

Aspects of renal physiology, nutrition and thermoregulation in the ground squirrel *Xerus inauris*

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Accepted: 20 October 1978

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ABSTRACT

The ground squirrel possesses very efficient kidney function which is reflected in a high urine:plasma concentration ratio, particularly during the summer months, and one of the highest relative medullary thicknesses recorded in mammals. The diet of these animals changes markedly from the wet to the dry season, as does the incidence of internal parasites. The flared, erect tail is used *inter alia* as a unique shading device as part of this species' complex thermoregulatory behavioural repertoire.

1 INTRODUCTION

The ground squirrel (Plate 1) enjoys a wide distribution in South Africa and is common in the central area, especially in the maize areas of the Orange Free State and Western Transvaal. It is also found throughout South West Africa, even occurring on the gravel plains of the Namib Desert (Coetzee, 1969).

In its natural habitat this small, diurnal mammal (300 – 500 g) excavates vast burrowing systems, an average colony consisting of 22 to 30 exit/entrance holes spread over an area of 200 to 400 m² (Zumpt, 1970). In fact, *Xerus* is probably the smallest diurnal mammal encountered in southern African deserts. As such it has to contend with extremely high surface soil temperatures and intense radiation without access to drinking water. Nothing, however, is known about its renal function and thermoregulatory behaviour which presumably are well adapted to the hostile environment which it inhabits.

The purpose of this study, therefore, was to assess renal efficiency in these animals by examining the morphology of the kidneys and the chemical composition of the urine and plasma. In view of the important influence of diet on water balance, this aspect was also investigated together with superficial observations on thermoregulatory behaviour.

2 PROCEDURE

2.1 Collection and analyses of plasma and urine samples

Animals were shot in the Okaukuejo area of the Etosha National Park and urine samples were collected within five minutes. Blood was removed from the jugular, the hepatic veins or the heart in a heparinized disposable syringe. The plasma was drawn off after 15 minutes of centrifuging in a clinical centrifuge and immediately cooled to -5°C in the field. Within three hours all samples were further cooled to -20°C in the laboratory. These samples were then stored at this temperature for several months until a detailed analysis could be performed. Urine was removed from

