

Comparative physiology of heat production in rodents under increasing salinity : The effects of habits and habitat

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ABSTRACT. Small mammals inhabiting environments that are either seasonally or perpetually dry, such as Mediterranean or desert ecosystems respectively, commonly have physiological capabilities that enable them to deal with water shortage. We compared results of thermoregulatory responses of rodent species inhabiting different habitats and having varying activity periods, when salinity increases in their water source, as often occurs in their natural habitats during the dry period.

Experimental animals were maintained on a diet of dry soy-beans and an increased salinity of their water source (2% agar gel), from 0.9% to 3.5% NaCl in mesic species and up to 7% in xeric species. While desert species could cope with high salinities in their water source, mesic species could not. Desert-adapted species depending on their preferred micro-habitats differ in their thermoregulatory responses. Rock dwellers, such as the golden spiny mouse *Acomys rus-satus* and the bushy tailed gerbil *Sekeetamys calurus*, reduce their resting metabolic rates (RMR) and increase nonshivering thermogenesis (NST) capacity in response to increasing salinity. In contrast, the deep burrowing fat jird *Meriones crassus*, increases RMR and only slightly increases NST-capacity.

Our study suggests that species occupying different habitats vary their thermoregulatory capabilities, in relation to dehydration and increasing salinity in the water source. This may be a consequence of adaptation from the original ecosystem to the current environment in which a species inhabits.

KEY WORDS : Nonshivering thermogenesis, resting metabolic rate, aridity, thermoregulation, kidney function

INTRODUCTION

Small mammals must find their food and water resources in their immediate surroundings. Therefore, they can be used as indicators of habitat quality. Israel, being a transition zone for biogeographically different regions (TCHERNOV & YOM-TOV, 1988), inhabits rodent species of different evolutionary origins. Furthermore, the landscape changes in relation to precipitation and altitude, from a sub-alpine ecosystem on Mount Hermon, through the Mediterranean and steppe ecosystems and finally to the extreme arid ecosystem. Rodent species show different distribution patterns, ranging from the occupation of a single ecosystem as the golden spiny mouse *Acomys russatus* (arid ecosystem), through to species with wide distributional ranges as in the case of the common spiny mouse *A. cahirinus* (arid, steppe and Mediterranean ecosystems).

A comparison of physiological variables, such as water economy and heat production, between different species from disparate environments, or divergent populations within the same species from distinct habitats, is of significant importance for the understanding of adaptation to the environment. Studies (SCHMIDT-NILSEN, 1964; SHKOLNIK & BORUT, 1969; WEISSENBERG & SHKOLNIK, 1994) have demonstrated that efficient water economy can be examined through the ability of the kidney to produce a

concentrated urine, and efficient heat economy is typified by resting metabolic rates (RMR) that are lower than the expected from body mass, according to allometric equations (KLEIBER, 1961; HART, 1971; HAIM & BORUT, 1981; HAIM, 1987; HAIM & IZHAKI, 1993). The relative medullary thickness (RMT) is an anatomical variable that can be used for predicting kidney function (SPERBER, 1944; SHKOLNIK, 1988; WEISSENBERG & SHKOLNIK, 1994). Therefore, it is expected that species with high RMT indices will be able to increase their urine concentration during spells of drought that lead to increased salinity of water sources.

Deserts can be cold at nights, and endotherms such as rodents that possess low RMR's have to increase heat production over a short period to maintain their body temperature (HAIM & LEVI, 1990). Nonshivering thermogenesis (NST) is an important mechanism for heat production in small mammals such as rodents (JANSKY, 1973). Furthermore, this mechanism has been found to compensate for the lower RMR values in species like desert rodents (HAIM & IZHAKI, 1993).

The objectives of this study were to compare the thermoregulatory responses of different rodent species subjected to osmolarity challenges. Specifically, to examine : (1) If such a challenge will have an impact on heat production, by means of NST? (2) If NST values can be related to the pattern of activity and habitat? This paper

compares five different species of rodents, some of an African origin, that occur in Israel, while others are of a Palearctic origin but occur also in Africa.

