Differential energy costs of winter acclimatized common spiny mice
*Acomys cahirinus* from two adjacent habitats

Michael Scantlebury*, Uri Shanas*, Hagai Kupshtein*, John R. Speakman**, Abraham Haim*

*Department of Biology, University of Haifa-Oranim, Tivon 36006, Israel
**Aberdeen Centre for Energy Regulation and Obesity (ACERO), School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, Scotland, UK
***ACERO, Rowett Research Institute, Aberdeen, Scotland AB21 9SB, UK*

Received 28 July 2003; received in revised form 10 November 2003; accepted 11 November 2003

**Abstract**

The common spiny mouse *Acomys cahirinus*, of Ethiopian origin, has a widespread distribution across arid, semi-arid and Mediterranean parts of the Arabian sub-region. We compared the daily energy expenditure (DEE), water turnover (WTO) and sustained metabolic scope (SusMS=DEE/resting metabolic rate) of two adjacent populations during the winter. Mice were captured from North- and South-facing slopes (NFS and SFS) of the same valley, comprising mesic and xeric habitats, respectively. Both DEE and SusMS winter values were greater in NFS than SFS mice and were significantly greater than values previously measured in the summer for these two populations in the same environments. However, WTO values were consistent with previously established values and were not significantly different from allometric predictions for desert eutherians. We suggest that physiological plasticity in energy expenditure, which exists both temporally and spatially, combined with stable WTO, perhaps reflecting a xeric ancestry, has enabled *A. cahirinus* to invade a wide range of habitats.

© 2003 Elsevier Inc. All rights reserved.

**Keywords:** *Acomys*; Energy; Doubly labelled water; Resting metabolic rate; Body temperature; Thermoregulation; Water turnover; Desert; Ecophysiology; Evolution

1. Introduction

The link between energy expenditure and physiological adjustment to the environment has been extensively studied and reviewed (McNab and Morrison, 1963; Degen, 1997; Lovegrove, 2000; Speakman, 2000). Small mammals such as rodents, that inhabit arid environments with restricted amounts of both water and food, characteristically have lower rates of energy expenditure and water turnover (WTO) than those occupying more mesic areas (Nagy and Peterson, 1988; Nagy et al., 1999). For species living in Mediterranean ecosystems, summer may be a physiologically demanding season when temperatures are maximal and the availability of moisture from the environment is minimal (Nevo, 1995). By comparison, for non-hibernating small mammals inhabiting cooler climates, winter is often considered the most energetically challenging period because low ambient temperatures require an increased energy intake (Speakman, 2000). Rodent
species inhabiting these cooler mesic areas typically have higher resting metabolic rates (RMR) and daily energy expenditures (DEE) than species from hot and xeric habitats (Haim and Izhaki, 1993).

We have previously shown that there are differences in energy expenditure and WTO between two populations of common spiny mice *Acomys cahirinus* inhabiting opposing slopes of the lower Nahal Oren (the ‘Evolution Canyon’; Nevo, 1995) during the summer (Scantlebury et al., 2003). Mice inhabiting the cooler, more mesic Northern-facing slope (NFS) had higher DEE but similar WTO compared with those inhabiting the warmer more xeric Southern-facing slope (SFS). These differences were interpreted as physiological adjustments to aridity and heat on the SFS. However, during the winter, minimal ambient temperatures in this area may fall as low as 8 °C, approximately 15 °C lower than during the summer (Shanas et al., 2002). At these temperatures hypothermia has been recorded in *A. cahirinus* (Haim and Rubal, 1994). Hence, the major challenge facing species like *A. cahirinus* during winter in the eastern Mediterranean ecosystem is probably to cope with low ambient temperatures during activity. The extent of this challenge may be different for mice inhabiting the NFS and the SFS as the different amounts of solar radiation received on the two slopes result in 3–4 °C lower minimal temperatures on the NFS (Pavlicek, personal communication). Due to this climatic variability, we predicted that energy expenditure and water turnover in NFS mice during winter would be higher than in SFS mice. We expected these differences to be more pronounced during the winter, than that previously measured during the summer, as the energy costs of thermoregulation are expected to increase. Therefore, the aim of the present research was to determine the DEE and WTO of NFS and SFS mice from the field during the winter, and to compare the levels of these traits to those measured in the same populations during the summer.

