



Temporal partitioning among diurnally and nocturnally active desert spiny mice: energy and water turnover costs

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Abstract

Nocturnal *Acomys cahirinus* and diurnally active *A. russatus* coexist in hot rocky deserts. Diurnal and nocturnal activity exposes them to different climatic challenges. A doubly-labelled water field study revealed no significant differences in water turnover between the species at all seasons, reflecting the adaptations of *A. russatus* to water conservation. In summers the energy expenditure of *A. russatus* tended to be higher than that of *A. cahirinus*. Energy requirements of *A. cahirinus* in winter are double than that of *A. russatus*, and may reflect the cost of thermoregulating during cold nights. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Two ecologically similar species of the genus *Acomys* coexist in hot rocky desert habitats in the south of Israel: the nocturnal common spiny mouse, *A. cahirinus*, and the diurnally active golden spiny mouse, *A. russatus*. A key field study revealed that the golden spiny mouse is competitively displaced into diurnality by its congener (Shkolnik, 1971). Later studies indicate that although the golden spiny mouse is active exclusively during the day, it retains the endogenous rhythmicity of a nocturnal mammal (Kronfeld et al., 1994; Kronfeld-Schor, 1998), and that its NST capacity in winter is similar to that of the common spiny mouse (Kronfeld-Schor et al., 2000).

The differing activity patterns of the two *Acomys* species in the shared habitat expose them to different climatic conditions. At Ein Gedi, where the two species coexist, the average maximal temperature in January is 20°C, and the average minimal temperature is 13°C. In July, the average maximal temperature is 38°C, and the average minimal temperature is 28°C (Jaffe, 1988). Being active during the night or during the day, therefore, subjects the two spiny mouse species to different environmental challenges. During summer diurnal activity of the golden spiny mouse may imply physiological costs in water turnover and metabolism, while during winter there may be a greater energetic cost of thermoregulation to be paid by the nocturnal common spiny mouse. Thus the physiological costs of diurnal and nocturnal activity may not only differ but may vary seasonally. Although spiny mice were subjects of a wealth of physiological studies (e.g., Shkolnik and Borut, 1969; Haim and Borut, 1981; Kam and Degen, 1993; Degen, 1994; Elvert et al., 1999; Kronfeld-Schor et al., 2000), the physiological costs involved in the

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temporal partitioning between the two species remain largely unstudied.

Here we used the doubly-labelled water (DLW) method to compare the physiological costs involved in the temporal separation in the field.

2. Materials and methods

Field research was carried out in the vicinity of the Ein Gedi Nature Reserve (31°28'N, 35°23'E, 100–350 m below sea level). Field metabolic rates and water turnover were measured in free-living individuals of both spiny mouse species using the DLW method (Lifson and McClintock, 1966; Nagy, 1980).

Sample collection: Mice of both species were trapped in February and August 1995, representing winter and summer, respectively. Captured individuals were weighed, sexed, and marked by toe clipping. Mice were given intraperitoneal injections of 0.2 ml of water containing 99 atoms of deuterium per 100 atoms of hydrogen, and 10 atoms of ^{18}O per 100 atoms of ^{16}O . The syringe was weighed before and immediately after injection (to 0.001 g) to determine mass of injectate. After 2 h, which is sufficient time for equilibration of the isotopes with body fluids (Karasov, 1981; Degen et al., 1986), a blood sample ($\sim 200\ \mu\text{L}$) was taken from the infraorbital sinus with a heparinized microhematocrit capillary tube (Fisherbrand). The mice were then released in the same place from where they were captured. During the following 1–6 days animals were recaptured (1–3 times), weighed, a blood sample was taken and the mice were released again. Blood samples were analyzed using mass spectrometer (Sitech SIRA, series II, Micromass).

Calculations: Total body water (TBW) of the mice was calculated from the dilution space of deuterium, and by drying other mice that accidentally died during this or other studies (seven individuals of *A. russatus* and two individuals of *A. cahirinus*) in 60°C until constant weight. Water turnover (WTO) was estimated from the decline over time in the specific activity of deuterium, and CO_2 production was estimated from the decline over time in specific activities of deuterium and ^{18}O (Lifson

and McClintock, 1966; Nagy, 1980). We assumed that $\text{RQ} = 0.83$, i.e., 1 ml CO_2 produced = 24.39 J, based on Gessaman and Nagy (1988) and calculations using data from Degen et al. (1986) for the calculation of field metabolic rates (FMR).