MATERIAL AND METHODS

Animals

Data were collected on the following rodents: Common spiny mouse (*Acomys cahirinus*), Golden spiny mouse (*Acomys russatus*), Bushy tailed gerbil (*Sekeetamys calurus*), Fat jird (*Meriones crassus*), Tristram's jird (*Meriones tristrami*) (Table 1). In all instances the experimental animals were fed crude soybeans that were dried for 48h at 60°C to a constant weight. Water was supplied in the form of 2% agar gel (20g of dry agar dissolved in 1000ml of de-ionized water) to which desired salinity levels were achieved by dissolving appropriate amounts of NaCl. Body mass was measured every second day, during the acclimation periods. When a loss of more than 20% in body mass was recorded, the experimental individual was removed from the experiment. Following each acclimation period (14 days) to a given salt concentration, urine volume, urine osmolarity and nonshivering thermogenesis (NST) variables were measured.

TABLE 1

Characteristics of the studied species, data are taken from HARRISON & BATES (1991).

Species	Region	Habitat	Activity
<i>A. russatus</i>	Xeric	Rock dweller	Diurnal
<i>A. cahirinus</i>	Mesic	Rock dweller	Nocturnal
<i>S. calurus</i>	Xeric	Rock dweller,	Nocturnal
<i>M. crassus</i>	Xeric	Burrow	Nocturnal
<i>M. tristrami</i>	Mesic	Burrow	Nocturnal

Urine collection and variables analysis

For each level of salinity, the animal was placed in a mesh net cage (19.5 x 11.5 x 9cm) above a sheet of Parafilm for a period of 24h. Urine was collected with a Pasteur pipette and subsequently placed into Eppendorf tubes and stored at 4°C every 6h. Urine volume was measured using a Gilson pipette to the accuracy of 1µl. Urine Osmolarity was measured using a Wescor 5500 Vapor Pressure Osmometer (PALGI & HAIM, 2003).

NST variables

Oxygen consumption (VO_2) was measured using an open flow system (DEPOCAS & HART, 1957). The air was pumped into the metabolic chamber using a pump (Aqua-Serene). Oxygen concentrations were measured from the air exiting the metabolic chamber using, an oxygen analyzer (Servomex 750A) connected to a multimeter (Tabor). The air was dried with a silica-gel column at the entrance and exit ports of the metabolic chamber.

Resting metabolic rate (RMR) was measured for each species as the minimal oxygen consumption (VO_{2Min}) at 1°C below its lower critical temperature. Body temperature (T_b Min) was measured at the end of VO_{2Min} measurements, by inserting a copper-constantan thermocouple 3cm deep into the rectum of the experimental individual. The thermocouple was connected to a TH-65 Wescor digital thermometer.

VO_{2NA} was measured as the maximal response of VO_2 to a noradrenalin (NA) injection (Sigma) 1.5mg/Kg (HELDMAIER, 1972; HAIM et al., 1995). Approximately 20min. after VO_{2NA} values were achieved and VO_2 levels started to decline, the experimental individual was removed from the metabolic chamber and its body temperature was measured once again and presented as T_{bNA} . NST-capacity was calculated as the ratio of VO_{2NA} to VO_2 Min (RON & HAIM, 2001; SCANTLEBURY et al., 2002).

Statistics: All values are given as mean \pm SD for $n = 7$. Results showed a normal distribution and therefore Student *t-test* was used for statistical analysis.

RESULTS

A marked difference was noted between species from mesic and xeric habitats. The xeric species comprising *S. calurus*, *A. russatus* and *M. crassus*, survived on agar with a 7% salinity, whereas the mesic species *M. tristrami* and *A. cahirinus* were only able to withstand 3.5% (Table 2). *Meriones crassus* showed the lowest drop of body mass (10.1%) when acclimated to 7% salinity (Table 2). The highest osmolarity values in urine were recorded in *A. russatus* and *M. crassus* (Table 3), and among the desert species the lowest values were found in *S. calurus*.