2. Materials and methods

Adult males and non-lactating adult females were trapped on the NFS (three males and two females) and SFS (four males and four females) of the lower Nahal Oren during mid-winter (end of January). We used the doubly labelled water (DLW) technique (Lifson and McClintock, 1966; Speakman, 1997) to determine DEE and WTO of mice in the field. The methodology for applying this technique in this species has been described previously (Scantlebury et al., 2003). Briefly, this involves capture of the animal and collection of a background blood sample, injection of DLW, collection of an initial enriched blood sample some 60 min after dosing, release of the animal back into the wild, recapture and a final blood sample being taken some 3–4 days post dose. The isotope ratios $^{18}$O/$^{16}$O and $^2$H/$^1$H from the blood samples are then analysed using gas source isotope ratio mass spectrometry (Optima, Micromass IRMS and Isochrom uG, Manchester, UK) prior to calculation of DEE (Speakman and Lemen, 1997). We took recaptured animals back to the laboratory where their RMR was measured using the set-up previously reported (Scantlebury et al., 2003). (M. Scantlebury et al., unpublished). Sustained metabolic scope (SusMS = DEE/RMR; Peterson et al., 1990), an index of how hard an animal is working, was determined for each population. WTO values (ml/day) were calculated using the measured deuterium elimination rates ($k_d$) and deuterium dilution spaces ($N_d$) (Lifson and McClintock, 1966; Nagy and Costa, 1980).

We used analysis of covariance (ANCOVA) to examine differences in body mass (g), DEE (kJ/g day), $N_d$ (ml), WTO (ml/100 g day) and SusMS (no units) between mice from all four groups (male and female mice from both the NFS and SFS populations). Slope of origin and sex were included as categorical factors. Body mass was included as an additional covariate when examining differences in DEE (kJ/day) and WTO (ml/day). We used initial values of body mass, as there was no significant change in body mass of mice between capture and recapture for either population (initial mass = 45.40, final mass = 42.78, $t$ = 2.16, $P$ = 0.07 for NFS mice and initial mass = 51.11 g, final mass = 48.67 g, paired $t$ = 1.37, $P$ = 0.24 for SFS mice).

3. Results

DEE (kJ/day) and mass-specific DEE (kJ/g day) were significantly higher in NFS mice than SFS mice ($F_{1,10} = 6.78, P = 0.026$ and $F_{1,10} = 6.58, P = 0.028$ for DEE and mass-specific DEE, respectively; Table 1). The absolute difference in DEE between the two populations amounted to 20.7 kJ/day, which was 27% of the mean expenditure.
across the two sites. Metabolic intensities (DEE/body mass) were also significantly different between the two sites, with mice from the NFS having metabolic intensities 40% greater than mice from SFS. SusMS for the NFS mice at 4.12 was significantly greater than for mice on the SFS, which averaged 2.64 ($F_{1,10}=8.39$, $P=0.016$). However, there were no significant differences in body mass, $N_d$, WTO or mass-specific WTO between mice from the two slopes. There were no significant differences in any of the measured variables between male and female mice. Nor were there any significant interactions between sex and site of origin for any of the measured variables.

4. Discussion

Previous measurements have shown that *A. cahirinus* from both extreme desert regions (Degen et al., 1986; Kronfeld-Schor et al., 2001) and Mediterranean areas (Weissenberg and Shkolnik, 1994) have both low energy expenditure and low WTO, which are characteristics of desert-living free-ranging eutherians (Degen, 1994). These attributes were also evident in mice collected from both slopes of the Nahal Oren during the summer (Scantlebury et al., 2003). In the present study, DEE and SusMS of mice were approximately twice the same values measured during the summer, and were subsequently not significantly different from allometric predictions for other mesic-living free-ranging eutherians (Table 2). During winter, NFS mice actually had significantly higher DEE values than predicted from allometric equations for desert rodents, whereas SFS mice

