

Seasonal Thermogenic Acclimation of Diurnally and Nocturnally Active Desert Spiny Mice

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Accepted 10/28/99

ABSTRACT

Diurnally active golden spiny mice (*Acomys russatus*) and nocturnal common spiny mice (*Acomys cahirinus*) coexist in hot rocky deserts of Israel. Diurnal and nocturnal activities expose these species to different climatic conditions. Nonshivering thermogenesis (NST) capacity of individuals of both species immediately upon removal from the field exhibited seasonal changes, with no significant interspecific difference. Colony-reared mice of either species transferred in the laboratory from long to short photoperiod increased NST capacity, though to a lesser extent than observed in the seasonal acclimatization. The underlying biochemical mechanisms of short photoperiod acclimation differed between the species. In both Cytochrome c oxidase (Cox) activity was higher in short as compared to long photoperiod. In short-photoperiod-acclimated *A. cahirinus* uncoupling protein (UCP) content in brown adipose tissue (BAT) was significantly higher than in long photoperiod, while in *A. russatus* there was no significant change. In *A. russatus* there was a significant increase in lipoprotein lipase (LPL) activity in BAT in short-photoperiod-acclimated individuals, while in *A. cahirinus* LPL activity was high under both acclimations. The low LPL activity in brown adipose tissue of desert-adapted *A. russatus* may facilitate lipid uptake in white adipose

tissue, an advantage in desert conditions where food is scarce and irregularly distributed in space and time.

Introduction

Two ecologically similar species of the genus *Acomys* coexist in hot rocky desert habitats in the south of Israel—the common spiny mouse, *A. cahirinus*, and the golden spiny mouse, *A. russatus* (Degen et al. 1986; Kronfeld et al. 1996). *Acomys cahirinus* is nocturnal, whereas *A. russatus* is diurnally active, with a peak of activity during midday in winter and two peaks (in the morning and in the afternoon) during summer (Shkolnik 1971; Kronfeld et al. 1996; Kronfeld 1998). The fossil record for species from this desert region is poor, but our knowledge of the biogeographic history of the region (Tchernov 1988) suggests that the two species have coexisted for millennia. The diurnal activity pattern of *A. russatus* is a result of competitive displacement by its congener (Shkolnik 1971).

In the Judean Desert, where the two *Acomys* species coexist, their differing activity patterns expose them to different climatic conditions to which they must adapt (Elvert et al. 1999; see also Jaffe 1988). Ambient temperatures show marked differences between day and night, with minima just before sunrise and maxima during early afternoon. Air temperatures in a sample rock crevice (where spiny mice shelter during periods of inactivity) did not show daily variation and were higher than nocturnal ambient temperatures and lower than diurnal ambient temperatures (Elvert et al. 1999). Spiny mice were subject to a wealth of physiological studies, with a focus on their adaptations to summer in their hot and arid environment (e.g., Shkolnik and Borut 1969; Haim and Borut 1981; Kam and Degen 1993; Degen 1994). Their adaptations to winter, however, have not been studied.

Small mammals cope with the drop in ambient temperatures in winter mainly by increasing their capacity for nonshivering thermogenesis (NST; Feist and Rosenmann 1976; Heldmaier et al. 1990) through uncoupling respiration in brown adipose tissue (BAT; Foster and Frydman 1978; Cannon et al. 1982). In winter, most species studied increase their brown fat mass (e.g., Lynch 1973; Heldmaier et al. 1986), as well as their biochemical properties, as a response to a short photoperiod even without changes in ambient temperature (Lynch 1970; Haim and Fourie 1980; Heldmaier et al. 1981). The biochemical responses to winter conditions include (a) an increase in the

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relative mitochondrial content of the tissue, measured by Cytochrome-c oxidase (Cox) activity (e.g., Klaus et al. 1988); (b) an increase in the concentration of uncoupling protein (UCP) that dictates the capacity of the proton conductance pathway (Himms-Hagen 1984; Cannon and Nedergaard 1985; Trayhurn et al. 1987); (c) an increase in the total amount of UCP, which determines the thermogenic capacity of the whole tissue (Trayhurn and Milner 1989); and (d) increased activity of lipoprotein lipase (LPL), a key enzyme mediating the uptake of fatty acids from circulating lipid-rich lipoproteins by peripheral tissues (Braun and Severson 1992). Activation of LPL increases the lipolysis and utilization of circulating blood triglycerides for mitochondrial oxidation in brown fat (Heldmaier et al. 1981; Bartness and Goldman 1988; Klingenspor et al. 1989).