TABLE 2

The response of body mass to increased salinity in the water source of dehydrated individuals, of different studied rodent species. Values presented as total body mass (gr) for 0.9%; 3.5% (mesic species) and 7% (xeric species) salinity of the water source and as the % difference between salinities. Data for *A. russatus* is from RON & HAIM (2001); for *A. cahirinus* from SHANAS et al. (2003); for *S. calurus* from PALGI & HAIM (2003); for *M. Crassus*, from HAIM (UNPUBLISHED) and for *M. tristrami*, from NEUMAN et al. (2000).

Species	Salinity (%)	Wb (gr)	Wb (%)
<i>A. russatus</i>	0.9	50.4	± 6
	7	39.0	± 8.2
<i>A. cahirinus</i>	0.9	43.1	± 7
	3.5	34.7	± 7.6
<i>S. calurus</i>	0.9	59.7	± 9.2
	7	48.9	± 5.5
<i>M. crassus</i>	0.9	100.1	± 15.8
	7	90.0	± 9.3
<i>M. tristrami</i>	0.9	79.2	± 8.3
	3.5	65.2	± 7.9

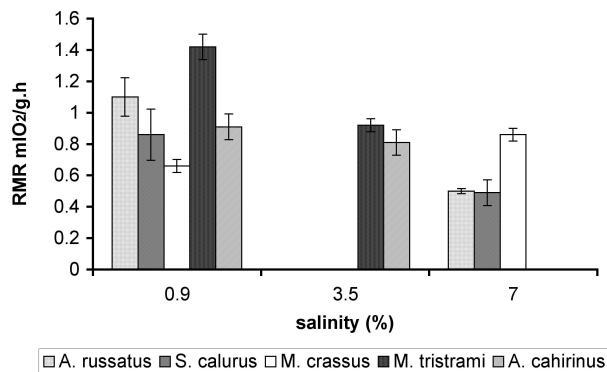


Fig. 1. – Resting metabolic rates RMR (mlO₂/g.h) of each studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data for *A. russatus* RON & HAIM (2001); data for *S. calurus* PALGI & HAIM (2003); data for *M. crassus* HAIM (UNPUBLISHED); for *M. tristrami* NEUMAN et al. (2000) and data for *A. cahirinus* SCANTLEBURY et al. (2002).

Apart from *M. crassus*, the RMR of all species showed a decrease as the salinity of the water increased (Fig. 1). The VO₂ response to NA increased significantly ($P < 0.01$) only in *M. crassus*, when the salinity in the water source was increased (Fig. 2). NST-capacity increased significantly ($P < 0.001$) with the rise in salinity only in *A. russatus* and in *S. calurus* (Fig. 3). T_b Min values generally decreased in all species, apart from *S. calurus* ($P < 0.05$ for *M. crassus* and $P < 0.01$ for *A. russatus*) as a response to the increase in salinity (Table. 3). The sharpest decrease (1.5°C) was observed in *A. russatus* and the lowest decrease (0.6°C) in *M. crassus* and in *M. tristrami*. The lowest T_b Min values were measured for *A. russatus* (34.8°C) under a salinity of 7% of the water source. The highest increase of T_b NA as a response to increase in salinity was observed in *M. crassus*, (1.5°C) while in some of the studied species as in *A. cahirinus* T_b NA val-

ues decreased (1.7°C) with the increase of salinity in the water source (Table 3).

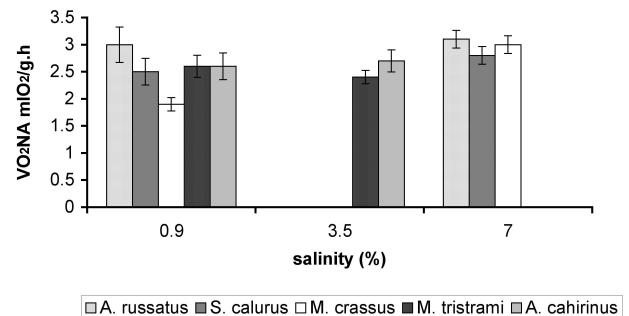


Fig. 2. – The maximal VO₂ (mlO₂/g.h) response to noradrenalin injection (VO₂NA) of each studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data sources are as in Fig. 1.