<table>
<thead>
<tr>
<th></th>
<th>SFS</th>
<th>SFS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
</tr>
<tr>
<td>$n$</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>50.01</td>
<td>39.85</td>
</tr>
<tr>
<td>S.D.</td>
<td>7.81</td>
<td>7.71</td>
</tr>
<tr>
<td>DEE (kJ/day)</td>
<td>113.00</td>
<td>74.40</td>
</tr>
<tr>
<td>S.D.</td>
<td>24.20</td>
<td>17.80</td>
</tr>
<tr>
<td>DEE (kJ/g-day)</td>
<td>2.34</td>
<td>2.18</td>
</tr>
<tr>
<td>S.D.</td>
<td>0.16</td>
<td>0.06</td>
</tr>
<tr>
<td>Nd (ml)</td>
<td>37.61</td>
<td>33.68</td>
</tr>
<tr>
<td>S.D.</td>
<td>8.94</td>
<td>13.57</td>
</tr>
<tr>
<td>WTO (ml/day)</td>
<td>6.38</td>
<td>3.31</td>
</tr>
<tr>
<td>S.D.</td>
<td>4.65</td>
<td>2.96</td>
</tr>
<tr>
<td>WTO (ml/100 g day)</td>
<td>9.20</td>
<td>13.34</td>
</tr>
<tr>
<td>S.D.</td>
<td>7.02</td>
<td>9.62</td>
</tr>
<tr>
<td>SusMS</td>
<td>4.77</td>
<td>3.14</td>
</tr>
<tr>
<td>S.D.</td>
<td>1.02</td>
<td>0.75</td>
</tr>
</tbody>
</table>

$n =$ sample sizes.

Table 2: Allometrically predicted values of daily energy expenditure (DEE; kJ/day), water turnover (WTO; ml/day) and sustained metabolic scope (SusMS; no units) from (1) Speakman (2000) (equation 3 for small mammals), (2) Nagy et al. (1999) (desert rodents), (3) Nagy and Peterson (1988) (desert eutherians in the field), (4) Nagy and Peterson (1988) (non-desert eutherians in the field), (5) Degen and Kam (1995) (eutherians) for common spiny mice *A. cahirinus* originating from North-facing slopes (NFS) and South-facing slopes (SFS)

<table>
<thead>
<tr>
<th>Predicted value</th>
<th>Source</th>
<th>NFS</th>
<th>%D</th>
<th>SFS</th>
<th>%D</th>
</tr>
</thead>
<tbody>
<tr>
<td>DEE (kJ/day)</td>
<td>1</td>
<td>90.47</td>
<td>8</td>
<td>84.05</td>
<td>-9</td>
</tr>
<tr>
<td>DEE (kJ/day)</td>
<td>2</td>
<td>65.75</td>
<td>48*</td>
<td>62.07</td>
<td>24</td>
</tr>
<tr>
<td>WTO (ml/day)</td>
<td>3</td>
<td>6.19</td>
<td>-17</td>
<td>5.53</td>
<td>15</td>
</tr>
<tr>
<td>WTO (ml/day)</td>
<td>4</td>
<td>13.93</td>
<td>-63*</td>
<td>12.77</td>
<td>-50**</td>
</tr>
<tr>
<td>SusMS</td>
<td>5</td>
<td>3.07</td>
<td>34</td>
<td>3.11</td>
<td>-15</td>
</tr>
</tbody>
</table>

* and ** indicate the results of $t$-tests at significance levels of $P<0.05$ and $P<0.01$, respectively, of the measured value from the predicted value. %D denotes the percent deviation of the measured value from the predicted value (a negative value indicates a lower measured value than the predicted value).
did not. Throughout the year DEE and SusMS values were consistently higher in NFS mice than SFS mice. Differences between mice from the two slopes may in part be accounted for by increased costs of thermoregulation (Kronfeld et al., 1998), which is required throughout the year on the cooler NFS. Energetic strategies adopted by the mice appear to vary seasonally. During the summer, a similar behaviour to desert-dwelling rodents is observed, with low RMR, DEE and SusMS values (Scantlebury et al., 2003). However, during the winter, DEE and SusMS values increase, signifying physiological adjustments to the more mesic conditions. In Israel, A. cahirinus ranges from extreme desert in the South (<50 mm annual rainfall), up to the Mediterranean live-oak maquis forests in the North (600–700 mm annual rainfall) (Nevo, 1985; Weissenberg and Shkolnik, 1994). This physiological plasticity may enable A. cahirinus to invade such a wide range of ecosystems (Weissenberg and Shkolnik, 1994).

