus musculus</em></td>
<td>20.2</td>
<td>164</td>
<td>81.2</td>
<td>Morris &amp; Bradshaw (1981)</td>
</tr>
<tr>
<td><em>Rattus fuscipes</em></td>
<td>13.9</td>
<td>223</td>
<td>103.3</td>
<td>Morris (1981)</td>
</tr>
<tr>
<td><em>Thomomys bottae</em></td>
<td>63.5</td>
<td>265</td>
<td>161.3</td>
<td>Morris (1981)</td>
</tr>
<tr>
<td><em>Praomys natalsi</em></td>
<td>99.4</td>
<td>256</td>
<td>169.0</td>
<td>Gettinger (1984)</td>
</tr>
<tr>
<td><em>Clethrionomys rubi</em></td>
<td>57.3</td>
<td>215</td>
<td>128.5</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Arvicola terrestris</em></td>
<td>15.8</td>
<td>361</td>
<td>171.1</td>
<td>Hölleman <em>et al.</em> (1982)</td>
</tr>
<tr>
<td><em>Sminthopsis crassicaudata</em></td>
<td>93.6</td>
<td>837</td>
<td>546.5</td>
<td>Grenot <em>et al.</em> (1984)</td>
</tr>
</tbody>
</table>

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influx rates can provide good estimates of food consumption rates (Benjamin, Degen, Brieghet & Tahhan 1973; Gettinger 1984). As mentioned, the vegetation during the present study was quite lush. After allowing for the formation of metabolic water the available water content in vegetation would represent at least 75% of the fresh weight and a similar available water content would prevail for invertebrate dietary items. In these circumstances it is unlikely that the rats were drinking. If these assumptions are correct the water influx rates represent the approximate consumption of 290 g fresh food/kg day and 100 g dry matter/kg day.

Drozd (1968) demonstrated energy assimilation efficiencies of about 85% for voles and mice consuming natural diets. If similar assimilation efficiencies prevail in P. natalensis then the metabolized energy of 1512 kJ/kg day represents an ingestion of 1780 kJ/kg day. Carbohydrate, protein and fat provide 17.20 and 39.3 kJ/g metabolizable energy respectively (Kleiber 1975). Since the estimated dry matter intake of P. natalensis, 100 g/kg day, provided 1780 kJ/kg day, i.e. 17.8 kJ/g, it appears that energy was derived predominantly from carbohydrates.

Water influx rates and metabolic rates may be subject to substantial seasonal variations. Pseudomys alboacinereus at two different study sites had water influx rates of 262 and 222 ml/kg day during winter compared with respective summer rates of 174 and 164 ml/kg day (Morris & Bradshaw 1981). The higher rates of water flux during winter in this species are associated with a winter rainfall pattern and a usually higher water content of food during this season. Perognathus formosus exhibits maximum metabolic rates of about 5.6 ml CO₂/h during the late northern winter months of February and March, about double the rates found in summer (Mullen & Chew 1973). Similar seasonal influences on metabolic rates have been found in free-living Dipodomys merriami (Mullen 1971). Increased metabolic rates during winter probably result from increased thermogenesis during cold conditions.

The present study was carried out during early summer in comparatively mild climatic and environmental conditions. It would be interesting to determine how the water and energy requirements of free-living P. natalensis vary under different climatic conditions, especially drought, and during breeding. P. natalensis is generally found in areas that experience wet, warm summers and dry, cool winters. It can therefore be expected that water influx rates may be lower in winter while CO₂ production rates are elevated. The energy costs of lactation can be expected to be high, as Mullen (1971) has demonstrated that lactating Perognathus formosus exhibit CO₂ production levels that are double those of non-lactating animals.

Considering the diversity of rodent species and habitats it is surprising how little published data are available on the energy and water requirements of free-living rodents. Further research in this area should reveal major inter-specific and seasonal differences in water and energy utilization in this important group of mammals.

Acknowledgements

This project was partially funded by the Council for Scientific and Industrial Research. We thank Prof. J. Skinner, Mammal Research Institute, University of Pretoria for providing research facilities and encouragement, Dr G.L. Dryden and C. Sapsford for their comments on the manuscript, and Graham Turner for operating the mass spectrometer.

References