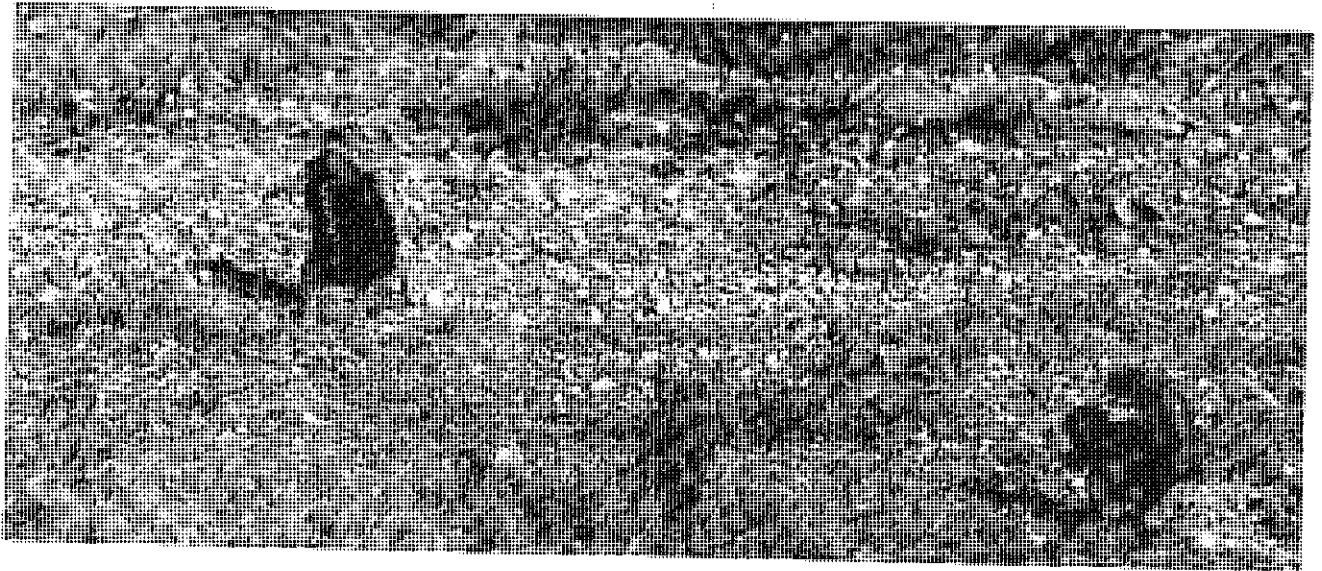


PLATE 1: Illustrating specialised thermoregulatory behaviour in *Xerus inauris*. The animals employ the flared tail for shading and orientate their bodies in the opposite direction from incoming insolation. Note the position of the shadows cast by the animals.

the bladder in a syringe and was cooled and stored in an identical manner to the plasma.

Samples were collected towards the end of February, 1976 which represents the height of the rainy season when free moisture and green vegetation are available, and at the end of August, 1976 when no free water was available and humidity was low (10 to 30 % rh).

The plasma and urine samples were analysed to determine the total osmolality as well as urea, sodium and potassium concentrations. Osmolalities were determined using an automatic osmometer (Advanced Instruments, model 6731 RAS). The concentration of urea was determined enzymatically using the method of Fawcett and Scott (1960) and a spectrophotometer at 546 nm. Sodium and potassium were determined using flame photometric techniques (Instrumentation Laboratory, IL 243).

2.2 Kidney dimensions

The mass of individual kidneys was determined. Length, width and depth dimensions were measured with a pair of calipers to the nearest mm and the kidney size was calculated as the cube root of the product of these dimensions (Sperber, 1944). The kidneys were bisected medially and the width of the cortex and the medulla were measured at 10 intervals along the periphery and the means were determined. The cortico-medullary ratio was calculated and the relative thickness of the medulla was determined using the formula:

$$\frac{\text{medulla thickness} \cdot 10}{\text{kidney size}} \quad (\text{Sperber, 1944}).$$

2.3 Stomach contents

The stomach contents of ground squirrels killed in the wet and dry season were analysed under a dissecting microscope. Five sub-samples were floated in water and the percentage area of dietary items was estimated with the aid of an ocular grid. Percentages thus obtained were interpreted as being percentages of total stomach contents. The incidence of parasitism was recorded.

2.4 Food selection

Observations on the food eaten by *X. inauris* were made with a telescope in the Etosha National Park between February and March in the wet season and again in August during the dry season, in 1976.

2.5 Thermoregulatory behaviour

While observing feeding habitats of the animals, incidental observations on thermoregulatory behaviour in relation to prevailing ambient temperature were recorded.

