

Differential osmoregulatory capabilities of common spiny mice (*Acomys cahirinus*) from adjacent microhabitats

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Abstract

The osmoregulatory function of common spiny mice *Acomys cahirinus* living on opposite slopes of the lower Nahal Oren ('Evolution Canyon') on mount Carmel, Israel, was investigated by increasing the salinity of the water source whilst maintaining a high-protein diet. The southern-facing slope (SFS) of this canyon differs from the northern-facing slope (NFS) as it receives considerably more solar radiation and consequently forms a more xeric, sparsely vegetated habitat. During the summer, mice living on the two opposite slopes significantly differed in their urine osmolality, which also increased significantly as dietary salinity increased. Offspring of wild-captured mice, born in captivity, and examined during the winter, continued to show a difference in osmoregulatory function depending on the slope of origin. However, they differed from wild-captured mice, as they did not respond to the increase in dietary salinity by increasing the concentration of their urine, but rather by increasing the volume of urine produced. This study shows that *A. cahirinus* occupying different microhabitats may exhibit differences in their ability to concentrate urine and thus in their ability to withstand xeric conditions. We suggest that they may also differ genetically, as offspring from the NFS and SFS retain physiological differences, but further studies will be needed to confirm this hypothesis.

Key words: ecophysiology, evolution, kidney, rodents, seasonality, *Acomys cahirinus*

INTRODUCTION

Species living in the Mediterranean ecosystem are often challenged by long periods of heat that are usually accompanied by high evaporative conditions. As all organisms depend on water for their survival, these environmental conditions impose certain physiological constraints. Conditions may be especially challenging for animals that live in the more xeric regions of this ecosystem (Degen, 1997). Within mammals, rodents are particularly susceptible to a high evaporative water loss because of their small body size and large surface area to volume ratio. Hence, they have developed mechanisms of decreasing water loss through a combination of behavioural and physiological means (Schmidt-Nielsen, 1964; Peinke & Brown, 1999). For example, they may conserve water by discharging concentrated urine, whilst gaining as much metabolic water and pre-formed water from their diet (Peinke & Brown, 1999).

MacMillen (1983) investigated the ecological significance of this mechanism on several rodent species and found that urine concentration was negatively correlated with mean annual rainfall. Thus, this trait may be used to convey the effects of environmental conditions,

and to shed light on the dynamic evolution of rodent species in this ecosystem. Several examples show how this trait differs among closely related rodent species, which occupy different ecological niches. Shkolnik & Borut (1969) compared golden spiny mice *Acomys russatus* with common spiny mice *A. cahirinus*. They found that the diurnal *A. russatus* exhibits superior capacities to concentrate urine than its close relative the nocturnal *A. cahirinus*. Similarly, Goyal *et al.* (1988) compared the osmoregulation of two Indian desert gerbil species, and found that urine osmolality of the diurnal *Tatera indica* was much higher than that of the nocturnal *Meriones hurrianae*. Interspecific studies, however, are limited in their predictive power of the environmental effects on physiology, because observed differences can always be attributable to phylogeny. Intraspecific differences, although harder to measure because of reduced variability, provide clearer indications of the cause and function of variations in physiology (Bartholomew, 1987). Weissenberg & Shkolnik (1994) studied two populations of *A. cahirinus*, one from the desert and one from a Mediterranean ecosystem. They found that the desert-living population had lower resting metabolic rate (RMR) values, water turnover rates, and were able to form more concentrated urine than the Mediterranean living population. Similarly, Haim, Plaut & Zobodat (1996) compared two populations

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of broad-toothed mouse *Apodemus mystacinus* from a Mediterranean ecosystem (Mount Carmel, Israel) and from a sub-alpine system (Mount Hermon). They found differences in the kidney morphology (relative medullary thickness, RMT) between the two populations, suggesting that mice from Mediterranean Mount Carmel had a superior ability to concentrate urine than those from sub-alpine Mount Hermon.

