Energetics and water economy of common spiny mice
*Acomys cahirinus* from north- and south-facing slopes of a Mediterranean valley

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Summary

1. A comparison was made of the daily energy expenditure (DEE), resting metabolic rate (RMR) and water turnover (WTO) of two populations of Common Spiny Mice *Acomys cahirinus* from north- and south-facing slopes (NFS and SFS) of the same valley, which represented ‘Mediterranean’ and ‘desert’ habitats, respectively.

2. An examination was made as to whether these physiological characteristics differed between mice that had been in the laboratory (outdoor conditions) for 2 months compared with mice captured from the field.

3. Mice from the field had greater RMR values than mice in the laboratory and NFS mice had greater RMR values than SFS mice. In the field, NFS individuals had greater DEE values than SFS individuals. Mass-specific RMR values of SFS mice were 20% less than the allometrically predicted value, whereas those of NFS were not. WTO and sustained metabolic scope (DEE/RMR) were lower in the field than in the laboratory.

4. The results indicate that physiological capabilities are phenotypically plastic, as differences exist between the field and laboratory and between NFS and SFS mice. Furthermore, they highlight the importance of using field studies for understanding the link between energetics and physiological adjustment to environmental conditions.

Key-words: Daily energy expenditure, doubly labelled water, ecological physiology, evolution, resting metabolic rate

Introduction

Energy has been suggested to be the universal currency of living systems and is required for all life-supporting activities, such as body maintenance, foraging, predator avoidance, growth and reproduction (McNab 1989; Speakman 2000). Many ecological and evolutionary theories have been concerned with acquisition and trade-offs associated with the allocation of resources, including energy (Gadgil & Bossert 1970; McNab 1980; Hennesman 1983). Traditionally, energy expenditure has been measured in the laboratory, under standard conditions, providing measurements of basal or resting metabolic rate (BMR or RMR; Brody 1945; Kleiber 1961). The metabolic rates obtained have been shown to depend on a variety of factors, such as body mass (Kleiber 1961), ambient temperature (Oliver & Fairchild 1984; Nagy & Gruchacz 1994), photoperiod (Heldmaier *et al.* 1982; Haim, McDevitt & Speakman 1995a), season (Corp, Gorman & Speakman 1997), latitude (Ellis 1984; Root 1988), altitude (Hayes 1989a, 1989b), diet (McNab 1980, 1986), habitat (Rubal, Choshniak & Haim 1992), zoogeographical origin (Lovegrove 2000) and phylogeny (Hayssen & Lacy 1985; Elgar & Harvey 1987). However, these values possibly bear little resemblance to daily energy expenditures measured in the field (FMRs), which vary uniquely between species and depend critically on other factors, such as the differences in seasonal supply of energy and water from the environment, the food source and digestibility (Nagy 1987; Nagy, Girard & Brown 1999; Speakman 2000). Therefore, it is generally accepted that experiments designed to measure the ecological significance of FMRs are most effective when combined with measurements of RMR of the same species under laboratory conditions (McNab 1989; Meerlo *et al.* 1997).

The link between energy expenditure and physiological adjustment to the environment has been extensively

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studied (McNab & Morrison 1963; Drent & Daan 1980; Lovegrove 2000; Speakman 2000). For example, animals originating from colder climates typically have higher RMR values than those from warmer areas (Haim, Rubal & Harari 1993). In contrast, animals that inhabit hot deserts, where water and food availability are limited and temperatures may reach extremes, characteristically have lower rates of energy expenditure and water turnover (WTO) than related non-desert species (Nagy 1987; Geffen et al. 1992; Seymour, Withers & Weather 1998). Rubal, Choshniak & Haim (1992) compared RMR values, food consumption and WTO rates in the laboratory between murid rodents from extremely different habitats. Their findings revealed that desert-living Golden Spiny Mice (Acomys russatus) had significantly lower metabolizable energy intakes, RMR values and WTO rates than temperate-living Broad-Toothed Field Mice (Apodemus mystacinus). These traits are assumed to be advantageous in an environment with low productivity, as they decrease the need of water and energy for body maintenance (Louw & Seely 1982).

