ENARA 288

J Comp Physiol B (1985) 155:211–218

Journal of Comparative Physiology B Biochemical, Systemic, and Environmental Physiology

© Springer-Verlag 1985

- no dates, lab study
- G. paeba, Aethomys namaquensis -

The effect of a high fibre diet on energy and water balance in two Namib desert rodents

Rochelle Buffenstein 1985
University of Cape Town, Rondebosch 7700, South Africa

Accepted July 14, 1984

Summary. The effect of dietary fibre content on food consumption, digestive ability and water balance was studied in two Namib desert rodents, *Aethomys namaquensis* and *Gerbillurus paeba*. In addition, changes in these factors were monitored when free water was withheld.

1. Daily energy expenditure (DEE) for *A. namaquensis* remained fairly constant and similar to that predicted by mass despite changes in food and water regimes. The DEE in *G. paeba* was more variable. On a millet (low-fibre) diet with ad lib. water DEE was 35% higher than the expected value. This increased still further within the first week of water deprivation before dropping back to pre-water deprivational levels once mass had stabilized. On the high fibre diet, the DEE of *G. paeba* was similar to that predicted by mass when water was freely available. This was reduced by half when the animals were water stressed, suggesting that *G. paeba* might employ torpor under these circumstances.

2. Water balance was assessed by measuring water intake and loss. Faecal water content when maintained on a millet diet was similar in both species, irrespective of whether water was freely available or withheld. However, urine concentrations and estimated evaporative water losses were higher in *G. paeba*. Observed differences in water loss are largely a function of variables related to weight specific metabolic rate. Differential water losses were offset by differences in metabolic water production, enabling both species to attain a positive water balance and survive indefinitely on a millet diet.

3. When provided with a more fibrous diet, low assimilation efficiency and the resulting increase in faecal production, coupled with increased faecal water content, increased faecal water loss to such an extent that it precluded the maintenance of a positive water balance in either species. Despite increased urine concentration and a decline in evaporative water loss, both species rapidly succumbed to chronic water deprivation.

Introduction

Deserts have been defined as 'areas where the environment places insurmountable obstacles in the way of its inhabitants' (Schmidt-Nielsen 1979). Consequently, interest in adaptation of animals to these environments is considerable (reviews: Schmidt-Nielsen 1964; Louw and Seely 1982; MacMillen and Hinds 1983).

The Namib desert, on the south-western coast of Africa, is an extremely arid environment in which the annual evapo-transpiration greatly exceeds the mean annual precipitation. This has had a profound effect on the quality and sources of food available to the rodent inhabitants. Potential foods vary in their preformed water content and in the degree of digestibility. The latter may affect energy and water balance, in that it controls the dietary energy and hence the amount of metabolic water liberated per gram of food consumed. In addition, it influences the amount of water lost through production of faeces (Withers 1982). Apart from the preformed water content, however, the importance of diet and digestive ability has

---

Abbreviations: *DEI* daily energy intake; *GEI* gross energy intake; *FE* faecal energy; *ME* energy from the mobilization or deposition of fat; *DEE* daily energy expenditure; *AE* apparent assimilation efficiency; *MWP* metabolic water production; *EWL* pulmo-cutaneous evaporative water loss; © SW change in the amount of stored water been generally overlooked in studies of water balance.

The rock rat, *Aethomys namaquensis*, and the pigmy gerbil, *Gerbillurus paeba*, whilst occupying different microhabitats in the Namib desert, are subject to similar energetic and water constraints. This study compares the energy and water balance of these two Namib species when the animals are fed low fibre (millet) and high fibre (bran) diets, both with and without drinking water.

Materials and methods

Experimental protocol. Rodents were trapped in the Namib Desert Park at Tumasberg (23° 29′S; 15° 32′E) and near Gobabeb (23° 34′S; 15° 03′E). Fifteen gerbils and twelve rock rats were housed individually in an air-conditioned laboratory (20 ± 2 °C, $52.3 \pm 9\%$ relative humidity) with a twelve hour photoperiod. Prior to experimental treatments, rodents were maintained in plastic hamster cages with a sand substrate. Sand was removed during experimental runs to prevent the contamination of food and faeces.

Over a six month period, all rodents were subjected to an experimental diet of golden millet followed by Kelloggs 'high bulk bran' (Table 1). A six week transition period occurred between these two experimental food treatments, during which the animals were provided an ad lib. supply of sunflower seeds, millet, oats, barley, bran and fresh vegetables. Throughout the transition period, the proportion of high bulk bran was gradually increased until, during the last week, a pure bran diet was supplied. It was only after this that the quantity of bran consumed was monitored. Bran was chosen as the high fibre food source after an abortive attempt at using dry lucerne as a food source. Bran was fairly stressful even under ad lib. water conditions, causing most rodents to lose weight.