Whilst previous intraspecific studies compared physiological differences between populations of rodents from different biogeographical ecosystems, a more sensitive design would be to compare individuals of the same species within the same ecosystem, or to compare individuals of the same species from the same locality but from different microhabitats. The 'Evolution Canyon' (Nevo, 1995, 1997) provides an opportunity for such a study. This canyon (lower Nahal Oren) breaks through the Carmel Mountain from east to west. Like many other canyons in the Mediterranean region, it has a south-facing slope (SFS) that receives considerably more solar radiation than the north-facing slope (NFS). Consequently, the SFS forms a more xeric, sparsely vegetated habitat than the closely located (200–500 m apart) and often forested NFS (Nevo, 1995).

The common spiny mouse *A. cahirinus* inhabits large areas of arid and semi-arid parts of the east Mediterranean region, and can be found in a wide variety of habitats, such as dry deserts close to human activity, as well as in cooler and more mesic places such as forests. These habitats are usually devoid of free accessible water thus *A. cahirinus* meet their water needs from preformed water in their food and from metabolized water (Mendelssohn & Yom-Tov, 1999). Desert-living common spiny mice have lower RMR and water turnover rates and are able to form more concentrated urine than their mesic counterparts (Weisenberg & Shkolnik, 1994). The common spiny mouse is found also on both the NFS and the SFS of the lower Nahal Oren (Blaustein, Kotler & Nevo, 1996). It was previously found that SFS mice have, similarly to their desert counterparts, a lower metabolic rate (Scantlebury *et al.*, 2002) and lower daily energy expenditure but not lower water turnover rate (Scantlebury *et al.*, 2003).

Because of the high evaporative conditions existing on the SFS, we hypothesize that SFS and NFS spiny mice may differ in their osmoregulatory capabilities and that the SFS mice will show increased capacity to conserve water and to deal with increased salinity in their diet compared with NFS mice. During the dry season, the vegetation in the Mediterranean ecosystem is expected to have an increased particle (or osmotic) concentration owing to higher evaporation of water (Main, 1986; Haim & Izhaki, 1994; Grammatikopoulos, 1999). Therefore, animals such as *A. cahirinus*, which may depend upon vegetation as a water source, face an increasing osmotic load as the dry season progresses. This effect is likely to be more marked on the SFS than the NFS. Thus to examine kidney function and the capacity to excrete the excess salt, animals may be challenged to drink saline solutions (MacMillen, 1983; Ron & Haim, 2001). The ability of rodents to concentrate urine has been used extensively as a measure for water

regulation efficiency (Schmidt-Nielsen, 1964; MacMillen, 1983; Weissenberg & Shkolnik, 1994).

The aims of this study were to test the above hypothesis by comparing the kidney function of SFS mice with NFS mice from the lower Nahal Oren, kept on a high protein diet, under increasing dietary salt intake, as measured by differences in the volume, osmolality, and particulates in the urine. The high protein diet forced the animals to consume increased amounts of the salty water that were necessary for the excretion of the toxic protein breakdown products. Furthermore, we aimed to test whether differences between individuals from the two slopes were retained in their offspring born in captivity.

METHODS AND MATERIAL

Animals

Founders

Mice were trapped on the SFS ($n = 20$) and NFS ($n = 21$) of Nahal Oren, on Mount Carmel, Israel ($32^{\circ}43'E$, $34^{\circ}58'N$), using Sherman live traps during June 1999. They were taken to the Department of Biology, University of Haifa-Oranim, and placed in individual cages ($c. 35 \times 25 \times 15$ cm) with sawdust as bedding. Cages were kept roofed outdoors, and exposed to ambient conditions during the summer ($c. 14L:10D$, min/max $28/37^{\circ}C$, 75% relative humidity (RH), 1999), and throughout the winter ($c. 10L:14D$, min/max $10/21^{\circ}C$, 68% RH, 1999–2000). Mice were offered rat chow and carrots when they were not undergoing experimentation, and with dry soybeans (42% protein) and 2% agar gel (20 g of dry agar dissolved in 1000 ml of de-ionized water), that provided the drinking water, during the experimentation periods, including the preceding acclimation period. Mice were observed for at least 2 weeks before acclimation periods (see below) to establish whether the females were pregnant. Only males and non-pregnant females were used. In both groups a similar proportion of males and females were studied. Experiments on founders were carried out in both summer and winter.