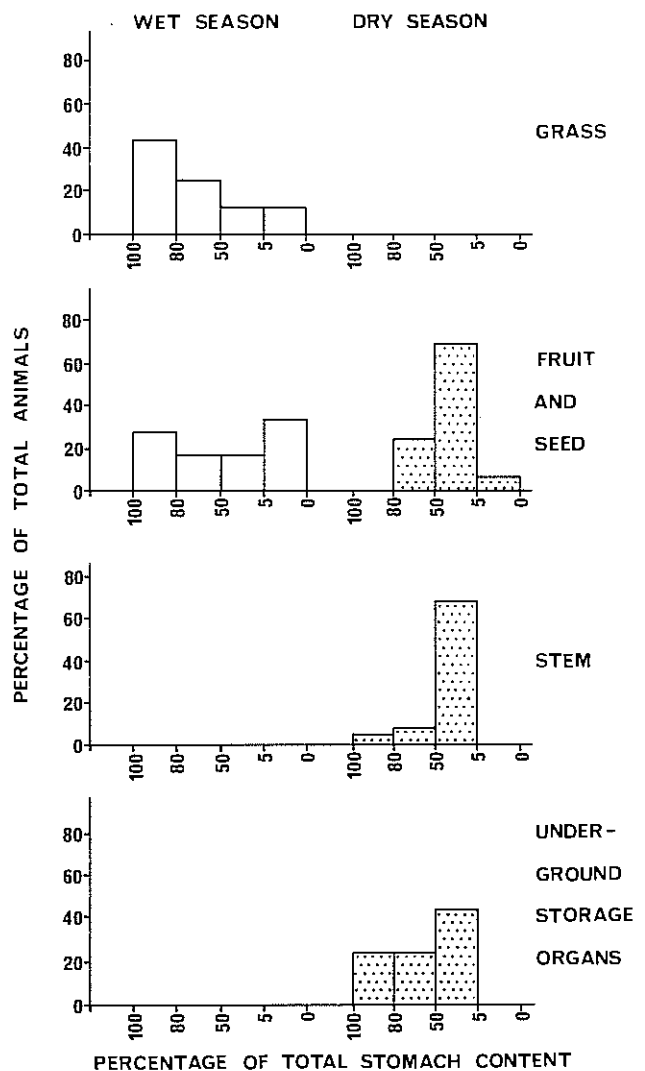


FIGURE 1: Stomach content analyses in *Xerus inauris*.

3 RESULTS

3.1 Plasma and urine analyses

The results of the plasma and urine analyses of *X. inauris* are given in Tables 1 and 2 respectively. Typical mammalian plasma characteristics are revealed. The high potassium concentrations are probably attributable to shock associated with death. The Student t-test showed that plasma urea levels increased significantly by a factor of two in the dry season ($p < 0.001$). Osmolality as well as sodium and potassium concentrations showed no significant seasonal variation ($p > 0.1$). All the urine constituents measured increased significantly in the dry season. Osmolality, potassium and urea increased by factors of 3.0; 3.6; and 3.4 respectively. These increases were all significant at $p < 0.001$ using the Student t-test. Sodium levels rose by a factor of 2.8 ($p < 0.05$).

3.2 Kidney dimensions

The kidney dimensions of *Xerus* are given in Table 3 and when these are compared with dimensions reported in the literature (Table 4), it is clear that the medullary thickness of *Xerus* is among the highest recorded to date.

3.3 *X. inauris* stomach contents

Fig. 2 is a summary of the major dietary components of *X. inauris* during the wet and in the dry seasons in the Okaukuejo area of the Etosha National Park. In the wet season grass and fruit comprise most of the diet. In 66.6 % of the animals investigated more than 50 % of the stomach contents was green grass. During the dry season, in spite of the presence of dry grass, the dietary items emphasized were underground storage organs, stem and fruit with the attendant seeds. No animal matter was detected in any of the stomachs. Thus, the Etosha National Park ground squirrels appear to be entirely herbivorous.

It is also of interest to note that the stomach of *Xerus* is capable of massive enlargement to accommodate the large intake of vegetable material. In this respect it was found that the ratio of the mass of the stomach contents to the total body mass was as high as 0.06:1. This represents 6 % of the animal's total body mass and is typical of an exclusively herbivorous animal. As would be expected, the animals possess an enlarged caecum where digestion of cellulose presumably takes place.

3.4 Food plants utilised by *X. inauris*

The vegetation favoured by *X. inauris* during February and March, 1976, is listed in Table 5. Unfortunately, it was not possible to estimate from stomach content analysis the proportion of the various plants consumed.

3.5 Stomach parasites

The incidence of parasitism fell from 75 % of the total number of animals in the wet season to 53 % in the dry season. The parasites were nematodes, belonging to the Ascaridae. Further identification was not possible. Infestation appeared to be associated with the consumption of green grass. All those individuals which had a high percentage of grass in their stomachs also contained numerous small parasites (<2 mm). The maximum number of these very small nematodes recorded from one individual was 10 000. All the nematodes found in the dry season were greater than 25 mm in length and many were about 70 mm long. The highest number found in one individual during the dry season was six.

3.6 Thermoregulatory behaviour

No attempt was made to examine thermoregulatory behaviour in detail. However, we wish to confirm an interesting behavioural mechanism, first suggested by Smithers (1971), namely the use of the flared tail as a shading device under conditions of intense solar radiation (Plate 1). In this plate it can be seen from the shadows cast by the animals that they orientate their bodies in such a way as to obtain maximum shading effect of the tails while foraging for food. This well synchronised orientation behaviour is only employed under conditions of high solar radiation when sun temperatures approach and exceed *ca.* 30°C. At lower ambient temperatures orientation is random. It should, however, be emphasized that flaring of the tail is not confined to thermoregulatory behaviour and is also frequently used as a behavioural signal during social interaction and during escape behaviour from predators. Available time, however, did not allow collection of quantitative data in regard to critical threshold temperature and wind speed at which tail shading takes place.

