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Urinary concentrating ability of four *Gerbillurus* species of southern African arid regions

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The four *Gerbillurus* species studied have efficient urinary concentrating capabilities. The renal morphology of all four species was similar, with a well-developed papilla renis extending into the ureter. Urine production and osmolality varied with protein content and potential water yield of different dietary regimes. When deprived of water on seed diets, each species produced a precipitate of allantoin in the urine which contributes to reducing overall water output. This is essential for water balance in their xeric habitats.

Introduction

The hairy-footed gerbils, *Gerbillurus tytonis*, *G. paeba paeba*, *G. vallinus vallinus* and *G. setzeri*, occur in arid regions of southern Africa and must rely on their food source for water. Regulation of water output (the summation of faecal, pulmocutaneous and urinary water) is essential to maintain positive water balance. The gerbils minimise evaporative cooling by use of burrows in daytime and restricting activity to night-time (Downs & Perrin, 1989*a*). They produce faeces with low water content (Downs & Perrin, 1989*b*), and reduce urinary water for increased water economy which is necessary for survival.

Urinary water loss is inversely correlated to urine concentrating ability (UCA). Production of a hypertonic urine is associated with increased medullary thickness and a counter-current system (Wirz *et al.*, 1951 *in* Khalil & Tawfic, 1963). Sperber (1944) found relative medullary thickness (RMT) of mammalian kidneys correlated positively with UCA and negatively with water availability. Renal anatomical characteristics are also used as indices for interspecific comparison of UCA (Geluso, 1978; Lawler *et al.*, 1986).

Objectives were (a) to establish if significant differences occur in UCA among the four taxa of *Gerbillurus* and (b) to determine the role of renal efficiency in maintenance of water balance.

Materials and methods

Gerbils were trapped during June 1986 and in March 1987 in south-west Africa/Namibia and in the Northern Cape Province of the Republic of South Africa. *Gerbillurus tytonis* were collected at Gobabeb (23°34'S, 15°03'E), *G. p. paeba* at Swakopmund (22°42'S, 14°31'E), *G. setzeri* at Rössing (22°24'S, 14°59'E) and *G. v. vallinus* near Kenhardt (29°38'S, 21°59'E). Animals were maintained in captivity as described previously (Downs & Perrin, 1989*b*).

Urine samples were used to quantify urine osmolality and urea concentrations for

Table 1. *Potential water yield and protein content of feeds given to the four* Gerbillurus *species during laboratory diet trials (Downs & Perrin, 1989b)*

Diet	Potential water yield (ml/g)	Protein content (kj/g dry mass)
Mealworms	0·8752	44·38
Sunflower seeds	0·7311	30·35
Millet seed	0·5335	10·00
Carrot	0·9455	13·25

animals subjected to water deprivation trials, each consisting of three stages. The effect of water deprivation, on three different diet regimes ranging in water yield and protein content as shown (Table 1) was examined. Gerbils were fed the respective diets with water and carrots for 4 days (stage 1) after which water was removed (stage 2). Daily carrot rations were withheld 4 days later (stage 3) when gerbils were fed treatment food only, for 4 days. Individuals were kept in metabolic cages (145 × 185 × 100 mm) with urine collecting trays. A gauze (1 mm²) separator prevented faeces from contaminating urine, which was collected under liquid paraffin to prevent evaporation. Urine samples were collected during the last 2 days of each stage.

Urine samples were collected during week-long tritium water-turnover experiments (Downs & Perrin, 1989b) when gerbils were subjected to one of the three diet regimes used in the deprivation trials. Experiments were conducted without water but each diet was supplemented with carrot. Total urine production for 24 h periods was obtained. For the final 4 days of the experiment, individuals were kept in metabolic cages. Urine was collected during the last 3 days of the diet trial. Urine samples of free-living gerbils were obtained during field water-turnover rate investigations in March 1988 (Downs & Perrin, 1989c), sealed in vials and stored at −4°C until analysed.

Urine analysis

Urine osmolalities (correct to 0·2% error) were measured with a cryoscopic osmometer (Gonotec Osmomat 030). Urine urea content (mM/ml) was determined using the spectrophotometric assay of Chaney and Marbach (in Henry, 1964). The range of concentrations where Beer's law is obeyed required dilution of urine subsamples. Crystalline precipitate in urine was extracted by the method of Buffenstein *et al.* (1985). Crystalline fractions from each gerbil species were examined by mass spectrometry (Hewlett Packard, GCMS 5890), using the direct insertion probe with the mass spectra measured at 70 eV using the selected ion mode, to confirm the precipitate was allantoin.