Offspring

Separate colonies of SFS and NFS mice were formed from the founder mice. Newborn mice were placed in sex-specific cages after weaning. Before the experiment (winter 2000–01) the mice were transferred into individual cages under the same conditions detailed above. Offspring were only tested during the winter.

Salinity changes

To simulate changes in osmotic load experienced in the wild, animals were exposed to increasing levels of salinity in their water source by dissolving NaCl into the agar.

The salt concentration was increased from 0.9% to 2.5% and 3.5% during the summer. Acclimation to each level of salinity lasted for at least 2 weeks. Since founders were not able to pass 2.5% salinity in the winter owing to loss of body mass (animals that lost 20% of their body mass were removed from the experiment), the salt concentrations of the agar that was offered to offspring were increased more gradually than in founders: 0.9%, 1.8% and 2.5%.

Urine collection

After 2 weeks of acclimation to a specific salinity, mice were transferred to metabolic cages (19.5 × 11.5 × 9 cm) with mesh floors above sheets of Parafilm for 24 h. They were provided with *ad libitum* soybeans and salty agar gel. Every 4 h the urine was collected from the Parafilm with a Pasteur pipette and stored in Eppendorf tubes below 4 °C until analysis.

Urine volume, osmolality, electrolytes and urea analysis

Within 24 h of collection, urine volume was measured ($\pm 1 \mu\text{l}$, Pipetman, Gilson), and the osmolality was determined by using a vapour pressure osmometer (Wescor 5500). Urine volume was normalized by dividing it with body mass. Sodium and potassium concentrations were determined within 2 weeks using a flame photometer (Sherwood 410). Chloride concentrations were determined by titration on a chloride analyser (Corning 925). Urea concentrations were determined using a commercial test kit (Sigma 640) on a spectrophotometer (Milton Roy Spectronic 401).

Statistics

The data were not normally distributed even after transforming. Therefore data were analysed by a non-parametric test for 2-way ANOVA, the Scheirer–Ray–Hare extension for Kruskal–Wallis test (Sokal & Rohlf, 1995). This test requires equal sample sizes so for uniformity, 6 datum points were randomly chosen for each salinity in the summer and winter, and 7 datum points for each salinity in the offspring group. ANOVA was run on Statview software for Macintosh, and the P values of H (SS/Ms total) were determined using a χ^2 table.

RESULTS

Urine volume

Founders

During the summer, a significant difference in the urine volume was found between north and south facing slopes ($H = 17.34$, $P < 0.001$). No significant difference was found among the different diet salinities ($H = 0.76$,

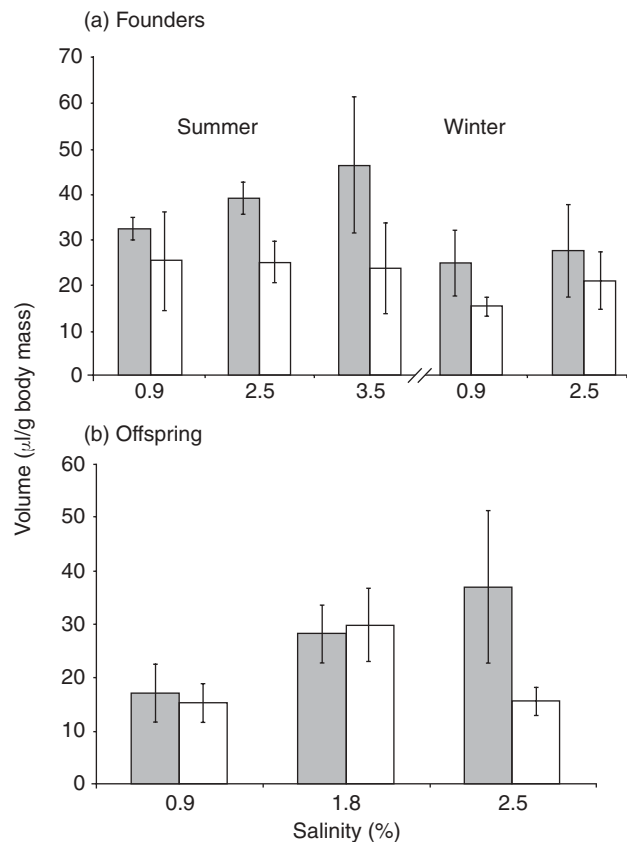


Fig. 1. The urine volume ($\mu\text{l/g}$ body weight \pm SE) of SFS (\square) and NFS (\blacksquare) *Acomys cahirinus* during summer and winter at different salinities.