Comparative interspecific studies of water economy and metabolic rates, however, are limited in their ability to provide understanding of physiological adjustments to the environment because observed differences may in part be attributable to phylogeny. Although this variability can be determined using large sets of data and knowledge of phylogenetic relationships between taxa (Harvey & Pagel 1991), this complication can clearly be avoided using within-species comparisons. Intraspecific differences, although harder to measure because of reduced variability, provide better indications of the cause and function of variations in energy expenditure due to environmental challenges. When such differences do occur, variations in RMR have been suggested to be a consequence of physiological adjustments to environmental conditions (Daan et al. 1989; Haim & Izhaki 1993; Mueller & Diamond 2001), which may also result in observed behavioural (Haim, Rubal & Harari 1993; Corp, Gorman & Speakman 1997, 1999) or reproductive (Johnson, Thomson & Speakman 2001) differences. Physiological adjustments to the environment may include genetic (Speakman & Johnson 2000) as well as plastic phenotypic components; the latter resulting either from different conditions during development (ontogenetic plasticity) or during adult life (acclimatization) (Sabat & Bozinovic 2000; Tracy & Walsberg 2001).

Northern- and southern-facing slopes (NFS and SFS) of valleys and wadis in the Mediterranean ecosystem offer a situation where closely located populations of the same species can inhabit very different habitats (Nevo 1995, 1997). The main environmental variable that shapes the two different habitats is incident solar radiation, which may be up to 300% greater on the SFS (Nevo 1995). An outcome of the increased radiation is greater water evaporative rates, which creates an increased xeric and less productive environment within a Mediterranean region (Broza & Nevo 1994). The direct result is a change in vegetation quality and cover on the two slopes with the SFS consisting of a mosaic of habitats with open park forests of Ceratonia siliqua—Pistacia lentiscus, savanna plant formations and bushy islands, while the NFS consists of dense live-oak maquis forest (Nevo 1997). Average yearly maximal temperatures are higher (up to 2°C) on the SFS than the NFS, while relative humidity is higher on the NFS (T. Pavliček, personal communication) and environments similar to ‘xeric savannah’ on the SFS and ‘temperate-mesic’ on the NFS are formed.

Common Spiny Mice (Acomys cahirinus Desmarest, 1819) inhabit both the NFS and SFS of the lower Nahal Oren, a wadi in the Carmel mountain range of Israel (Blaustein, Kotler & Nevo 1996). These mice do not dig burrows but inhabit exposed rocky crevices. Therefore, they are especially susceptible to climatic variability, for example high daytime temperatures, and face very different physiological challenges in these two areas. We aimed to examine the hypothesis that the differences in daily energy expenditure (DEE), RMR and WTO observed in populations of A. cahirinus over a large geographical scale, between individuals inhabiting deserts compared with those inhabiting mesic areas (Weissenberg & Shkolnik 1994), might also exist at a much smaller scale on the mesic and xeric NFS and SFS of Nahal Oren. Further, we aimed to determine whether there were any differences in these variables between individuals that had been acclimatized to outdoor laboratory conditions for 2 months (where food and water were not limiting) compared with individuals that were freshly captured from the field, during the dry summer period.

Materials and methods

Laboratory studies

Acomys cahirinus were trapped from the NFS and SFS of the lower Nahal Oren, Mount Carmel (32°43’ E, 34°58’ N), Israel, and taken to the Department of Biology at the University of Haifa-Oranim during the summer (June). Traps were set in the evening and collected in the early morning. Mice weighed between 40 and 60 g. Mice were placed individually in cages (35 × 25 × 15 cm3) and exposed to the outdoor ambient conditions of the dry season (approx. 14L: 10D, min./max. 28 °C/37 °C, 75% RH). All individuals were provided with a treadmill in which they could exercise at will. Body mass was measured daily (Sartorius 0-1 g) to establish if any of the females were pregnant. Pregnant individuals were not used. Mice were offered a rodent chow (Koffolk, Israel, 21% crude protein, 4% crude fat, 4% cellulose, 13% moisture, 7% ash, 18.7 kJ g−1 gross energy) ad libitum and agar gel (20 g of agar gel dissolved in 1000 ml of water made up to
FIELD STUDIES