In contrast to the variation in energy expenditure, observed between populations and across seasons, WTO values remained low throughout the year and were not significantly different from the allometric prediction for desert eutherians (Table 2). During the winter, animals increased their DEE, and the ratio of WTO to DEE was about half of the values measured in the summer in both populations (Scantlebury et al., 2003). Consequently, as there were no sources of free water in the study area, this suggests that the winter diet consisted of less water, relatively, than the summer diet and mice increased the energy density of their food. Degen et al. (1986) compared the DEE, WTO and diet of three sympatric desert-living species, A. cahirinus, golden spiny mouse (Acromys russatus) and bushy-tailed gerbils (Seketamys calurus). The latter two are able to survive in extremely arid areas where A. cahirinus is absent. The results of their study showed that whereas A. cahirinus required a high dry matter intake, compared with the other two species, it also required a high water intake. They suggested that one reason that A. cahirinus could be excluded from extremely arid areas is if stomach volume were limiting. This is because they would be forced to obtain more water from energy-poor sources, such as snails (e.g. the land snail, Pomatias olivieri; Broza and Nevo, 1994) and insects, and consequently they may not be able to consume enough dry matter to meet energy requirements. Constraints such as stomach volume might also be important in the present study. Given that DEE increases to almost double the value in winter than in summer, A. cahirinus may be unable to increase their metabolizable energy intake during the winter without switching to a more energy-dense diet.

Weissenberg and Shkolnik (1994) compared WTO between two populations of A. cahirinus, one from Eilat (extreme desert) and one from the Galilee (a mesic Mediterranean area). They found that, under controlled laboratory conditions, WTO was 36% lower in mice from Eilat than those of the Galilee. However, when WTO was measured in free-ranging mice in their natural habitats, WTO rates were similar and close to that measured in Galilee animals in the laboratory. One possibility is that the Eilat mice select a diet with an increased water content (e.g. one which contains many snails and insects), to enable them to thermoregulate in hot and dry conditions. In both the current study and that of Weissenberg and Shkolnik (1994), no significant differences in WTO were observed between free-living populations of A. cahirinus. Hence, mice seem to be able to manipulate water intake and water loss to maintain approximately constant WTO under a variety of conditions. It is unclear what mechanisms they may use, but physiological means, such as osmoregulation (Shanas et al., 2003) may be important. Alternatively, behavioural mechanisms such as diet selection and activity patterns (e.g. being active during cooler periods of the day) may also be used. Further work is needed on this topic.

A low water requirement may have been maintained in A. cahirinus when it colonised mesic Mediterranean habitats because it provided an advantage in a heterogenic habitat in which the dry season is hot and long (up to 9 months), and in which large areas are sparsely vegetated. In such areas, A. cahirinus may have an advantage over common mesic-originating species, such as the broad-toothed wood mouse Apodemus mystacinus, which has higher water and energy requirements (Haim and Rubal, 1994). The Mediterranean ecosystem on Mount Carmel is vulnerable to fire (Naveh, 1990), which removes the arboreal cover on both slopes. Following such events, the survival of A. cahirinus could be enhanced, as it will have an advantage re-colonising the recovering ecosystem, when water sources are scarce (Haim et al., 1997).
Acknowledgments

This work was supported in part by grants from the Israel Science Foundation, Israel Academy of Science and Humanities to AH (298/97-2) and from the Royal Society (SV/ISR/NVB) and British Ecological Society (SEPG-1878) to MS. We would like to thank the two anonymous referees for their helpful and constructive comments with which this manuscript was greatly improved.

References