We studied the seasonal thermogenic acclimatization of wild-caught *A. cahirinus* and *A. russatus* and the role of photoperiod and the underlying biochemical mechanisms in acclimatized mice taken from zoo colonies. We measured NST capacity of individuals of both species within 24 h of their removal from the field and of short- and long-photoperiod-acclimated individuals in the laboratory. We also measured BAT mass, protein content, cell number, Cox activity, UCP content, and LPL activity in BAT in short- and long-photoperiod-acclimated individuals of both species.

Material 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).

A total of 48 individuals (six of each species at each season: February, representing winter; May, representing spring; August, representing summer; and November, representing fall) were trapped in the study site, weighed, and brought into the laboratory within 24 h for measurement of noradrenalin induced nonshivering thermogenesis (NA-NST). NST was measured during the day (before noon) in both species (both have nocturnal body temperature rhythms [Kronfeld 1998]) in a metabolic chamber. Ambient temperature (T_a) was 31°C for *Acomys russatus* and 28°C for *Acomys cahirinus*, just below the lower critical point of each species (as described in Böckler et al. 1982). Oxygen consumption ($\dot{V}O_2$ = resting metabolic rate, RMR) was recorded until it reached a steady state (minimum stable reading); NA was injected (1.5 mg/kg body mass), and the metabolic response was recorded for at least 30 min ($\dot{V}O_{2NA}$). O_2 consumption was measured in an open-circuit system (Depocas and Hart 1957; Hill 1972), using airflow of 480–600 mL/min. Chamber volume was 900 mL. NST capacity was calculated as the net increase in the metabolic rate caused by the NA injection (oxygen consumption following the injection minus oxygen consumption before the injection). Mice were released at the site of capture at the end of each measurement session.

Animals from the same area bred and raised in colonies at

Oranim and at the Meier Segal Garden for Zoological Research of Tel Aviv University were used in the laboratory experiments. The effect of photoperiod was tested on a total of 12 individual animals (six animals from each of the species, three males and three females) taken from the colony, housed in individual cages, and acclimated to long (16L : 8D) photoperiod ($T_a = 28^\circ\text{C}$). Each species was kept in a separate room. When kept separately under laboratory conditions, the two species are nocturnal (Rubal et al. 1992). After 21 d, the animals were weighed and tested for RMR and NA-NST as described previously. Immediately afterward, the photoperiod was changed to 8L : 16D (short photoperiod, with no change in ambient temperature), and the animals were weighed and tested for RMR and NA-NST after 7, 21, and 42 d.