Mice were trapped from the NFS and SFS of Nahal Oren towards the end of the dry season (end of August). Only adult males and adult non-lactating females were used. Body mass was recorded (Ohaus Scout 0·1 g) and individuals were marked by toe clipping. An initial blood sample was taken by tail tipping, and the mice were injected with doubly labelled water (DLW) (see below). A second blood sample was taken 1 hour after the DLW injection to estimate initial isotope enrichments. The mice were then released at the capture site. Labelled animals were recaptured 3 or 4 days post-dose, after which a final blood sample was taken. Recaptured animals were then taken to the laboratory where their RMR was measured.

DAILY ENERGY EXPENDITURE (DEE) AND WATERTurnover (WTO)

DEE and WTO were determined for mice in both the field and laboratory using the DLW technique (Lifson & McClintock 1966; Speakman 1997). On day one, the animals were weighed and approximately 200 μl of blood was obtained by tail tipping and flame-sealed into glass capillaries (Vitrex, Camlab Ltd, Cambridge, UK). Each sample was used to determine background isotope enrichments of D2H and 18O. Immediately afterwards, a known mass of DLW (0·3 ml) (10% APE-enriched 18O water (APE = atom percent excess; Enritech Ltd, Rehovot, Israel) and 99% APE-enriched D2H water (MSD Isotopes Inc., Pointe-Claire, Quebec) mixed in a ratio of 20 : 1) was administered intra-peritoneally (IP). Syringes were weighed before and after administration (0·0001 g, Sartorius 4-figure balance) to calculate the mass of DLW injected. Blood samples were taken after 1 hour to estimate initial isotope enrichments. To estimate the isotope elimination rates, mice in the laboratory were blood sampled at 48 and 96 h post-injection while mice injected in the field were recaptured and blood sampled at 72 h or at 96 h post-dose (if not captured at 72 h). Blood samples were taken within half an hour of whole 24-h periods following injection to minimize errors involved with daily fluctuations in isotope elimination rates (Speakman & Racey 1988).

Capillaries that contained the blood samples were vacuum distilled (Nagy 1983) and water from the distillate was used to produce CO2 and H2 (Speakman 1997; Ward et al. 2000). 18O : 16O and D : H isotope ratios were analysed using gas source isotope ratio mass spectrometers (Optima, Micromass IRMS and Isochrom pG, Manchester). 18O and D injectate enrichments (p.p.m.), elimination constants (k_e and k_d), dilution spaces (N_e and N_d), initial and final pool sizes were calculated as recommended by Speakman (1997) (specifically, the ‘plateau’ method was used to estimate initial isotope enrichments with the ‘percentage mass’ method of calculating final pool sizes). The ‘plateau’ method assumes that the initial blood sample is taken at a time when the administered isotope has equilibrated with the animal’s body water pool and reached a maximal value, before a significant amount of isotope has been washed out of the body. The ‘percentage mass’ method assumes that the ratio of isotope pool size to body mass measured initially, remains constant for the duration of the experiment. Hence, if the body mass of the animal changes, then the final isotope pool size can be calculated from the initial percentage pool size and the final body mass. The single-pool calculation method was used to calculate CO2 production (Speakman 1997, equation 7·17). DEE was calculated using a computer program that took into account the effects of small deviations from 24 h for the sampling intervals and the effects of mass changes on body water pool size over the experimental period using a direct proportional correction (Lemen & Speakman 1997). WTO values (ml day−1) were calculated using the measured deuterium elimination rates (k_d, per day) and deuterium dilution spaces (N_d, ml) (Lifson & McClintock 1966; Nagy & Costa 1980) as:

\[
WTO = k_d N_d \times F, \tag{1}
\]

where \( F \) is the fractionation factor of the isotope (= 0·941, Speakman 1997). We examined whether the DEE and WTO values obtained were different from allometrically predicted values (Nagy & Peterson 1988; Nagy 1999; Speakman 2000). Pooled values of sustained metabolic scope (SusMS, DEE/RMR, Peterson, Nagy & Diamond 1990) and water economy index (WEI, WTO/DEE, Nagy & Peterson 1988; Nagy & Gruchacz 1994) were also compared between mice from the two sites (see below).