For the first two weeks of each experimental food treatment, free water was supplied. During this period, food and water consumption were monitored. Water bottles were then removed and exogenous water was supplied in the form of lettuce. Lettuce was gradually eliminated over an eight day period; five days thereafter, daily energy intake (DEI) and associated parameters were monitored. Water deprivation experiments were terminated when two animals of each species had succumbed to hydropenia (deprivation of water).

All rodents were subjected to a sequence of two different water regimes: (i) an ad lib. supply, (ii) the withholding of all exogenous water. After experimental periods of six and twelve days, urine, faecal samples and 200 μl of blood were collected.

Energy balance measurements. An energy balance was calculated by assuming that energy intake should equal energy expended plus changes in energy stored within the body:

$$DEE = GEI - (FE + U) + ME$$

where DEE is the daily energy expenditure; GEI is the gross energy intake; FE is the faecal energy; U is urine energy content (ignored in these calculations because it has been reported to constitute a neglibible fraction of energy exchange; Grodzinski and Wunder 1975); ME is the energy content of changes in fat stores. The daily energy intake (DEI), often referred to as energy assimilated, was determined gravimetrically as the difference between the energy content of food consumed (Gross Energy Intake; GEI) and faeces produced per day. Food consumption was determined by initially supplying a known quantity of food greatly in excess of the rodents' requirements. Unconsumed food was collected and weighed after six and twelve days. Control samples of food were monitored to correct for any weight changes due to desiccation or water absorption. Faecal production was determined by collecting all the faeces produced during the monitored periods. The energy content of the food and faeces was determined by microbomb calorimetery.

Table 1. Food values of the two diets supplied to the animals

	Millet	High-bulk bran
Energy ($kJ \cdot g^{-1}$)[a]	20.88	18.15
Protein (%)	12.7	18.0
Carbohydrate (%)	57.4	72.0
Fat (%)	3.5	1.4
Crude fibre (%)	0.4	6.0
Dietary fibre (%)	1.0	30.0
Preformed water (%)	9.0	5.0

[a] Energy content was determined in this study. All other millet values were taken from Leung and Rao (1972). High-bulk bran data were supplied from the cereal manufacturers, Kelloggs (Braamfontein)

'Apparent' assimilation efficiency (AE) was calculated as:

$$AE = 100 \times DEI/GEI.$$

Daily energy expenditure (DEE) differed from DEI because of changes in the energy stores within the body. Only non-breeding adult rodents were used and thus it was assumed that changes in weight were due to fat deposition or mobilization only. Daily energy expenditure was thus calculated by correcting DEI for energy changes due to the mobilization and deposition of fat (23.36 $kJ \cdot g^{-1}$ of fat mobilised and 33.9 $kJ \cdot g^{-1}$ of fat deposited; Jagosz et al. 1979). The DEE values determined this way are maximal estimates.

Water balance measurements. Water balance measurements were based on the assumption that water intake equals water loss. Water intake was determined by weighing the drinking bottles initially and again at the end of the two six-day monitoring periods. Control bottles were kept so as to enable correction for water loss due to evaporation and handling. Preformed water in the millet and bran was determined by drying known quantities of seed at 60 °C to constant mass. Metabolic water was calculated assuming 0.03 ml water per kJ of energy expended (Schmidt-Nielsen 1975).

Faecal water content was determined from faeces voided whilst the rodents were handled. Faeces were weighed to the nearest 0.01 mg as soon as possible after voiding, and then again after they were dried at 60 °C to constant mass.

Water loss in the urine was determined by collecting 24-h urine samples under light liquid paraffin on the sixth and twelfth day of each experiment. Each urine sample was weighed and its mass converted into volume using a correction obtained from the weight of a 10 μl aliquot of that sample.

Pulmocutaneous evaporative water loss (EWL) and changes in stored water were not measured, however, minimum and maximum estimates were extrapolated from the water balance equation:

$$D + P + MWP1 + MWP2 + \copyright SW = U + F + EWL$$

where D is water drunk; P is preformed water in food; MWP1 is the metabolic water produced from oxidization of the food eaten; MWP2 is the metabolic water produced as a result of the oxidization of mobilised fat; © SW is the change in stored water; U is water lost in urine; F is water lost in faeces; and EWL is evaporative water loss. Minimum and maximum estimates of EWL are calculated from the water balance equation, by assuming that weight changes are either entirely due to fat mobilization (MWP2) or are due to dehydration (© SW).