Kidney morphology

Kidneys of laboratory and field animals were removed immediately after euthanasia (with 0·5 ml of SAFFAN, Glaxovet). Kidneys were fixed in Bouin's solution (Culling *et al.,* 1985) for 24 h before storage in 70% alcohol. Formalin-fixed kidneys were obtained from wild caught *G. p. paeba* and *G. tytonis*. Kidney length, width at mid-point, and thickness were measured using vernier calipers accurate to 0·01 mm. Kidney sections were stained with Ehrlich's haemotoxylin stain and eosin counterstain (Culling *et al.*, 1985). Remaining kidneys were cut mid-sagittally and examined under a dissecting microscope. Outer cortex

and medullary zone widths were measured using a calibrated ocular micrometer eyepiece graticule. Cortex (Fig. 1) width was measured from the kidney surface to the corticomedullary junction (visible at the level of arcuate vessels). Medullary zone width was inclusive of the papilla renis, from the corticomedullary junction to the tip of the papilla including the length of the papilla. It was calculated as the kidney surface to papilla tip width minus the cortex width. Mid-sagittal kidney sections were photographed and drawn.

Determination of renal indices

Data were used to calculate two renal indices known to be good indicators of UCA (Geluso, 1978; Heisinger & Breitenbach, 1969).

1. Relative medullary thickness (RMT)—(Sperber, 1944),

$$RMT = \frac{10 \times \text{Absolute medullary width (mm)}}{\text{Length} \times \text{Width} \times \text{Thickness of kidney (cm)}}.$$

2. Per cent medullary thickness (PMT)—(Heisinger & Breitenbach, 1969),

$$PMT = \frac{100 \times \text{(Medullary width)}}{\text{(Cortical + Medullary width)}}.$$

Statistical analysis

Descriptive statistics, 'Student' t-tests and one-way anova used Minitab 5 and Statgraphics software packages. The significance level used was 0·05.

Results

Kidney anatomy

Figure 1 shows the renal macro-anatomical features of the four *Gerbillurus* taxa studied. All species have simple, unilobular kidneys with an elongated papilla renis extending into the ureter. Each species has a type II (Schmidt-Nielson, 1977) renal pelvis with fornices
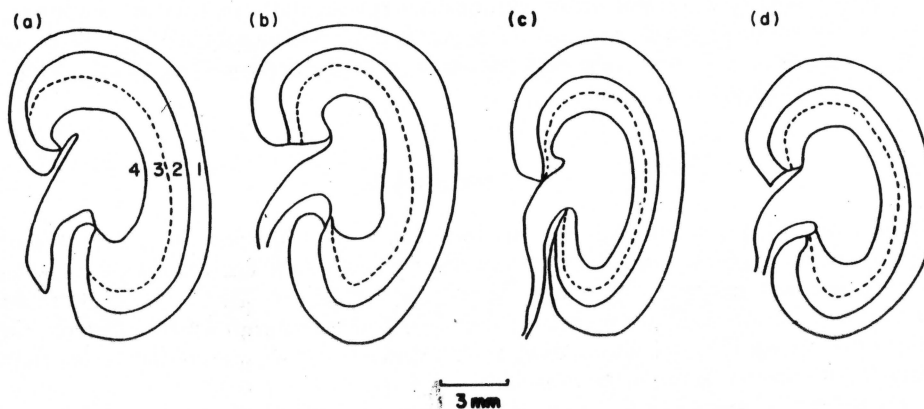

Figure 1. The renal structure of four *Gerbillurus* species: (a) *G. v. vallinus*; (b) *G. setzeri*; (c) *G. tytonis*; and (d) *G. p. paeba*. (1 = cortex; 2 = distal medulla; 3 = proximal medulla; 4 = pelvic region.)

penetrating the outer medulla. Fornices were lined with cuboidal or squamosal epithelium while the renal papillary epithelium was cuboidal.

Renal indices

Renal indices, RMT and PMT, are presented in Table 2. Since indices of wild and laboratory gerbils did not differ significantly ($p > 0.05$), samples were pooled for interspecific comparisons. The RMT and the PMT of *G. tytonis* and *G. p. paeba* were significantly lower than those of *G. setzeri* ($p < 0.05$). The RMT of *G. v. vallinus* was similar to those of *G. tytonis* and *G. p. paeba*, whereas the PMT of *G. v. vallinus* was intermediate between these two species and that of *G. setzeri*.