RESTING METABOLIC RATE (RMR)

RMR was determined as minimal oxygen consumption (VO2) after an initial hour of minimal stable recordings when animals were seen to be inactive using an open-circuit respirometry system (Depocas & Hart 1957; Hill 1972). On the two occasions that animals did not settle down, these data were rejected. A metabolic chamber (1100 ml volume) was immersed in a temperature-controlled water bath (Neslab EX-500, West Shore Technologies Inc., Michigan, USA) and maintained at the lower critical point (28·0 ± 0·5 °C) (Weissenberg & Shkolnik 1994). Dried air (silicagel, TamRoad; Sigma-Aldrich Co. Ltd, Dorset, UK) was pumped into the chamber at a rate of 500 ml min−1 providing positive pressure throughout. The flow rate was controlled by a mass-flow controller (Platon Instrumentation, Roxpur Measurement & Control Ltd, Bramley, Hants, UK) placed upstream of the
metabolism chamber, which was calibrated with a bubble flowmeter (Bennett, Clarke & Jarvis 1992) every 2 weeks. We verified that there were no air leaks in the system before each measurement. Measurements of VO2 were taken every 2 min during the minimal phase of the T cycle (10:00–15:00) (Kronfeld et al. 1994; Haim, McDevitt & Speakman 1995b; Haim & Zisapel 1999) using an oxygen analyser (Servomex 570A, Servomex Group Ltd, Crowborough, Sussex, UK) connected to a Tabor multimeter (Tabor Electronics Ltd, Tel Hanan, Israel) for fine resolution. Depressions in oxygen concentration were approxi-
mately 0·25–0·4%. The oxygen analyser was calibrated to an upper value (20–95% O2, atmospheric) prior to the measurement of each animal and to a lower value (0·0% O2, N2 gas) every 2 weeks. VO2 was converted to kJ using an oxygen equivalent of 20·51 kJ/l O2 (Hardy 1972). All results were corrected to standard temperature and pressure (STP). RMR values were compared with allometrically predicted values (Kleiber 1961; Speakman 2000).

Results

BODY MASS

Although there was no overall difference in body mass among the four groups of mice (NFS and SFS mice in both the field and laboratory) (ANOVA $F_{3,26} = 1·99$, $P = 0·14$), there was a significant interaction between site of origin and Laboratory/Field (ANOVA $F_{1,16} = 4·91$, $P = 0·036$). Within the laboratory NFS mice tended to be heavier than SFS mice, whereas within the field SFS mice tended to be heavier than NFS mice (Table 1).

DAILY ENERGY EXPENDITURE (DEE)

DEE values of mice in the field were significantly lower than those in the laboratory (ANOVA $F_{1,22} = 5·10$, $P = 0·034$) when body mass was included as a covariate and site of origin and Laboratory/Field were included as factors. There was no significant interaction between site of origin and Laboratory/Field (ANOVA $F_{1,22} = 1·61$, $P = 0·218$). Within the field subgroup mass-specific DEE and whole-animal DEE values of NFS mice were significantly higher than those of SFS mice ($t = 2·69$, $P = 0·03$).