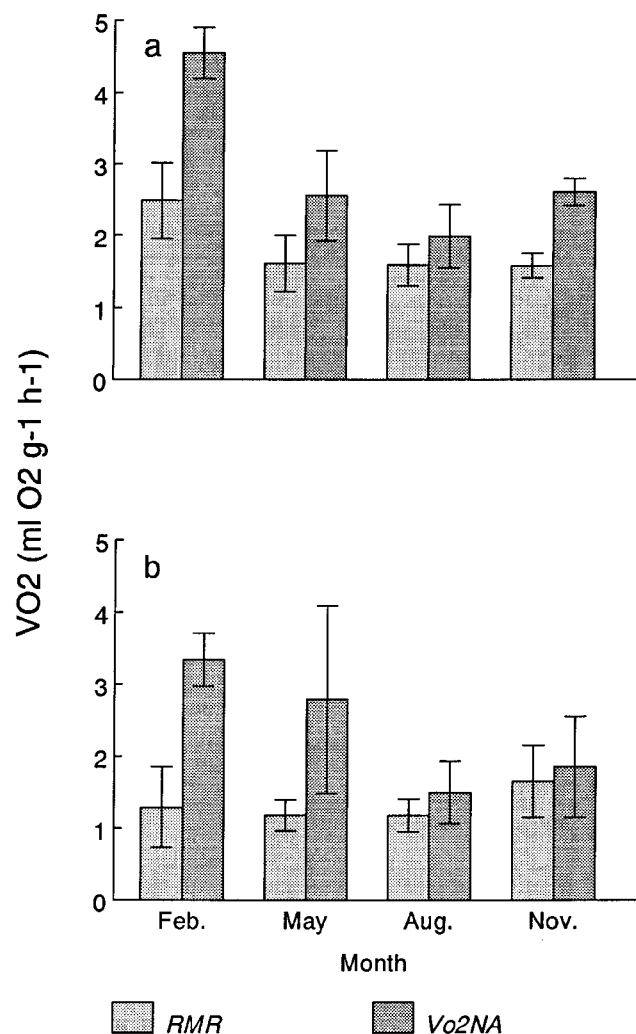


Figure 1. $\dot{V}O_2$ and $\dot{V}O_{2NA}$ (NA = induced oxygen consumption) of *Acomys cahirinus* (a) and *Acomys russatus* (b) during the different seasons of the year, measured immediately after capture at Ein Gedi ($n = 6$, mean \pm SE).

Twenty-four individual animals (12 individuals from each species) were taken from the colony at Oranim, housed in individual cages, and acclimated to long (16L : 8D, $n = 6$ for each species, three males and three females) or short (8L : 16D, $n = 6$ for each species, three males and three females) photoperiods ($T_a = 28^\circ\text{C}$ in both acclimations). Individuals of each species were kept in a separate room. After 3 wk, animals were weighed and then killed using CO_2 (since both species are nocturnal under these conditions, they were killed at the same time, 1000–1400 hours), and their total brown fat (interscapular, dorsal cervical, subscapular) was excised, weighed, and immediately frozen on dry ice. The tissue samples were stored at -70°C for further analysis. Before the assays, all tissue samples were ground to powder in liquid nitrogen.

Lipoprotein lipase (LPL) activity was assayed according to Klingenspor et al. (1989) and expressed as mU (=1 nmol oleate released per min). Cytochrome-c oxidase activity was measured polarographically in a Hansa Tech electrode (Bachhofer, Reutlingen) as described by Rafael (1983) and Rafael et al. (1985). Protein concentration in tissue homogenate was measured by the method of Bradford (1976). Due to the sensitivity of the assay, the sample preparation for the protein determination included a 20-fold dilution of the original tissue homogenate in phosphate buffered saline (PBS). Uncoupling protein 1 was immunodetected on a Western blot. Immunodetection of UCP1 was performed using enhanced chemiluminescence (Amersham Buchler). Total adipose tissue protein (10 μg per lane) was separated in a discontinuous SDS-polyacrylamide gel (3% stacking gel, 10% running gel) and blotted to a nitrocellulose membrane (Hybond C, Amersham Buchler). Rabbit anti-hamster UCP1 antibodies that were purified as described previously (Klingenspor et al. 1996) with a second antibody conjugated to peroxidase (ECL, Amersham; Ricquier et al. 1983) were used as primary antibodies. To check for the efficiency of protein transfer and for equal loading, gels and membranes were stained with Coomassie blue and Ponceau red. UCP concentration was expressed as relative units (RU), as

determined from densitometry readings (as in Klingenspor et al. 1996). DNA content, as an index of the cell number, was measured according to Labarca and Paigen (1980).

All results are given as mean \pm SE. The statistical significance of differences between groups was assessed by Student's t -test (two-tailed) and by one- or two-way ANOVA. Significance level was $P < 0.05$.