Urine production

Table 3 reports specific urine production for each dietary regime with carrots as a water supplement. *Gerbillurus tytonis* and *G. setzeri* produced significantly less urine on sunflower seeds than on mealworms or millet seed ($p < 0.05$). *Gerbillurus p. paeba* had a significantly lower urine production on the sunflower seeds than on mealworms ($p < 0.05$). Urine production of *G. v. vallinus* was significantly lower on sunflower seeds than on millet seeds ($p < 0.05$).

Urine production did not differ significantly among the four taxa on sunflower seeds ($p > 0.05$); however, on mealworms, *G. p. paeba* produced significantly less urine than the other three taxa ($p < 0.05$). On millet seeds *G. p. paeba* produced significantly less urine than *G. tytonis* and *G. v. vallinus*.

Urine osmolality

Urine osmolalities (osmol/kg) of the four *Gerbillurus* species on different diets are presented in Table 4. *Gerbillurus tytonis* showed no significant difference in osmolality among the diet regimes with supplementary water ($p > 0.05$). Without water and fed mealworms, the osmolality increased four-fold and was significantly different from the other two stages of water deprivation on this diet ($p < 0.05$). On millet seeds, there was only a 1·8 increase in the urine osmolality.

Gerbillurus p. paeba had no significant difference in osmolality among the three stages of water deprivation, on each diet regime, or among diets at each stage ($p > 0.05$). Urine osmolality of *G. v. vallinus* during stage 3 of water deprivation for each diet, was significantly higher than during the previous two stages. In stage 3 of water deprivation, there was no significant difference in osmolality among diets for *G. v. vallinus* ($p > 0.05$). However, osmolality during the first two stages of water deprivation differed significantly between the millet seed and mealworm diets compared with the sunflower seed diet.

Table 2. *Renal indices of four* Gerbillurus *species*

Species	n	RMT	PMT
G. tytonis	27	6·26 ± 0·31	83·41 ± 0·68
G. p. paeba	25	5·97 ± 0·29	85·27 ± 0·57
G. v. vallinus	2	6·14 ± 0·10	87·53 ± 0·72
G. setzeri	5	8·35 ± 0·43	89·09 ± 0·91

Mean value ± S.E.; RMT, relative medullary thickness (Sperber, 1944); PMT, per cent medullary thickness (Heisinger & Breitenbach, 1969).

Table 3. *Urine production (ml/day) of four species of* Gerbillurus *when feeding on three respective dietary treatments*

Species	Body mass (g)	Mealworm + carrot urine volume			Body mass (g)	Sunflower + carrot urine volume			Body mass (g)	Millet + carrot urine volume		
		x ± S.E.	Min.	Max		x ± S.E.	Min	Max		x ± S.E.	Min	Max
G. tytonis	33·3	0·99 ± 0·108 (17)	0·20	1·65	32·9	0·12 ± 0·033 (13)	0·02	0·40	36·9	1·28 ± 0·675 (2)	0·60	1·95
G. p. paeba	27·9	0·26 ± 0·071 (8)	0·05	0·65	27·2	0·08 ± 0·018 (14)	0·02	0·20	29·4	0·28 ± 0·025 (2)	0·25	0·30
G. v. vallinus	37·6	0·46 ± 0·216 (7)	0·04	1·55	47·4	0·29 ± 0·066 (12)	0·05	0·76	40·3	0·89 ± 0·603 (8)	0·08	2·00
G. setzeri	32·8	0·76 ± 0·174 (12)	0·20	1·97	41·8	0·06 ± 0·019 (11)	0·02	0·23	29·9	0·10 ± 0·057 (8)	0·05	0·18

Mean ± S.E.; Min, minimum urine produced per day; Max, maximum urine produced per day; Number of animals in parentheses.

Table 4. *Urine osmolality (osmol/kg) of four* Gerbillurus *species on different diets*