RESTING METABOLIC RATE (RMR)

Mice in the field had significantly higher RMR values than in the laboratory (ANOVA $F_{1,17} = 4·49$, $P = 0·049$) and NFS mice had significantly higher RMR values than SFS mice (ANOVA $F_{1,17} = 5·08$, $P = 0·038$) when body mass was included as a covariate with site of origin and Laboratory/Field included as factors (Table 1). There was a significant interaction between site of origin and body mass (ANOVA $F_{1,17} = 6·29$, $P = 0·023$), indicating SFS mice were heavier in the field and NFS mice were heavier in the laboratory. In the laboratory there was a significant positive correlation between body mass and RMR in NFS mice (least squared regression, $F = 9·48$, $r^2 = 0·629$, $P = 0·037$), but not in SFS mice ($F = 0·06$, $r^2 = 0·01$, $P = 0·81$). In contrast, in the field, there was no correlation between body mass and RMR in NFS mice ($F = 1·41$, $r^2 = 0·22$, $P = 0·289$) or SFS mice ($F = 0·36$, $r^2 = 0·06$, $P = 0·571$). Sustained metabolic scope (DEE/RMR) values were 2·03 and 2·18 in NFS and SFS mice in the laboratory, respectively. However, values were lower for mice from the field, 1·75 in NFS mice and 1·53 in SFS mice.

WATERTurnover (WTO)

When testing the results obtained from all four studied groups of mice a significant difference in WTO was noted (one-way ANOVA, $F_{3,27} = 7·53$, $P < 0·001$, Table 1). Within sites, values were significantly higher for mice kept in the laboratory compared with those of the field ($t = 3·69$, $P = 0·003$ for NFS mice and $t = 2·08$, $P = 0·03$ for SFS mice). Within the laboratory groups, values of WTO were significantly higher in NFS mice than SFS mice ($t = 2·34$, $P = 0·037$). However, among the mice from the field, WTO values were similar between NFS and SFS mice ($t = 0·1$, $P = 0·92$). The water economy index (WEI, WTO/DEE) was greater in NFS than SFS mice in the laboratory
Predicted value | Laboratory | Field |
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<tbody>
<tr>
<td>DEE (kJ day(^{-1}))</td>
<td>1</td>
<td>86.99*** (−40)</td>
</tr>
<tr>
<td>DEE (kJ day(^{-1}))</td>
<td>2</td>
<td>82.59*** (−38)</td>
</tr>
<tr>
<td>DEE (kJ day(^{-1}))</td>
<td>3</td>
<td>63.76* (−19)</td>
</tr>
<tr>
<td>RMR (ml O(_2) g(^{-1}) h(^{-1}))</td>
<td>4</td>
<td>1.44*** (−20)</td>
</tr>
<tr>
<td>RMR (kJ day(^{-1}))</td>
<td>4</td>
<td>30.25 (−16)</td>
</tr>
<tr>
<td>RMR (kJ day(^{-1}))</td>
<td>5</td>
<td>26.88 (−6)</td>
</tr>
<tr>
<td>WTO (ml day(^{-1}))</td>
<td>6</td>
<td>5.83*** (52)</td>
</tr>
<tr>
<td>WTO (ml day(^{-1}))</td>
<td>7</td>
<td>13.30*** (34)</td>
</tr>
<tr>
<td>SusMS</td>
<td>8</td>
<td>3.09*** (−34)</td>
</tr>
</tbody>
</table>

*, ** and *** indicate the results of \(t\)-tests at significance levels of \(P < 0.05, < 0.01, < 0.001\), respectively, of the measured value from the predicted value.

†ml O\(_2\) was converted into kJ day\(^{-1}\) using an oxygen equivalent of 20.51 kJ l O\(_2\) (Hardy 1972).

In agreement with this hypothesis, a recent study on the body temperature \((T_b)\) daily rhythms of *A. cahirinus* from the two populations (NFS and SFS mice) (Shanas et al. 2002) showed that NFS mice exhibited lower in the field than in the laboratory. This was surprising given that animals usually expend less energy in the laboratory than in the field because they have no need to expend energy on activities such as foraging, predator avoidance or territorial maintenance (McNab 1989). Our animals behaved differently in laboratory and field conditions. In the laboratory, where water and food were not limiting factors, they appeared able to waste more water and energy compared with in the field. In contrast to DEE values, RMR values were higher in mice from the field than in those from the laboratory. Of the four groups of mice, three had RMR values that were 20% less than the allometric prediction and only NFS mice in the field had RMR values that were not significantly different from the predicted value (Table 2).