Results

Body mass (Bm) of field-trapped individuals did not show a significant seasonal change and was 33.4 ± 1.2 for *Acomys cahirinus* and 42.6 ± 1.7 for *Acomys russatus*. RMR of trapped individuals of both species measured in the laboratory did not show a significant seasonal change (one-way ANOVA, Fig. 1).

Nocturnal *A. cahirinus* and diurnal *A. russatus* showed very similar seasonality in their NST capacity in the field (Fig. 1). Their NST capacity in summer (August) was significantly lower than their NST in winter (February; $P < 0.01$; Table 1). *Acomys cahirinus* increased its NST capacity in winter by 170%, and *A. russatus* by 112%. There were no significant differences between the two species in NST capacity for the different seasons.

In both species, short photoperiod acclimation in the laboratory caused a significant (one-way ANOVA, $P < 0.05$) increase in NST capacity, which reached maximal level after 21 d (Fig. 2; Table 1). The maximal NST capacity as a result of short photoperiod acclimation was higher (but not significantly so) in *A. cahirinus* than that of *A. russatus* (Table 1).

Body mass of individuals of both species did not differ between the two photoperiod acclimations in the laboratory (Table 2). No effect of photoperiod on brown fat mass (as absolute value and also as percent of body mass) or in the lipid-free dry weight of the brown fat was detected in either species (Table 2). In both species there was no effect of photoperiod on BAT DNA (mg g^{-1} Bm) content (Table 2).

Both species responded to short photoperiod acclimation by an increase in BAT Cytochrome-c oxidase (Cox) activity. Cox

Table 1: Nonshivering themogenesis (NST) capacity ($\dot{V}\text{O}_2$, $\text{mL g}^{-1} \text{h}^{-1}$) of spiny mice in winter and summer immediately upon removal from the field and in long and short photoperiod in the laboratory

Spiny Mice	February	August	Photoperiod	
			Short	Long
<i>Acomys cahirinus</i>	$2.25 \pm .20^a$	$.32 \pm .10$	$1.86 \pm .11^a$	$.69 \pm .11$
<i>Acomys russatus</i>	$2.06 \pm .15^{a,b}$	$.45 \pm .08$	$1.36 \pm .16^a$	$.64 \pm .05$

Note. NST capacity calculated as the net increase in the metabolic rate caused by the noradrenalin (NA) injection. $n = 6$, mean \pm SE. There was no significant difference between the two species under the same conditions and in the same season ($P > 0.05$).

^a Significant difference from individuals of the same species in August ($P < 0.01$).

^b Significant difference between February and short photoperiod or August and long photoperiod of individuals of the same species ($P < 0.01$).

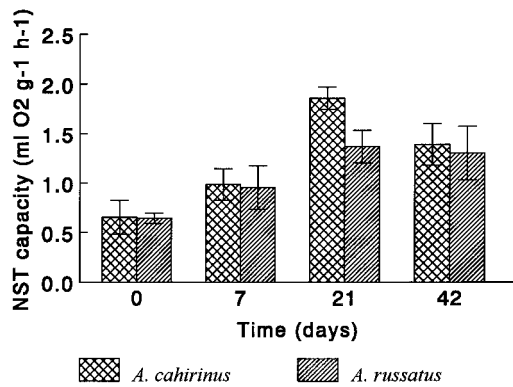


Figure 2. Mean NST capacity (mL O₂ g⁻¹ h⁻¹), calculated as the net increase in the metabolic rate caused by the NA injection, of *Acomys cahirinus* and *Acomys russatus* acclimated to long (0) photoperiod and 7, 21, and 42 d of short photoperiod ($n = 6$, $T_a = -28^\circ\text{C}$, mean \pm SE).

activity (U g⁻¹ Bm) was low in long photoperiod and increased by 100% in *A. cahirinus* and 52% in *A. russatus* after 3 wk acclimation to short day ($P < 0.05$; Table 2; Fig. 3).

In short photoperiod, *A. russatus* BAT LPL activity (mU Bm⁻¹, $P < 0.05$; mU g⁻¹ Bm, $P = 0.061$) was elevated 100% above the activity level in long photoperiod (Table 2; Fig. 3). *Acomys cahirinus*, however, showed no significant change in BAT LPL activity level between short and long photoperiods.