$P > 0.05$). However, it seems (Fig. 1a) that the urine volume of NFS mice increases as the salinity increases. During the winter no difference was found between slopes ($H = 1.01$, $P > 0.05$) or among salinities ($H = 0.07$, $P > 0.05$). The mass of the animals decreased in the summer from 45.17 to 40.23 to 35.74 g in SFS mice and from 47.55 to 47.13 to 40.79 g in NFS mice owing to increasing salinity acclimations. In the winter, the mass decreased from 49.49 to 45.22 g in SFS, and from 52.82 to 49.12 g in NFS.

Offspring

The urine volume of NFS mice was significantly higher than the volume of SFS mice ($H = 5.65$, $P < 0.05$). Salinity had a significant effect on the urine volume ($H = 23.48$, $P < 0.001$). In NFS mice, urine volume increased along with the increased diet salinity, while in SFS mice it increased from 0.9% to 1.8% and then decreased at 2.5%. The statistical difference in volume is mainly caused by the decreased volume in SFS at 2.5% (Fig. 1b). Unlike founders, the mass of offspring did not show a decreasing trend with the increased diet salinity. Average mass in SFS offspring varied from 50.32 to 53.59 to 52.68 g, and in NFS offspring from 43.43 to 46.15 to 44.91 g with the increased diet salinity.

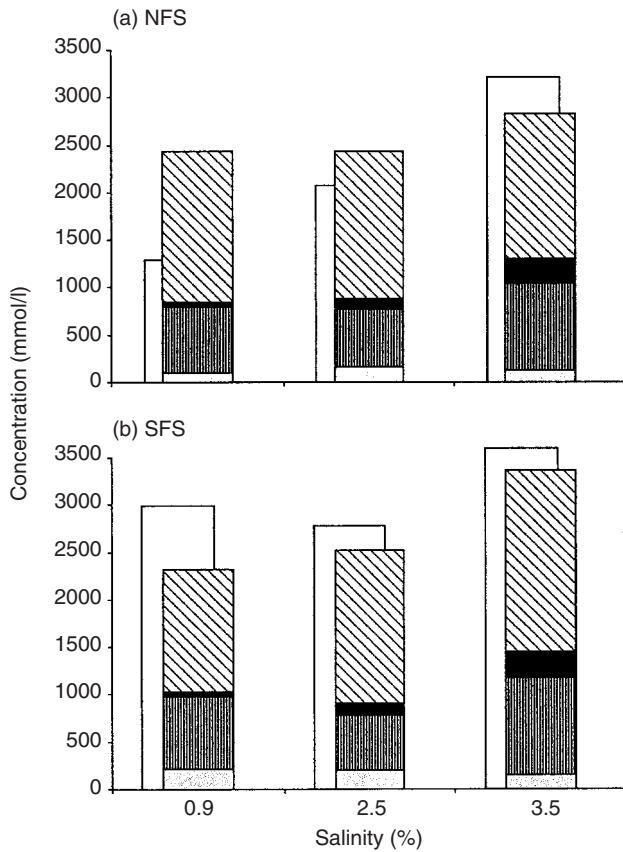


Fig. 2. The urine osmolality (mmol/l) (\square), and concentration (mmol/l) of potassium (\square), chloride (\blacksquare), sodium (\blacksquare) and urea (hatched) of founder *Acomys cahirinus* at different diet salinities during summer.

