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The effect of water stress on growth and renal performance of juvenile Namib rodents

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Deprivation of water had a profound effect on newly weaned juvenile Namib rodents. Growth rates were depressed and the juveniles consequently reached reproductive maturity later than siblings reared with a free supply of water. In addition, renal performance (as indicated by maximum urine concentration and relative medullary area) was superior in juveniles maintained without an exogenous water supply. Maximum urine concentrations were approximately 1.5 times greater than those of siblings reared with a ready supply of water, suggesting that lack of water in the diet of juveniles has a profound effect on nephron production and development.

Introduction

Arid zones are characterized by infrequent, discrete and largely unpredictable rainfalls (Noy-Meir, 1973) and the Namib desert is no exception. In fact, records of no rainfall for several consecutive years are quite common. It is a well documented phenomenon that arid-adapted adult rodents can survive indefinitely in the absence of free water (Schmidt-Nielsen & Schmidt-Nielsen, 1953; MacMillen & Lee, 1967). Whilst most animals synchronize breeding with the rainy season (Poulet, 1972), the continued success of any small mammal living in these areas depends on its ability to reproduce when conditions are stressful, albeit at a lower rate than when conditions are optimal. Very little is known about the impact of environmental conditions on the development and survival of the offspring of desert rodents. Baverstock & Watts (1975) have reported that growth of offspring is at a depressed rate when lactating rodents are deprived of water. Hewitt (1981) found that juveniles subjected to a diet which included deprivation of water or a high filtered load exhibited renal hypertrophy.

This paper examines the effect of deprivation of water on the development of juvenile Namib rodents from the time they are first weaned.

Methods

Experimental protocol

Eight pregnant *Aethomys namaquensis* and three pregnant *Tatera leucogaster* were collected in the arid zones of Namibia. (*A. namaquensis*: Seeheim 26°50′S–17°45′E, and Tsumis 23°43′S–17°28′E and *T. leucogaster*: Ganab 23°10′S–15°32′E.) Average litter size for

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A. namaquensis was 2.63 ± 0.18; $n = 8$ and for *T. leucogaster* was 4.33 ± 0.33; $n = 3$. The juveniles were removed from their mothers when weaned and the siblings separated into two groups: (i) with an *ad lib* supply of water (FW); (ii) those maintained without free water (F). An attempt was made to separate siblings equally. In instances where the litter size was three, one juvenile was maintained on an *ad lib* supply of water and the remaining two were deprived of water. Both groups were provided with an *ad lib* supply of mixed bird seed. Survival, growth and renal performance of animals within these two groups were then compared.

Growth rates

All juveniles were weighed regularly to the nearest 0.01 g. Reproductive state was determined by examining the external genitalia. Males were considered reproductively mature when testes had descended.

Urine and blood collection and analysis

Urine samples were collected by housing each rodent in a small glass aquarium (300 × 230 mm), which was placed upside down on a stainless steel mesh grid. Urine was collected under light liquid paraffin placed in a container underneath the grid. The urine was pipetted out and stored in plastic vials (Eppendorf 1.5 ml) and frozen (−15°C) until analysis. Only urine uncontaminated by faeces was collected. Blood samples were taken from the canthal sinus of the anterio-dorsal aspect of the orbit. Blood was collected in heparinized capillary tubes and centrifuged for 5 minutes. Haematocrit readings were taken before the plasma was separated from the packed cells and frozen until analysis. Urine and blood concentrations were monitored by measuring their osmolality. This was determined using a vapour pressure osmometer (Wescor, model 5100B).

Kidney morphology

Relative medullary area (RMA) measurements were used as indicators of renal performance. These measurements have been found to give better predictions of maximum urine concentration than measurements of relative medullary thickness (Brownfield & Wunder, 1976). At the end of the experimental period, all animals were sacrificed and their kidneys removed. One kidney from each animal was fixed in 10 per cent formal saline, embedded in paraffin wax, sectioned at 7–10 μ and stained with PAS and haematoxylin. This staining technique accentuates the cortico-medullary boundary. Mid-sagittal sections were placed in the negative holder of a photographic enlarger and the image projected onto paper. The outline of the organ and the cortico-medullary junction were traced onto the paper at a magnification of approximately 20. The cortical and medullary areas were carefully cut out and weighed. The RMA was determined as a ratio of these two weights. Statistical analysis included Student *t*-tests and linear regressions (Zar, 1974). Data were considered statistically significant at $P \leq 0.05$. Unless otherwise stated, mean values and standard errors are given.

Results

Mortality

During the 50 days of monitoring, 36·4 per cent of the juvenile *A. namaquensis* in group F died. In addition, one sickly animal was provided with water and excluded from further data. No juvenile *A. namaquensis* in group FW died (Table 1). No juvenile *T. leucogaster* from either group died or were excluded during the experimental period.

Growth

Differences in growth rates in juvenile *A. namaquensis* in group F and FW (as determined by comparing the slopes of regression lines in Fig. 1) were significant ($P \leq 0.001$). Juveniles maintained without a free water supply grew more slowly and 3 weeks after weaning showed only 58 per cent of the increase in mass of those in the FW group. Similar trends were observed in juvenile *T. leucogaster* (Table 1). *A. namaquensis* had, however, significantly greater growth rates than *T. leucogaster* in the same group ($P \leq 0.01$ for the F group and $P \leq 0.001$ for the FW group). Reproductive maturity was reached later in both species in the F group. Descended testes were only observed when the male juveniles were approximately 53 days old, whereas descended testes were observed 8–10 days earlier in males maintained in the FW group.