Diet	G. tytonis Mean ± S.E. (n)	G. p. paeba Mean ± S.E. (n)	G. v. vallinus Mean ± S.E. (n)	G. setzeri Mean ± S.E. (n)
Millet + C	2·21 ± 0·97 (2)	1·73 ± 0·29 (3)	1·94 ± 0·74 (9)	4·19 ± 0·59 (2)
Millet only	3·64 ± 0·94 (6)	3·12 ± 0·79 (3)	4·64 ± 0·96 (3)	2·99 ± 1·33 (5)
SS + C + W	2·60 ± 0·54 (9)	3·39 ± 0·61 (5)	2·50 ± 0·51 (6)	3·26 ± 0·28 (9)
SS + C	3·29 ± 0·26 (22)	3·20 ± 0·38 (17)	3·70 ± 0·15 (17)	3·50 ± 0·29 (17)
SS only	—	2·64 ± 0·14 (3)	4·51 ± 0·99 (5)	4·29 ± 0·14 (2)
M + C + W	1·27 ± 0·55 (8)	3·69 ± 2·29 (10)	3·24 ± 1·28 (6)	3·18 ± 1·12 (9)
M + C	1·85 ± 0·19 (30)	2·18 ± 0·55 (12)	2·03 ± 0·29 (6)	2·04 ± 0·33 (20)
M only	4·59 ± 1·32 (4)	4·65 ± 1·65 (12)	5·66 ± 1·23 (6)	4·63 ± 0·78 (4)
Field	4·05 (1)	4·36 ± 0·44 (2)	—	4·65 ± 0·67 (9)

SS, sunflower seeds; C, carrots; W, drinking water; M, mealworms; n, number of animals.

Table 5. *Ratios of mean osmolality to mean volumes of urine produced per day (osmol day/kg ml)*

Diet	G. tytonis	G. p. paeba	G. v. vallinus	G. setzeri
Mealworms + carrot	1·87	8·26	4·41	2·68
Sunflower seeds + carrot	27·65	39·51	12·63	60·34
Millet seeds + carrot	1·73	6·30	2·18	41·95

Table 6. *Maximum urine osmolality value (osmol/kg) of four* Gerbillurus *species*

	G. tytonis	G. p. paeba	G. v. vallinus	G. setzeri
Mealworm only	6·129	6·997	7·144	5·398
Sunflower seed	—	2·848	6·125	4·437
Millet seed	5·213	4·097	5·925	5·219
Field	3·152	4·800	—	5·648

When fed mealworms, *Gerbillurus setzeri* had a significantly higher urine osmolality compared to the other two stages of water deprivation ($p < 0·05$). Comparison of each stage of water deprivation among diets for *G. setzeri* showed a significantly higher osmolality for the sunflower seed/carrot diet compared with the mealworm/carrot diet.

For interspecific comparison of UCA, ratios of mean osmolality for each stage of the respective diet treatments divided by mean volume of urine produced were calculated (Table 5). Ratios increased greatly on the sunflower seed/carrot diet.

Mean urine osmolalities of *G. tytonis*, *G. p. paeba* and *G. setzeri* collected at Gobabeb during March 1988 are shown in Table 4. Values approximated those obtained in stage 3 of diet treatments. Maximum urine osmolalities for laboratory and field *Gerbillurus* species are shown in Table 6.

Table 7. *Urea concentration (mM/ml) of urine of four* Gerbillurus *species on different diets*

Diet	G. tytonis Mean ± S.E. (n)	G. p. paeba Mean ± S.E. (n)	G. v. vallinus Mean ± S.E. (n)	G. setzeri Mean ± S.E. (n)
Mealworms + C + W	1·813 ± 0·550 (6)	2·039 ± 0·928 (4)	1·662 ± 0·439 (4)	2·758 ± 0·090 (2)
Mealworms + C	2·941 ± 0·412 (9)	3·053 ± 0·796 (14)	2·897 ± 0·630 (10)	2·324 ± 0·722 (16)
Mealworms only	2·475 ± 0·424 (2)	— (1)	2·768 (2)	2·685 ± 0·285 (3)
Sunflower seed + C + W	4·769 ± 0·532 (6)	2·592 ± 1·154 (2)	3·352 ± 0·105 (3)	3·951 ± 0·103 (2)
Sunflower seed + C	2·343 ± 0·530 (6)	2·265 ± 0·439 (6)	2·363 ± 0·518 (19)	1·671 ± 0·459 (8)
Sunflower seed only	—	3·668 ± 0·180 (2)	4·000 ± 0·705 (3)	3·206 ± 0·128 (2)

n, number of animals; C, carrots; W, drinking water.