Osmolality

Founders

During the summer (Fig. 2) a significant difference in urine osmolality was found between slopes ($H = 12.68$, $P < 0.001$). A significant difference was found also among salinities ($H = 34.65$, $P < 0.001$). Urine osmolality increased along with the increased diet salinity in NFS mice, however in SFS mice it seems that osmolality was already high at 0.9%. During the winter (Fig. 3) there was no significant difference in urine osmolality between slopes ($H = 0.45$, $P > 0.05$). Urine osmolality, however, showed a significant increase along with diet salinity ($H = 6.5$, $P < 0.05$), though, as in the summer, this trend seems to be more pronounced in NFS mice than in SFS mice (Fig. 3).

Offspring

There was no difference in urine osmolality between the two slopes ($H = 0.53$, $P > 0.05$). However, urine

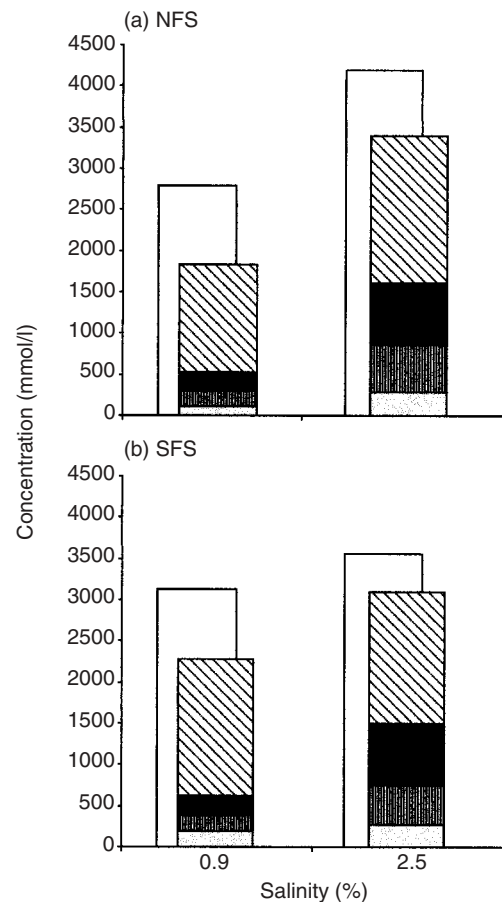


Fig. 3. The urine osmolality (mmol/l) (\square), and concentration (mmol/l) of potassium (\square), chloride (\blacksquare), sodium (\blacksquare) and urea (hatched) of founder *Acomys cahirinus* at different diet salinities during winter.

osmolality decreased significantly ($H = 45.27$, $P < 0.001$) along with the increased diet salinity (Fig. 4).

Potassium ion concentration [K^+]

Founders

During the summer (Fig. 2) [K^+] was significantly higher in the SFS mice compared to NFS mice ($H = 13.08$, $P < 0.001$), but no significant difference was found among salinities ($H = 4.87$, $P > 0.05$). During the winter (Fig. 3) there was no difference in [K^+] between slopes ($H = 1.89$, $P > 0.05$), but [K^+] increased significantly along with the increased diet salinity ($H = 10.59$, $P < 0.01$).

Offspring

[K^+] was found to differ significantly both between slopes ($H = 7.19$, $P < 0.01$) and among salinities ($H = 67.51$, $P < 0.001$), being higher on the SFS and decreasing along with the increased diet salinities (Fig. 4).