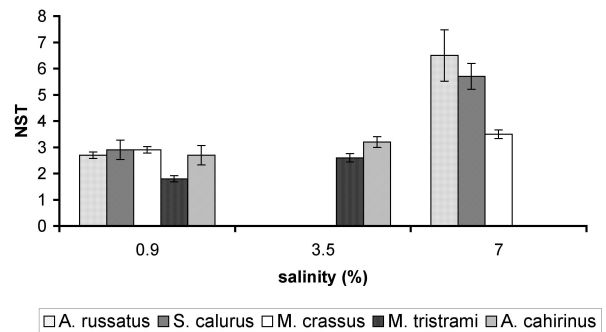


Fig. 3. – Nonshivering thermogenesis NST-capacity (VO₂NA/RMR) of the studied species under control conditions (0.9% salinity of the water source) and of maximal salinity (3.5% for mesic species and 7% for the xeric ones). Data sources are as in Fig. 1.

TABLE 3

Minimal body temperature (T_b Min) and the maximal body temperature response to a noradrenalin injection (T_b NA), maximal urine concentration of each species at control and in maximal salinity of the water source. RMT relative medullary thickness. Values for T_b are taken from RON & HAIM (2001) for *A. russatus*; from SCANTLEBURY et al. (2002) and SHANAS et al. (2003) for *A. cahirinus*; from PALGI & HAIM (2003) for *S. calurus*; from HAIM (UNPUBLISHED) for *M. crassus* and from NEUMAN et al. (2000) for *M. tristrami*. RMT values for *A. cahirinus* are taken from WEISSENBERG & SHKOLNIK (1994) for all other species values are taken from BROSH (1971).

Species	Salinity (%)	T_b Min	T_b NA	Osmolarity	RMT*
<i>A. russatus</i>	0.9	36.3±0.3	38.2±0.8	5353±725	11.4
	7	34.8±1.1	37.8±1.3	9123±3292	
<i>A. cahirinus</i>	0.9	36.7±0.8	37.5±0.3	3006±485	9.3
	3.5	35.0±0.9	35.8±0.7	3389±623	
<i>S. calurus</i>	0.9	37.3±0.2	39.6±0.9	3197±1167	9.03
	7	37.4±0.6	39.7±0.7	7091±1729	
<i>M. crassus</i>	0.9	35.8±0.5	36.8±0.7	2450±830	10.3
	7	35.2±0.3	38.3±0.3	9642±2066	
<i>M. tristrami</i>	0.9	36.8±0.6	38.0±0.5	1500±120	8.2
	7	36.2±0.5	37.7±0.4	3210±523	

* Values are taken from BROSH, 1971; for *A. cahirinus* from WEISSENBERG & SHKOLNIK, 1994.

DISCUSSION

Many desert rodent species show low RMR values (DEGEN, 1997). This physiological trait enables them to conserve water and to keep a balanced heat exchange. In addition, for species that do not engage in reproduction annually as a result of the harsh unpredictable desert conditions, lower RMR values could result as an adaptive longevity trait (HAIM, 1987; HAIM & IZHAKI, 1993). However, in deserts, nights can be cool even during summer. Therefore, increased NST is an important and efficient mechanism for heat production and thermoregulation in a cold environment (HAIM & LEVI, 1990). It was also noted that acclimation to heat or dehydration increases NST-capacity (Fig. 3), compared with control groups at 0.9% salinity (HOROWITZ & SAMUELOFF, 1989; YAHATA et al., 1999; RON & HAIM, 2001).