One possible reason that NFS mice had relatively higher RMR values might be because the NFS is a cooler and more mesic and productive environment (Nevo 1995). This is consistent with the suggestion that higher metabolic rates are generally associated with environments of higher productivity (McNab 1983, 1986; Mueller & Diamond 2001). In addition, on the NFS, *A. cahirinus* coexists with the Palaearctic-originating Broad-Toothed Field Mouse *Apodemus mystacinus*, which is active under cooler conditions and has RMR values similar to the expected allometric value (Harrison & Bates 1991; Haim & Rubal 1994). While SFS mice may benefit from a low RMR, NFS mice may be selected for a higher RMR to enable them to compete more effectively with the *Apodemus*. In agreement with this hypothesis, a recent study on the body temperature \((T_b)\) daily rhythms of *A. cahirinus* from the two populations (NFS and SFS mice) (Shanas et al. 2002) showed that NFS mice exhibited...
an acrophase in $T_9$, 6 h before SFS mice, which is assumed to be the result of earlier activity (Aschoff 1982). This difference may possibly serve to avoid competition with Apodemus. Hence, NFS mice may maintain RMR values that are appropriate for higher productivity and higher energy costs on the NFS, compared with mice from the SFS. Current measurements of RMR were 30–50% higher than previously reported for postabsorptive desert- and Mediterranean-adapted A. cahirinus (0.71, SD = 0.13 and 0.88, SD = 0.08 ml O$_2$ g$^{-1}$ h$^{-1}$, respectively, Weissenberg & Shkolnik 1994). Variation in water economy was also found among populations of A. cahirinus from different geographical localities. A population from the Galilee (temperate Mediterranean) had a 40% higher WTO than one from Eilat (extreme desert) when measured in the laboratory (Weissenberg & Shkolnik 1994). However, in the field, during the hot summer month of August, WTO rates were similar. Our results showed that WTO values were lower in mice from the field than those in the laboratory, and, in agreement with the above study, we also found no significant difference in WTO between mice from the NFS and SFS in the field measured at the end of August. Although WTO values of mice in the field were not significantly different from allometric predictions for desert eutherians, values for mice in the laboratory were significantly greater than allometric predictions for desert eutherians. All four groups of mice had WTO values that were significantly lower than allometric predictions for non-desert eutherians (Nagy & Peterson 1988) (Table 2). Previous research has shown that if a water source is available, common spiny mice may be active at high ambient temperatures and thermoregulate using high cutaneous evaporative rates (Shkolnik & Borut 1969). Hence, WTO rates are likely to have been higher in the laboratory than the field, because water was not a limiting factor in the laboratory (Golightly & Ohmart 1984).

It has been suggested that water turnover and energy expenditure are necessarily linked for animals that do not drink, as water intake must come from metabolism of foodstuffs and preformed water in food (MacFarlane et al. 1971; Yousef et al. 1974). The energy requirement of desert-living Kit Foxes Vulpes vulpes macrotis may be met before their water requirements—animals appear to be foraging more for dietary water than energy (Golightly & Ohmart 1984). In the current study, in the laboratory, NFS mice had a greater WEI than SFS mice or NFS mice from the field. Hence, NFS mice increased their WTO relative to their DEE when they were taken into the laboratory, whereas SFS mice did not. WEI values of both laboratory and field mice were greater than the minimal predicted values for desert mammals that are able to survive on a diet of dried substrates alone (Withers, Louw & Henschel 1980). Consequently, mice in the field may have consumed some material with high water content, such as the land snail Pomatias olivieri (Arad 1993; Broza & Nevo 1994).

It is tempting to assume that the observed differences in physiological characteristics are an outcome of differences in local environmental conditions. However, with only two different localities it was not possible to determine whether other factors may have contributed to this variation (Garland & Adolph 1994). Comparative energetic measurements were different in the four groups of mice, indicating phenotypic plasticity; in particular, our results emphasize the importance of using field studies to provide a better understanding of physiological adjustments to the environment.

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