4 DISCUSSION

The plasma analyses of *X. inauris* revealed typical mammalian characteristics. *X. inauris* showed an increase in all blood solutes in the dry season, with the exception of potassium. The increase in urea is statistically significant (Table 1). This increase in plasma concentration could possibly improve water economy by reducing the kidney load, and would facilitate water retention by the plasma.

When the urine osmolality of *Xerus* is compared with that of other species (Table 4) it appears as if *Xerus* possesses kidneys which are among the most efficient examined to date. In the rat, cat, man, dog, kangaroo rat and jerboa the osmotic ceiling of the urine can be increased by raising the concentration of urea in the urine (Schmidt-Nielsen *et al.*, 1961b). The vast increase in urinary urea and osmolality that occurred in the dry season suggests that *X. inauris* may employ a similar strategy (Table 2).

Most plants do not accumulate sodium and chloride ions to any great extent and herbivores as a consequence tend to be chronically short of these electrolytes (Potts & Parry, 1964). Mammalian homeostasis requires a high plasma level of sodium and chloride and efficient reabsorption of these electrolytes from the urine is very important. The very low levels of sodium in the urine of *X. inauris* in the wet season (Table 2) implies a low sodium level in the diet and an extremely efficient reabsorption of sodium in the kidney. As green grass was the major dietary component in the wet season, it is very likely that these grasses are exceptionally low in sodium (Fig 2).

The higher sodium in the urine in the dry season may be a result of both a higher sodium intake as well as the more efficient reabsorption of water by the kidney. Zumpt (1970) reported that the major food items of *X. inauris* from South Africa are bulbs, corms, roots, green grass, seeds and stems. The results in this investigation support this view (Fig 2, Table 5). However, he also records finding termites, beetles, locusts and other insects in *X. inauris* stomachs. This was particularly so during the breeding season between July and September. It is therefore surprising that during the wet season in the Etosha National Park, when sodium seems to be in short supply, *X. inauris* do not eat insects. This, however, may be due to the relatively small size of our sample.

The maximum renal efficiency of *Xerus* is not apparent from the blood and urine samples. However, kidney structure reflects maximum urine concentrating ability and when this is examined the position of this species, in terms of arid-adaptiveness, becomes apparent.

Table 4 shows the position of various mammals with respect to relative medullary thickness and the maximum urine concentration measured. The bontebok (*Damaliscus dorcas dorcas*) shows a similar urine concentrating ability to the domestic cat whereas the springbok (*Antidorcas marsupialis*) has a slightly lower efficiency than the white rat and is, therefore, superior to *D.d. dorcas*. *X. inauris* falls within the class of desert rodents.

Based on its exceptionally high relative medullary thickness it can be predicted that *X. inauris* should have a maximum urine concentrating ability in the region of 6 890 mOsm/l. This would be one of the highest values recorded in mammals and it would be extremely interesting to test these animals under controlled laboratory conditions to confirm this prediction. These results also suggest that the dry season at Etosha National Park is not sufficiently stressful to elicit maximum urine concentrating potential in *X. inauris*, as the maximum osmolality recorded was only 3 280 mOsm/l. Presumably preformed water in the food and metabolic water is sufficient to meet the requirements of *X. inauris* in the dry season. Moreover, efficient thermoregulatory behaviour probably minimises excessive water loss.

Research on American ground squirrels has shown that these animals employ various strategies to improve water economy in addition to efficient renal function. One of the most important strategies has been the minimisation of water loss by efficient thermoregulation in hot environments (Hudson *et al.*, 1972). This has been achieved in several ways. In North America arid-adapted ground squirrels permit their body

temperature to increase to as much as 45°C before seeking thermal refuge in their burrows, where excess heat can be off-loaded by flattening the body against the cool earth. Most ground squirrels have low basal metabolic rates thus minimising endogenous heat production and, furthermore, peripheral blood circulation can be voluntarily reduced. Under extreme stress, ground squirrels pant and spread saliva over their fur. To what extent *X. inauris* employs these strategies of water conservation and the degree of saving that they would result in is not known.

5 ACKNOWLEDGEMENTS

We wish to thank the Division of Nature Conservation and Tourism for permission to carry out this investigation, and the CSIR for financial assistance.