Statistical analysis: All the results are given as mean \pm SE. The statistical significance of differences between groups was assessed by ANCOVA (STATISTICA).

3. Results

For the DLW measurements, during February, four *A. cahirinus* and six *A. russatus* were recaptured at least twice (two *A. cahirinus* and three *A. russatus* were recaptured three times). During August, two *A. cahirinus* and three *A. russatus* were recaptured at least once (one *A. cahirinus* was recaptured twice).

Mean body mass of both species did not increase or decrease significantly between captures, indicating that the rodents were maintaining steady-state water and energy budgets. Individuals of *A. russatus* are significantly heavier than the individuals of *A. cahirinus* ($p < 0.05$, Table 1). The average TBW volume based on drying the animals was $59.9 \pm 2.4\%$ ($n = 7$) for *A. russatus* and $61.3 \pm 5.7\%$ ($n = 2$) for *A. cahirinus*. The average TBW volume based on the dilution space of deuterium was $44.6 \pm 2.1\%$ ($n = 19$) and $51.1 \pm 2.5\%$ ($n = 8$), respectively. WTO rates calculated using the TBW volume results from drying the animals ranged between 2 and 5 ml H_2O per day (Table 1) with no significant difference between seasons and between species ($p > 0.05$).

CO_2 production of *A. cahirinus* in the field during February was double that of *A. russatus* ($p < 0.05$, Table 1). During August CO_2 production of *A. cahirinus* was 65% that of *A. russatus* (Table 1).

4. Discussion

The energy requirements of the common spiny mice in the field in winter are double than that of golden spiny

Table 1
 CO_2 production, water turnover (WTO), and body mass in free-living spiny mice (mean \pm SE)

	<i>Acomys cahirinus</i>		<i>Acomys russatus</i>	
	February	August	February	August
r CO_2 ml d $^{-1}$	2440 \pm 524 ^{a,b}	1621 \pm 31	1053 \pm 142 ^a	2477 \pm 523
WTO ml d $^{-1}$	4.30 \pm 1.14	2.43 \pm 0.7	4.65 \pm 0.68	3.52 \pm 0.31
Body mass g	41 \pm 3 ^b	32 \pm 5 ^b	49 \pm 6	44 \pm 1
n	4	2	6	3

^aSignificant difference from individuals of the same species in summer ($p < 0.05$).

^bSignificant difference between the two species in the same season ($p < 0.05$).

mice. In summer, the trend appears to reverse, but the difference between the species is not significant, possibly due to our small sample size. Population densities of both species in this habitat are very low (e.g., Shargal et al., 2000), so capturing and recapturing rates were very low.

Field metabolic rate reflects the costs of basal metabolism, thermoregulation, locomotion, feeding, predator avoidance, reproduction and other costs. The two species are similar in morphology and ecology. They overlap in habitat use (Shargal et al., 2000), food habits (Degen et al., 1986; Kronfeld-Schor and Dayan, 1999), and onset of reproductive season (Kronfeld et al., 1996; Shargal et al., 2000). There is even an overall similarity in their foraging ecology, in particular in summer (Jones, personal comm.). The major difference between the two species is their diametrically opposite activity patterns (Shkolnik, 1971; Kronfeld et al., 1994; Kronfeld-Schor, 1998), which expose them to different climatic conditions.

During their hours of inactivity, spiny mice are found in rock crevices where the temperatures are not extreme and remain fairly constant. Throughout our year of research (1995) the minimal air temperature (10°C) was recorded at night during winter, while the temperature inside rock crevices remained constant at 18°C (Elvert et al., 1999). Thus, nocturnally active common spiny mice were exposed to significantly lower ambient temperatures than diurnally active golden spiny mice were. Therefore, the greater energy expenditure of the common spiny mouse during winter may reflect the greater cost of maintaining homeothermy while active during the colder hours of the night.