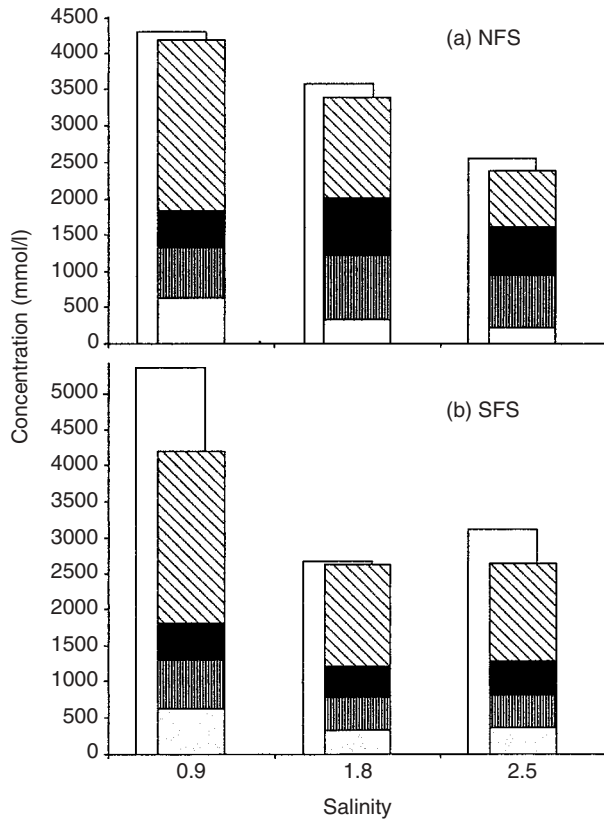


Fig. 4. The urine osmolality (mmol/l) (\square), and concentration (mmol/l) of potassium (\square), chloride (\blacksquare), sodium (\blacksquare) and urea (\square) of offspring *Acomys cahirinus* at different diet salinities during winter.

Chloride concentration [Cl^-]

Founders

[Cl^-] did not differ between slopes in either season ($H = 0.86$, $P > 0.05$, $H = 0.19$, $P > 0.05$ for summer and winter, respectively; Figs 2 & 3). It increased significantly, however, in both seasons along with increased diet salinity ($H = 42.76$, $P < 0.001$, $H = 19.62$, $P < 0.001$ for summer and winter, respectively; Figs 2 & 3).

Offspring

[Cl^-] was significantly higher in NFS mice ($H = 12.62$, $P < 0.001$) and it decreased significantly along with the increased diet salinities ($H = 13.03$, $P < 0.01$; Fig. 4).

Sodium ion concentration [Na^+]

Founders

[Na^+] did not differ between slopes in either season ($H = 0.67$, $P > 0.05$, $H = 0.09$, $P > 0.05$ for summer and winter, respectively; Figs 2 & 3). However, it increased

significantly in both seasons along with the increased diet salinity ($H = 94.06$, $P < 0.001$, $H = 23.35$, $P < 0.001$ for summer and winter, respectively; Figs 2 & 3).

Offspring

[Na^+] was significantly higher in NFS mice than SFS mice ($H = 18.74$, $P < 0.001$; Fig. 4), but did not vary with the increasing salinities ($H = 0.30$, $P > 0.05$).

Urea

Founders

Urea concentrations did not differ between slopes in either season ($H = 0.012$, $P > 0.05$, $H = 1.62$, $P > 0.20$ for summer and winter, respectively; Figs 2 & 3). In the summer urea concentrations increased significantly along with the increased diet salinity ($H = 2.08$, $P < 0.001$, Fig. 2), however no significant difference was noted in the winter ($H = 2.18$, $P > 0.05$; Fig. 3).

Offspring

Urea concentrations significantly differed between slopes ($H = 6.22$, $P < 0.05$) and decreased significantly along with the increased diet salinity ($H = 66.04$, $P < 0.001$; Fig. 4).

DISCUSSION

Rodents from xeric environments are expected to have increased urine concentration capabilities compared to their mesic counterparts (Schmidt-Nielsen, 1964). In this study we found that individuals of the same species from the same geographic locality (two slopes of a canyon) but different microhabitats (xeric on the SFS, and mesic on the NFS) could show similar divergence in their kidney functions.

The measured volume of urine was significantly lower in SFS mice than in NFS mice in the summer, suggesting that SFS mice are more adapted to xeric conditions in their water economy capabilities. This result supports previous studies where it was demonstrated that SFS mice have lower metabolic rate (Scantlebury *et al.*, 2002). Lower metabolic rates may also explain the decreased urine volume found in SFS mice in this study, since it implies decreased water loss and decreased concentrations of nitrogenous waste. It was found that body mass decreased as dietary salinity increased (the effect of salinity on the body mass of spiny mice on the two slopes has been reported and discussed in Scantlebury *et al.*, 2002). Urine volume (normalized to body mass) did not change as diet salinity was increased, suggesting that mice were not limited by water intake. Generally, when water availability is limited, animals respond by decreasing the