Urea

Table 7 presents the urea concentration in urine for each stage of water deprivation for the sunflower seed and mealworm diets. The amount of urea (mM/ml) excreted in the urine of *G. tytonis* and *G. v. vallinus* was significantly lower for mealworm and sunflower seed diets in stage 1 compared to stage 2 of water deprivation ($p < 0.05$). *Gerbillurus p. paeba* had no significant difference in urea concentration for each stage of water deprivation within or between diet treatments ($p > 0.05$). *Gerbillurus setzeri* had no significantly lower urea production on sunflower seeds and stage 2 of water deprivation compared to the other two stages. This species had significantly lower urea content on sunflower seeds/carrot than on mealworms/carrot ($p < 0.05$). *Gerbillurus v. vallinus* had a significantly higher urea production on the sunflower seeds than on mealworms when water and carrots were available. However, there was no change for the subsequent two stages of water deprivation. Generally, mean urea production was greater on sunflower seeds than mealworms for each stage of water deprivation.

Allantoin

Low resolution mass spectrometric analysis of urine crystalline fractions confirmed the precipitate was allantoin in all *Gerbillurus* taxa. However, the amount of precipitate was affected by diet and water availability: variation occurred among species and individuals. *Gerbillurus v. vallinus* produced the greatest amount of precipitate (an average of 0·04 mmol/day) on all diet regimes. The other species produced less precipitate when deprived of water except for stage 3 on millet seeds when precipitate production was similar in all species.

Discussion

Renal structure and urinary concentrating ability

The relationship between renal structure and degree of UCA of desert rodents has been extensively studied (Sperber, 1944; Schmidt-Nielsen & O'Dell, 1961; Hewitt, 1981). Most desert rodents, including *Gerbillurus*, have increased medullary widths, an elongated

papilla renis extending into the ureter, and exceptional UCA to minimise urinary water loss.

The four gerbil species studied have simple (Sperber, 1944) kidneys, with characteristic outer and inner medullary zones and an elongated papilla extending into the ureter, conforming to other desert rodents including *Psammomys obesus* (Schmidt-Nielsen & O'Dell, 1961), *Jaculus jaculus*, *Gerbillus gerbillus* (Khalil & Tawfic, 1963), *Notomys alexis* (MacMillen & Lee, 1969) and *Tatera indica* (Goyal *et al.*, 1988).

Morphological renal characters are reliable indicators of UCA, particularly RMT (Sperber, 1944), PMT (Heisinger & Breitenbach, 1969) and the relative medullary area (RMA) (Brownfield & Wunder, 1976). *Gerbillurus setzeri*, a gravel plains species, had significantly higher RMT and PMT values than the two dune species, *G. tytonis* and *G. p. paeba* and should therefore have greater UCA. Although osmolality and urea concentrations were similar in all species, total urine volume for *G. setzeri* was lower, indicating a greater reduction in overall urinary water loss, supporting the validity and reliability of RMT and PMT indices.

Goyal *et al.* (1988) reviewed data on RMT and osmolality and derived the following equation:

$$y = (306 \cdot 7 + 524 \cdot 5x)10^{-3}$$

where y = osmolality (osmol/kg) and x = RMT.

Predicted osmolalities are $3 \cdot 6$, $3 \cdot 4$, $3 \cdot 5$ and $4 \cdot 7$ for *G. tytonis*, *G. p. paeba*, *G. v. vallinus* and *G. setzeri* respectively, and approximate values obtained for water-derived laboratory animals and field animals. It appears that animals were under considerable water stress in the field during March, which is corroborated by low water-turnover rates at this time (Downs & Perrin, 1989c).

Studies of desert rodents including *Psammomys obesus* (Jamieson *et al.*, 1979) and *Neotoma albigula* (Schmidt-Nielsen, 1977), emphasise the importance of the renal pelvis in hyperosmotic urine production. Goyal *et al.* (1988) have suggested that more concentrated urine in *T. indica* than *Meriones hurrianae*, is a consequence of increased papilla renis length since UCA is positively correlated with papilla renis length (MacMillen & Lee, 1967, 1969). The correlation between pelvis structure, papilla renis length and UCA is corroborated in this study of *Gerbillurus*.

Renal concentrating ability and water availability

Studies of renal morphology and physiology indicate a positive association between a species distribution and its ability to conserve water (Schmidt-Nielsen, 1961; Heisinger & Breitenbach, 1969; Geluso, 1978). UCA is determined by the capacity to minimise water loss and is assessed by the total number of solutes in the urine (Louw *et al.*, 1972). Convergent trends in kidney structure and UCA typify small mammals from diverse desert habitats, e.g. rabbits (Heisinger & Breitenbach, 1969), hedgehogs (Yaakobi & Sholnik, 1974), insectivorous bats (Geluso, 1978), and cricetid and heteromyid rodents (MacMillen & Hinds, 1983).