Renal performance

The RMA and observed maximum urine concentrations were significantly greater ($P \leq 0.05$) in juvenile *A. namaquensis* maintained without water (Table 1). Similar trends were observed in juvenile *T. leucogaster*; however, RMA values and urine concentrations were considerably greater than those of *A. namaquensis*. Plasma concentrations, on the other hand, were similar irrespective of group or species ($P \leq 0.10$).

Discussion

Very little information is available concerning the field biology of Namib desert rodents. The scant available data suggest that they are primarily granivorous (Withers, 1979) and that breeding rodents have been collected shortly after the rains (Christian, 1979; Withers, 1983). In the laboratory, absence of water during the first 2 months after weaning had a profound effect on body growth and on renal performance. This no doubt resulted from an attempt to balance their water requirements with that available. Not only were their

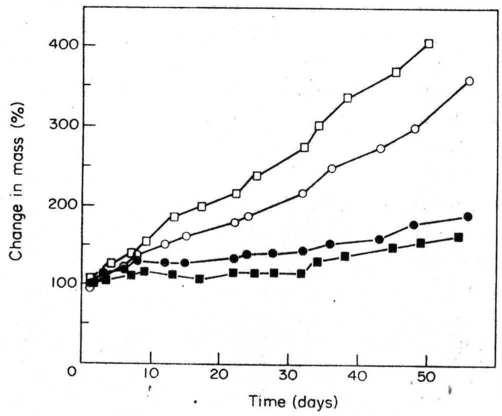

Figure 1. Mean changes in body mass for (■ □) *Aethomys namaquensis* and (● ○) *Tatera leucogaster*. Solid symbols (■ ●) represent juveniles reared in the absence of water and open symbols (□ ○) represent juveniles reared with water freely available.

Table 1. *A comparison of growth rates and renal performance in juvenile rodents reared in the absence of water (F) and with water freely available (FW)*

	FW			F			P†
	x̄	se	n	x̄	se	n	≤
				Aethomys namaquensis			
Mortality (%)	0·00	—	—	36·40	—	—	
Max. urine conc. (mOsm. l^{-1})	3490·00	236·00	6	4835·00	449·00	7	0·03
Max. plasma conc. (mOsm. l^{-1})	353·00	9·00	6	366·00	11.00	7	0.44
RMA	0·99	0·11	6	1.34	0·07	7	0·02
Change in mass at 3 weeks (%)	216·00	21·00	6	115·00	11·00	7	0·001
Growth rate equation*	$y = 94{\cdot}2$	$+ 6{\cdot}16x$		$y = 103{\cdot}0$	$+ 0{\cdot}84x$		0·001
				Tatera leucogaster			
Mortality (%)	0·00	—	—	0·0	—	—	
Max. urine conc. (mOsm. l^{-1})	4753·00	355·00	4	7767·00	652·00	3	0·007
Max. plasma conc. (mOsm. l^{-1})	360·00	21·00	4	374·00	21·00	3	0·773
Change in mass at 3 wks (%)	178·00	8·00	4	132·00	3·00	3	0·002
Growth rate equation*	$y = 91{\cdot}2$	$+ 4{\cdot}45x$		$y = 107{\cdot}1$	$+ 1{\cdot}35x$		0·001

* The equation represents the linear regression through the data in Fig. 1; y is change in mass (%), x is time (days).
† is the probability of data being significantly different.

growth rates approximately 60 per cent of that of their siblings in FW, but these animals took longer to become reproductively active. In the field, when water is scarce, there is a concomitant decline in food supply and it is possible that, under these conditions, growth rates would be depressed even more severely. Lowered growth rates, coupled with delayed onset of reproductive maturity and breeding would maintain energy requirements at a minimal level, and would thus enhance the chance of survival under adverse conditions. Conversely, when resources are readily available, rapid growth and the early attainment of reproductive maturity would ensure that the bulk of the available energy is channelled into reproduction.

Renal performance

The juveniles in group F produced a significantly ($P \leq 0.05$) more concentrated urine than those in group FW, when both groups were deprived of water. Plasma concentrations, on the other hand, were similar, suggesting that kidney concentrating ability was better in juveniles reared without water. Indeed, their RMA measurements were significantly greater ($P \leq 0.05$) than those of juveniles in FW and also than those obtained from field collected adults (in preparation). These findings suggest that the low water in the diet of newly weaned animals can significantly alter their kidney morphology leading to an increase in renal medullary tissue. Hewitt (1981) found similar increases in RMA and suggested that water deprivation in immature murids induced kidney growth and the development of substantially more nephrons with long loops of Henle, thus compensating for the reduced water availability.

It could be argued that with the higher mortality rate in the F group, the observed changes in renal efficiency are due solely to selection of those juveniles with more efficient kidney genotypes rather than changes directly induced by water stress. Whilst this is no doubt true to a certain extent, it does not apply to *T. leucogaster*, where no mortality occurred. Furthermore, the differences in kidney concentrating ability between siblings with or without water were so marked that they strongly suggest that a lack of water in the diet has a profound effect on nephron development.

It was also found that the water deprived siblings of both species voided a significantly ($P \leq 0.05$) more concentrated urine than any field collected animal, again suggesting that the results obtained were not simply due to selection of better adapted individuals within the population. Water deprived *T. leucogaster* produced the most concentrated urine of all the experimental animals. In fact, maximum urine concentrations of these individuals were within the same range as that of *Notomys alexis* (MacMillen & Lee, 1967) and *Leggadina hermansburgensis* (MacMillen *et al.*, 1972), animals purportedly producing the most concentrated urine. In the light of these findings, care should be taken when interpreting comparative data on renal performance of field caught animals. Obviously, a knowledge of the early life history is essential, if meaningful comparisons are to be made.

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