These animals maintained high LPL activity levels in both photoperiod acclimations (Table 2; Fig. 3).

In short photoperiod, *A. cahirinus* brown fat UCP content as measured by Western blot was elevated (50% U Bm⁻¹, 75% U g⁻¹ Bm, $P < 0.05$) above the level in long photoperiod (Table 2; Fig. 3). *Acomys russatus* showed no significant change in BAT UCP content between short and long photoperiods (Table 2; Fig. 3).

Discussion

Both spiny mouse species showed a very clear seasonality in NST capacity in the field. However, the NA-NST capacity during winter for these species is only 38% and 46% (for *Acomys cahirinus* and *Acomys russatus*, respectively) of that expected on the basis of an allometric relationship between body mass and NST based on rodents from cold climates (Heldmaier 1971). This is in accord with Saarela and Hissa (1993), who suggested that species living in warm-temperate climates exhibit only about 50% of the NST capacity expected for their body mass.

There were no significant differences in NST capacity between the species in any season, including winter. NST capacity mainly reflects the animal's potential of producing heat through uncoupled respiration, which is not necessarily realized at all times. Possibly *A. russatus* retains a relatively high NST capacity in anticipation of a few exceptionally cold days during winter. Moreover, in spite of their diurnal activity throughout their lifetimes, golden spiny mice retain nocturnal endogenous

Table 2: Effect of long and short photoperiod acclimation (21 d) in the laboratory on *Acomys cahirinus* and *Acomys russatus*

Photoperiod	<i>Acomys cahirinus</i> ($n = 6$)		<i>Acomys russatus</i> ($n = 6$)	
	Long	Short	Long	Short
Bm (g)	54.9 \pm 1.7	51.51 \pm 2 ^a	65.1 \pm 4.6	74.21 \pm 3.8
BAT (g)72 \pm .1	.62 \pm .07	.68 \pm .13	.76 \pm .21
RMR (mL O ₂ g ⁻¹ h ⁻¹)	1.2 \pm .07	1.3 \pm .09	1.5 \pm .3	1.3 \pm .06
NST capacity (mL O ₂ g ⁻¹ h ⁻¹)7 \pm .11 ^b	1.9 \pm .11 ^a	.6 \pm .05 ^b	1.4 \pm .16
LPL activity (U total BAT ⁻¹)74 \pm .19 ^a	.76 \pm .18	.21 \pm .02 ^b	.51 \pm .13
Cox activity (U total BAT ⁻¹)	29.4 \pm 8.4	57.1 \pm 9.2	46.5 \pm 3.7 ^b	77.5 \pm 11.3
Protein (mg mL ⁻¹)	49 \pm 11 ^a	53 \pm 4 ^a	83 \pm 8	77 \pm 9
UCP (RU total BAT ⁻¹)	56 \pm 12 ^b	83 \pm 12	66 \pm 7	50 \pm 11
Lipid-free dry weight (mg mL ⁻¹)	109.6 \pm 11.9	104.3 \pm 8.7	122.9 \pm 18.7	106.6 \pm 12.7
DNA (ng g ⁻¹ BAT)	170 \pm 36	219 \pm 20	242 \pm 38	246 \pm 41
DNA (ng g ⁻¹)	106 \pm 13	131 \pm 11	142 \pm 8	147 \pm 4

Note. Bm = body mass, BAT = brown adipose tissue mass, RMR = resting metabolic rate, NST = nonshivering thermogenesis capacity, LPL = lipoprotein lipase activity, Cox = Cytochrome-c oxidase activity, protein content, UCP = uncoupling protein content; mean \pm SE.

^a Significant difference from individuals of *A. russatus* acclimated to the same photoperiod.

^b Significant difference from individuals of the same species acclimated to short photoperiod.