In summer, it is possible that a greater energetic cost is paid by the golden spiny mouse because it is active during hot hours when thermoregulation requires energy expenditure (see Degen, 1997). The maximal air temperature recorded at day during this summer (1995) was about 45°C, while the temperature inside rock crevices did not show daily variations, and remained constant at about 35°C (Elvert et al., 1999).

Field metabolic rates (FMR) of desert eutherian mammals are about 30% lower on average than nondesert eutherians (Nagy, 1987), an advantage in a low productivity habitat (Louv and Seely, 1982). During February, FMR was 100 and 55% of the expected for desert eutherians, for *A. cahirinus* and *A. russatus*, respectively (Table 2). During August FMR was 70 and 97% of the expected for desert eutherians, for *A. cahirinus* and *A. russatus*, respectively (Table 2) (Eq. (12), Nagy, 1987, Table 4). The relatively low FMR values may result, at least in part, from the low basal metabolic rates reported for these species (Haim and Borut, 1981; Rubal et al., 1992; Weissenberg and Shkolnik, 1994; Kronfeld-Schor et al., 2000). The low ratios of FMR to RMR (Table 2) indicate that the energetic costs of living in excess of RMR are also relatively low in these mice (Nagy and Gruchacz, 1994).

There is no significant difference in the rate of water turnover (WTO) between *A. cahirinus* and *A. russatus*. WTO measured in the field was low, 77 and 86% in winter, 65 and 61% in summer, respectively (Table 3), of the expected for desert eutherians ($y = 0.145x^{0.954}$, where Y is water flux rate (in ml/day) and x is body mass (in g), Eq. (6), Nagy and Peterson, 1988), reflecting their specific mechanisms for conserving water in their natural habitat (e.g., Shkolnik and Borut, 1969; Shkolnik, 1971; Kam and Degen, 1991, 1993; Weissenberg and Shkolnik, 1994).

In sum, our results suggest that in terms of energy expenditure, diurnal activity in the desert may be more costly in summer, while nocturnal activity is more costly in winter. Golden spiny mice do not pay a greater price in water turnover than do common spiny mice. Their superior physiological adaptations (e.g. Shkolnik and Borut, 1969; Kam and Degen, 1993; Degen, 1994; Degen, 1997) coupled with behavioral adaptations (e.g., foraging only in the shade under and between boulders, Jones, personal comm., and in the cooler hours of the day, Shkolnik, 1971), enable them to be diurnally active even in summer, without paying a significant cost in water turnover.

Table 2

Measured and predicted field metabolic rate (FMR, Eq. (12), Nagy, 1987), the ratio between resting metabolic rate (RMR, from Rubal et al., 1992; Haim and Borut, 1981; Weissenberg and Shkolnik, 1994) and FMR, and the ratio between measured and predicted FMR in free-living spiny mice^a

Month	Species	FMR (kJ day ⁻¹) Measured	FMR (kJ day ⁻¹) Predicted	RMR FMR ⁻¹	FMR (%) Measured/predicted
February	<i>Acomys russatus</i>	37.97 ^a	68	0.47	55
	<i>Acomys cahirinus</i>	59.45	60	0.42	100
August	<i>Acomys russatus</i>	60.72	63	0.29	97
	<i>Acomys cahirinus</i>	34.4	49	0.72	70

^aSignificant difference between the two species in the same season ($p < 0.05$).

Table 3

Measured and predicted water flux (Eq. (6), Nagy and Peterson, 1988) in free-living spiny mice^a

Month	Species	Measured water flux (ml day ⁻¹)	Predicted water flux (ml day ⁻¹)
February	<i>Acomys russatus</i>	4.65	5.94
	<i>Acomys cahirinus</i>	4.3	5.01
August	<i>Acomys russatus</i>	3.52	5.36
	<i>Acomys cahirinus</i>	2.43	3.96

^aNo significant differences were found.

Understanding the physiological costs of nocturnal and diurnal activity is crucial for understanding the evolution and maintenance of temporal partitioning in this unique system, and may help us gain insight into the selective pressures involved in the evolution of activity patterns of small mammals in desert environments.

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