volume of urine excreted and by increasing its concentration (e.g. in springhares *Pedetes capensis*; Peinke & Brown, 1999; in the desert mouse opossum *Thylamys pusilla*; Diaz, Ojeda & Dacar, 2001). The current results suggest that *A. cahirinus* are able to survive on a diet with high osmolarity and maintain water balance. The ability of both NFS and SFS mice to concentrate the urine well above 3000 mosmol kg⁻¹ shows that they both are relatively adapted to xeric conditions (Peinke & Brown, 1999), though their urine concentration capacity is still lower than that of their desert counterparts, *Acomys russatus* (Weissenberg & Shkolnik, 1994). In general, as diet salinity increased, the urine osmolality of mice increased in both seasons. However, it seems that the osmolality of the SFS mice was already high at low salinity levels and did not change with increasing salinity. These results suggest that SFS mice maintain a low urine volume and high urine osmolality throughout the year, perhaps as an adaptation to the more xeric conditions on the SFS compared with the NFS. Thus, increasing dietary salinity apparently 'forces' NFS mice to improve their physiological performance to match a xeric-like water regulation, such as the SFS mice demonstrate.

As expected, mice increased sodium and chloride excretion as dietary salinity increased in both summer and winter. The increased electrolyte excretion is probably a direct cause of their increased presence in the water source. Choshniak & Mualem (1997) studied the electrolyte absorption of the *A. cahirinus*. Their results suggest an electro-neutral transport mechanism irrespective of feeding regime. Thus, it is not expected that the observed differences in electrolyte levels found in our study are a result of changes in food consumption, but rather a result of changes in water salinity. The discrepancy between the measured osmolality and the sum of the concentrations of the measured constituents might be caused by an additional constituent in the urine, for example a bivalent ion, that was not analysed in this experiment.

The response of the offspring was unexpected. We anticipated that urine osmolality would increase with increasing dietary salinity as it did in the founders. However, the opposite occurred; osmolality decreased with salinities for both slopes and the urine volume increased. Offspring may have responded to increased dietary salinity by consuming increased quantities of water, producing the observed increase in urine volume. This resulted in significant decreases of [K⁺], [Cl⁻] and urea. An increase in urine volume with a corresponding decrease in urine osmolality was also observed in the mink *Mustela vison* (Eriksson, Valtonen & Makela, 1984) and naked mole rat *Heterocephalus glaber* (Urison & Buffenstein, 1994) for similar conditions (increasing water salt concentrations from 0.9% to 3.0% and from 0.5% to 2%, respectively). This does not, however, explain the observed differences between offspring and founders. Differences may have arisen because offspring were born and raised in captivity and at no stage during their development was water a limiting resource. We suggest that the offspring may have used an alternative uneconomic way to deal with increasing salinity, by

consuming increasing amounts of water, instead of limiting the amount of water consumed and increasing urine osmolality. None the less, differences in physiological capabilities between mice from the two slopes are retained in almost all measures in the offspring, implying that there may be a genetic basis for this phenomenon.

A major difference in urine osmolality was noted between summer and winter measurements of founders. *Acomys cahirinus* increased urine osmolality to higher values during the winter. This is contrary to the expectation that arid adapted granivores (whose primary source of water is from oxidative metabolism) characteristically have low winter and high summer values of urine osmolality (MacMillen, 1983). Even though wild *A. cahirinus* are known to consume land snails *Promatias* during the dry summer months (Broza & Nevo, 1994), we still expected them to have higher urine osmolality in the summer whether they were challenged with a high salinity diet in the wild or in the laboratory. One possible explanation for the higher winter osmolality is that under the colder winter conditions, mice consumed more soybeans (42% protein) to thermoregulate. This may have forced them to excrete more urea and consequently consume more water. Since the water consumed contained high concentrations of salt, this resulted in an increased salt excretion in the urine.

This study is complimentary to an increasing body of evidence suggesting that *A. cahirinus* from the NFS and SFS of Nahal Oren show differences in their physiological capabilities (Afik *et al.*, 2000; Scantlebury *et al.*, 2002; Shanas *et al.*, 2002). We suggest that further studies should be carried out to examine genetic differences between NFS and SFS mice, as even the offspring from the two slopes exhibit different physiological capabilities.

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