We show that rock dwelling, desert rodent species such as, *A. russatus* and *S. calurus* can further decrease their RMR values (RON & HAIM, 2001; PALGI & HAIM, 2003), in response to increasing salinity (of dehydrated individuals). In contrast, the soil form burrow dwelling *M. crassus*, a desert adapted species (HAIM & TCHERNOV, 1974), did not reduce its RMR under the same conditions (Fig. 1). As the thermal refuge for rock dwellers is less efficient than a deep burrow (HAIM et al., 1998), it is proposed that the difference in habitat may play an important role in the thermoregulatory response to dehydration. A decrease in RMR values was noted also in the two mesic species at 3.5% salinity, but these RMR values are much higher than those of the rock dwelling desert adapted species at 7% salinity and are close to those of *M. crassus* at 7% salinity (Fig. 1).

The absence of a significant change in VO_2NA , apart from the increase observed in *M. crassus*, suggests that although the response to increased salinity is a reduction in RMR, it seems to have no effect on the response to noradrenalin (Fig. 2). These results tend to suggest that the number and sensitivity of the adrenalin receptors in the brown adipose tissues (BAT) do not change under the current conditions of dehydration, as was suggested by REDLIN et al. (1992) for the difference in thermogenic capacity of juvenile rats.

Food consumption (apparent digestible dry matter intake – ADDMI – and digestible energy) responds to photoperiodic manipulations (HAIM & LEVI, 1990). Yet, the observation that VO_2NA increases in *M. crassus* as a result of dehydration may indicate that decreased food quality, increases the number or affinity of the adrenergic receptors in this species. In addition to a secure thermal refuge, *M. crassus* has an efficient kidney and among the tested desert species, has the highest ability to concentrate its urine at 7% salinity (Table 2). This finding supports the kidney anatomy where the relative medullary thickness (RMT) is high (10.3, BROSH, 1971).

In *S. calurus*, T_bMin does not decrease in response to an increase in salinity. Body temperature is the outcome of two opposite physiological processes, namely heat production and heat dissipation. In *S. calurus* heat production (as reflected by VO_2) decreases and has the same value as *A. russatus*. Yet, in *A. russatus* T_bMin drops at 7% salinity by 1.5°C. This drop of T_bMin (Table 2) may be a direct

result of the decrease in heat production with or without any change in heat dissipation. In *S. calurus* the decrease in heat production with the increase in salinity is accompanied by a decrease in heat dissipation and as a result T_bMin does not decrease. However, in the case of *M. crassus*, T_bMin decreased by 0.6°C although heat production increased. Therefore, it is suggested that in *M. crassus*, the desert burrow dwelling species, heat dissipation increases with the increasing of salinity.

As both spiny mice are rock dwellers with a poor thermal refuge that use evaporative mechanism for heat dissipation (SHKOLNIK & BORUT, 1969; WEISSENBERG & SHKOLNIK, 1994), the decrease in T_bMin is assumed to be an important contribution for thermoregulation, as it conserves water. In contrast, the bushy tailed gerbil *S. calurus*, shows the same distribution pattern as *A. russatus* and the same habitat, but is nocturnal and digs shallow burrows, which may be used as a thermal refuge (HARRISON & BATES, 1991; PALGI & HAIM, 2003). Under such conditions, it can maintain its T_bMin values even under dehydration conditions, whereas the diurnal *A. russatus* low T_b values, will enable it to forage for longer periods under the hot conditions during day time in its habitat (HAIM et al., 1998).

In conclusion, the results of our study indicate that thermoregulatory mechanisms in different rodent species, respond differently to dehydration caused by a high protein diet and increasing salinity of the water source. Desert species can tolerate higher salinity values, twice those tolerated by mesic species. Thermoregulatory response varies between the different species and is affected by the time of activity (habits) and by the species habitat. The spiny mice of the genus *Acomys* are dependent on their kidneys for survival in the desert since they have a poor thermal refuge and use water for evaporative cooling. This latter phenomenon may indicate that the origin of this genus is from an environment where water was not limited. Therefore, when facing water shortage in xeric environments, spiny mice decrease their T_bMin values and as consequence conserve water.

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