Increased UCA may be related to increased dietary protein and decreased water potential (MacMillen & Hinds, 1983; Lawler & Geluso, 1986). In this study, UCA has been further examined by the ratio of osmolality to urine production. Ratios increased greatly for each taxon of *Gerbillurus* on sunflower seeds compared to other diets; *G. setzeri* also showed an increase on millet seed. Thus, diets with low potential water yield and high protein contents maximised UCA. Many desert rodents, including *Gerbillurus*, are independent of exogenous water because of diet selection, renal efficiency, and behavioural and morphological attributes.

All *Gerbillurus* taxa are nocturnal, opportunistic omnivores; however species differ in

body size. Mean masses (g) of wild-caught *G. setzeri, G. v. vallinus, G. tytonis* and *G. p. paeba* were 34·9, 34·3, 24·6 and 22·5 respectively (pers. obs.). Lawler & Geluso (1986) examined the relationship between body mass and UCA in six species of sympatric desert heteromyid rodents with similar dietary habitats and life histories: renal morphology was highly and negatively correlated with body mass. In this study, however, *G. setzeri,* the largest species, has greater UCA which is confirmed by renal indices. *Gerbillurus v. vallinus* and *G. setzeri* occupy gravel plains whereas the other two species are restricted to dune or sandy soils. Heisinger *et al.* (1973) found that cricetid rodents have increased renal efficiency with decreased water availability, suggesting small changes in water availability select for structural and functional changes in the kidneys. The efficiency of *G. setzeri* kidneys to other *Gerbillurus* species, is a likely consequence of decreased food availability, with high potential water yields and/or increased aridity of its environment.

Although *G. p. paeba* has an efficient renal function, it cannot survive on a dry grass seed diet without succulent supplements (Louw, 1972). Mean urine osmolality was 2860 m-osmol/l when gerbils received lettuce, but when removed, osmolality increased to 4035 m-osmol/l. These values are within the range obtained for *G. p. paeba* in this study during different stages of water deprivation. Each gerbil species lost mass when fed only millet or sunflower seed while they maintained mass when fed on mealworms without supplementary water (Downs & Perrin, 1989*b*). The osmolalities obtained during stage 3 of the sunflower and mealworm diets fell within the range obtained during water deprivation by Buffenstein *et al.* (1985).

Increased urine osmolality on sunflower and mealworm diets compared to the millet seed diet are a consequence of increased protein load (Downs & Perrin, 1989*b*). Similarly, Yaakobi & Shkolnik (1974) found increased dietary protein increased urine osmolality. Selection of insects by gerbils increases water and protein intake. Removal of by-products of protein metabolism without concomitant increase in water loss enables the gerbils to survive without exogenous water, but when insect availability is low, gerbils are forced to supplement the diet with succulent vegetation.

Urine concentrating ability and the excretion of precipitate in the urine

Buffenstein *et al.* (1985) reported the excretion of allantoin in the urine of hydropenic cricetid rodents, including *G. p. paeba*. The crystalline precipitates in the urine of each gerbil species studied was identified as allantoin, and its concentration increased with water deprivation and/or lower potential water yield of the diet. Conversion of 1 mole of urea to allantoin increases water conservation by 1·5 moles (Stryer, 1981). The gerbils conserved more than 0·6 ml of water per animal per day on millet seed without water because of allantoin production. *Tatera leucogaster* and *Desmodillus auricularis* excrete allantoin (Buffenstein *et al.,* 1985) but there are no other reports of desert rodents producing a supersaturated urine; however the dassie, *Procavia capensis,* has a renal function near maximum efficiency and produces urine supersaturated with calcium carbonate (Louw *et al.,* 1972). Production of supersaturated urine is probably a consequence of the role of the renal pelvis in the modification of the urinary concentration and composition (Schmidt-Nielsen, 1977).

The renal indices, UCA, and allantoin excretion indicate efficient renal capabilities in the four *Gerbillurus* species. Plasticity in maximum UCA on different diets was dependent on potential water yield. The potential to increase UCA with decrease in potential water yield of the diet enhances water conservation in gerbils and their ability to survive in arid habitats where food resources are ephemeral and scarce. *Gerbillurus* is a monophyletic group (Qumsiyeh *et al.,* 1987) representing old inhabitants of the arid regions (Meester, 1965). Similarities in renal morphology and UCA, particularly allantoin production, suggest these adaptations were inherited from a common ancestor. However, increased

efficiency of UCA occurs locally, depending on food availability and aridity of the specific habitat.

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