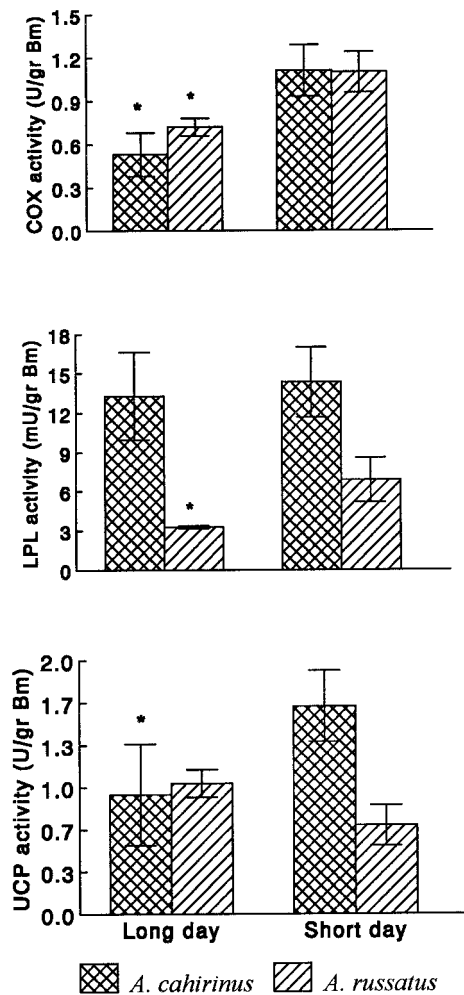


Figure 3. Cox activity ($U\ g^{-1}$ body mass), LPL activity ($RU\ g^{-1}$ body mass), and UCP content ($U\ g^{-1}$ body mass) of *Acomys cahirinus* and *Acomys russatus* acclimated to short (8L:16D) and long (16L:8D) photoperiod (21 d acclimation, $T_a = -28^\circ C$ in both acclimations). Asterisk represents significant difference ($P < 0.05$) from the same species acclimated to short photoperiod.

rhythms (Kronfeld 1998) and return to nocturnal activity in the absence of common spiny mice (Shkolnik 1971; Shargal 1997). Thus, it may be selectively advantageous to retain the high NST capacity appropriate for nocturnal activity.

An alternative hypothesis is that the NST capacity of golden spiny mice is evolutionarily constrained and reflects their past as nocturnally active mammals. The degree of NST capacity should be related to the most extreme cold conditions that an animal is expected to encounter. Since reaching maximal NST capacity requires at least several days (Heldmaier et al. 1981), it is crucial that animals will not be misled by warm spells within the cold period and reduce their NST capacity. Control

of NST capacity by day length obviates this problem. However, control by this cue also implies that an animal that has shifted to being active in a warmer environment but with the same day length may retain its original cold-adapted NST capacity for an extended period of time.

In the laboratory, NST capacity reached maximal values after 3 wk of acclimation to short photoperiod (Fig. 2). In *A. russatus*, however, these values remained significantly lower than those of mice captured in the field in February (Table 1). A similar but not significant trend was observed in *A. cahirinus* (Table 1). A possible explanation for this phenomenon may be that the seasonal acclimation of NST in these species occurs in response to a combined action of short photoperiod and other seasonal changes, such as cold or changes in diet. In most small mammals studied so far a combined exposure to short photoperiod as well as cold will induce maximum thermogenic acclimation, with photoperiod accounting for ca. 50% of the response (Heldmaier et al. 1989).

In both *Acomys* species there is no effect of photoperiod acclimation on brown fat mass, cell number, or protein content. This result is not surprising since the mice were fed ad lib., and brown fat mass reflects primarily the state of energy balance and the level of lipid stores (Steinlechner 1980; Rafael 1983; Trayhurn and Milner 1989).

The changes in Cox activity between short and long photoperiods indicate that both species increased the total respiratory capacity and the mitochondrial content of their total brown fat depot, as well as per unit mass of brown fat, in accord with the observed increase in NST capacity.