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TABLE 1: Plasma analyses of *Xerus inauris*

SEASON	N	MEAN	S.D.	RANGE
		Osmolality (mOsm/l)		
Wet	21	240,95	±62,72	168 – 412
Dry	10	257,70	±22,29	220 – 290
		Sodium (mEq/l)		
Wet	22	183,50	±41,79	121 – 281
Dry	10	206,50	±17,81	184 – 242
		Potassium (mEq/l)		
Wet	22	16,65	± 4,68	8,3 – 23
Dry	10	14,61	± 2,81	11,5 – 21
		Urea (mg/100 ml)		
Wet	22	44,62	±16,20	10,4 – 70,4
* Dry	10	86,31	±16,69	54,2 – 105,8

* Significant difference between wet and dry season concentrations ($p < 0,001$)

TABLE 2: Urine analyses of *Xerus inauris*

SEASON	N	MEAN	S.D.	RANGE
		Osmolality (mOsm/l)		
Wet	18	634,1	± 442,8	180 – 1572
**Dry	9	1934,4	± 636,9	1260 – 3280
		Sodium (mEq/l)		
Wet	20	9,9	± 18,9	1 – 74
* Dry	10	27,6	± 22,3	6 – 70
		Potassium (mEq/l)		
Wet	20	152,6	± 76,8	54 – 281
**Dry	10	555,6	± 72,4	448 – 684
		Urea (mg/100ml)		
Wet	20	2526,1	±1559,9	932 – 4658
**Dry	10	8666,5	±3036,6	5721 – 13509

** Significant difference between wet and dry season concentrations ($p < 0,001$)

* Significant difference between wet and dry season concentrations ($p < 0,05$)

TABLE 3: Kidney dimensions of *Xerus inauris*

	N	MEAN	S.D.	RANGE
Mass (g)	44	1,1	±0,21	0,74 – 1,69
Size (mm)	44	12,1	±0,84	10,30 – 14,30
Medulla (%)	10	77,7	±3,60	73,10 – 83,80
Cortex (%)	10	22,3	±3,60	16,20 – 26,90
Relative medullary thickness	10	12,4	±1,16	10,70 – 14,10
Kidney size/body mass × 10 ³	44	2,3		

TABLE 4: Relative medullary thickness (*) and maximum urine/plasma osmotic ratios in selected animals.

Animal	Relative medullary thickness	Maximum urine/plasma osmotic ratio
Beaver (<i>Aplodontia rufa</i>) ¹	1,3	2,7
Man (<i>Homo sapiens</i>) ²	3,0	4,2
Cat (<i>Felis domesticus</i>) ¹	4,8	—
Bontebok (<i>Damaliscus dorcas dorcas</i>) ³	4,9	5,4
Springbok (<i>Antidorcas marsupialis</i>) ⁴	5,5	8,3
White rat (<i>Rattus rattus</i>) ²	5,9	8,9
Jerboa (<i>Jaculus jaculus</i>) ¹	9,3	—
Gerbil (<i>Gerbillus gerbillus</i>) ²	10,5	14,0
Ground squirrel (<i>Xerus inauris</i>) ⁵	12,4	14,9**
Desert mouse (<i>Psammomys obesus</i>) ¹	12,9	17,0

* Calculated as $\frac{\text{medulla thickness (mm)} \cdot 10}{\text{kidney size}}$

Sources: Chew, 1965¹; Gordon, 1972²; van Zyl, 1978³; Hofmeyr & Louw, 1977⁴; and present investigation⁵

** Theoretical maximum

TABLE 5: Plants eaten by *Xerus inauris* in the Etosha National Park during February to March 1976.

1. Grasses: *Aristida edsonionis*
Aristida hordeacea
Enneapogon brachystachyus
Eragrostis annulata
Eragrostis echinocloidea
Eragrostis glandulosipedata
Monelytrum Luederitzianum
Setaria verticillata
Sporobolus tenellus
Tragus racemosus
Urochloa brachyura
2. Herbs: *Erucastrum arabicum*
Geigeria odontoptera
Heliotropium ovalifolium
Hirpicium gazanioides
Sida hoepfneri
3. Shrubs: *Cyathula hereroensis*
Leucosphaera bainesii
Salsola tuberculata