In short-photoperiod-acclimated *A. cahirinus*, UCP content in BAT was significantly higher than in long photoperiod, while in *A. russatus* there was no significant change. However, in *A. russatus* there was a significant increase in LPL activity in short photoperiod-acclimated individuals, while in *A. cahirinus* individuals such an effect was not observed, and LPL activity was high (not significantly different from LPL activity in short-photoperiod-acclimated *A. russatus*) under both acclimations.

LPL is distributed in different tissues, among them white adipose tissue (WAT) and BAT, and its activity can be regulated in a tissue-specific manner. This implies that fatty acid utilization can be monitored according to the metabolic demands of individual tissues so that the degradation of triacylglycerol-rich lipoproteins can be targeted to specific sites (Braun and Severson 1992). The significant increase in LPL activity in *A. russatus* suggests that it regulates NST capacity at the level of lipid uptake in BAT.

The intracellular lipid stores in BAT can only supply substrate for a few hours near maximum NST, and the BAT has to rely on substrate import for continued thermogenesis (Klingenspor et al. 1989). LPL is a key enzyme mediating the uptake of fatty acids from the circulation (Braun and Severson 1992) and is considered to be rate limiting for the delivery of triglyceride fatty acids to different tissues (Bessesen et al. 1995). In Djun-

garian hamsters, when body mass increases in spring, a combined decrease of LPL activity in BAT and the increase of LPL activity in WAT redirect circulating lipids from combustion by NST in BAT to storage in WAT (Klingenspor et al. 1993). Likewise, studies have consistently documented increased LPL activity in WAT and decreased LPL activity in BAT in obese rats relative to lean rats (Bertin et al. 1985; Bessesen et al. 1995). These data suggest that the metabolic partitioning of triglyceride fatty acids favors storage over oxidation in obese rats (Bessesen et al. 1995).

In our zoo colonies (Tel Aviv and Oranim), where both species are kept with food ad lib., we noticed a high occurrence of obesity in *A. russatus*, but not in *A. cahirinus*. The low values of LPL activity measured in *A. russatus* during long-photoperiod acclimation (in comparison with the values measured in *A. cahirinus*) and the obesity observed when fed ad lib. may suggest that in *A. russatus* the metabolic allocation of triglyceride fatty acids favors storage over combustion by NST in BAT, and this may have a selective advantage in desert ecosystems, where food is limited and the chances of becoming obese are extremely small. *Acomys russatus* occurs only in hot rocky deserts and has well-documented physiological adaptations to desert life (e.g., Shkolnik and Borut 1969; Degen et al. 1986; Kam and Degen 1993). *Acomys cahirinus* is found also in the Mediterranean region, ranging as far north as Turkey (Mendelssohn and Yom-Tov 1999), and while it can persist in rocky deserts, it is not primarily a desert mammal. In general it is not as adapted to desert life as *A. russatus*, and this difference in LPL activity probably reflects this fact.

In sum, while NST capacity of both species increases in winter (and short photoperiod), no interspecific differences were found. This implies that *A. russatus* retain the ability to be active under similar cold conditions, as do *A. cahirinus*, possibly due to an evolutionary constraint. It appears that the two species regulate their NST capacity at different levels. The low LPL level in BAT of *A. russatus* may facilitate lipid uptake in WAT, an advantage in desert conditions where food is scarce and irregularly distributed in space and time.

Acknowledgments

We thank A. Landsman for his cheerful help in the field; the Ein Gedi Field School of the Society for the Protection of Nature in Israel for their warm hospitality and help; the Nature Reserves Authority for their helpful cooperation; I. Coshniak for being so generous with his equipment and advice; A. Shkolnik for his help and support in every stage of this research; The Meier Segal Garden for Zoological Research at Tel Aviv University for the maintenance of a captive spiny mouse colony; H. Kosik for the maintenance of a spiny mouse colony at Oranim; and T. H. Kunz, A. Shkolnik, D. Simberloff, and three anonymous reviewers for their comments on an earlier draft

of this manuscript. This research was supported by the German-Israeli Foundation for Scientific Research and Development grant I-264-203.11/92.

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