On the sixth and twelfth days of each experiment 200 µl of blood were taken from the canthal sinus on the anteriodorsal aspect of the orbit, according to the method of Halpern and Pacaud (1951). After haematocrits were taken, plasma was separated and frozen in sealed capillary tubes.

Statistical analyses included Student's *t*-tests and, where applicable, paired *t*-tests (Zar 1974).

Results

Both species survived water deprivation when provided with millet. However neither species survived water deprivation when their diet consisted only of high bulk bran. On the bran diet, three *G. paeba* died within seven days of water-deprivation and two *A. namaquensis* died on the eighth day. The severity of the bran diet in the absence of free water is also indicated by the rapid weight loss shown by both species (Fig. 1).

Energy balance

Water available

i) Millet: Both species when provided with millet showed similar digestive ability ($P \geqq 0.10$) and changes in mass ($P \geqq 0.10$). However, species differences in rates of food consumption, faecal production and GEI (Tables 2 and 3) were significant ($P \leqq 0.05$), resulting in very different DEIs and DEEs ($P \leqq 0.001$). This difference in DEE does not merely reflect differences in mean body mass, for percentage deviations were significantly different from values predicted by mass for a granivorous rodent using Grodzinski and Wunder's (1975) allometric equation.

ii) Bran: Despite the fact that bran was gradually introduced into the diet, this food was generally avoided. DEI values when bran was the only food source were insufficient to meet the DEE requirements and even under conditions of ad lib. water, mass declined. The apparent assimilation efficiency of this diet was low (Table 3), reflecting the high fibre content of this food supply, and no species difference was observed.

Water deprived

i) Millet: Gerbillurus paeba and *A. namaquensis* showed different dietary responses to water deprivation when maintained on a millet diet. *Gerbillurus paeba* lost weight rapidly and, if mass change is assumed to result from fat mobilization, DEE increased during the first week of deprivation of water. Once body mass stabilized DEE rates returned to within the range observed under ad lib. water conditions (Table 2). *Aethomys namaquensis* lost weight more gradually but continued to do so for much longer (Fig. 1). No significant changes in DEE were observed in any of the energetic balance variables monitored on the millet diet in the presence and absence of drinking water (Table 2) in this species.

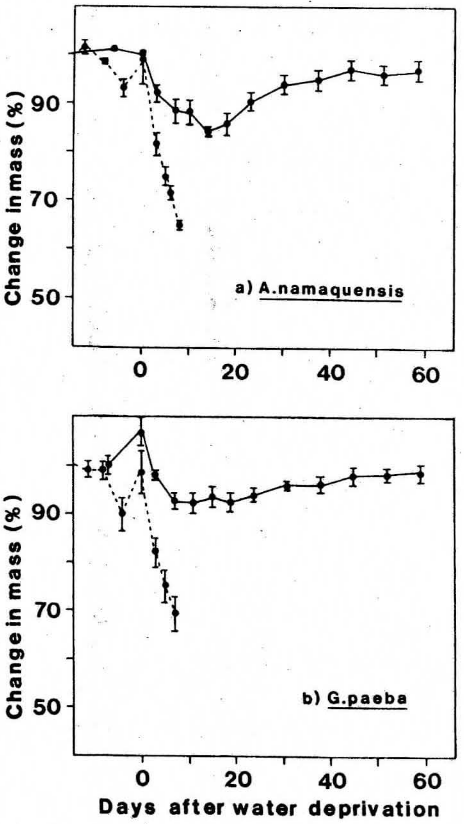

Fig. 1. Changes in mass for *Aethomys namaquensis* (top) and *Gerbillurus paeba* (bottom) when deprived of water on i) a low fibre diet of millet (solid lines) and ii) a high fibre diet of bran (dashed lines). Values are means ± SEM

ii) Bran: The DEI of both species declined significantly with water deprivation on a bran diet; although the AE of both species remained unchanged (Table 3). Both species rapidly lost weight and it is assumed therefore that they responded to this decline in energy intake by mobilising fat reserves. In *A. namaquensis*, there was complete compensation such that DEE was similar under both treatments of water, whereas in *G. paeba*, there was a 45% decline in DEE after water deprivation.

Table 2. Influence of water availability on the energy balance of *Aethomys namaquensis* and *Gerbillurus paeba* when maintained on a low fibre diet (millet)

	$+H_2O$		$-H_2O$ 1 week		$-H_2O$ 2 weeks	
	$\bar{x}$ ±	SD	$\bar{x}$ ±	SD	$\bar{x}$ ±	SD
Aethomys namaquensis						
No. of animals	8		8		8	
Mean weight (g)	51.86	10.63	47.73	11.07	46.53	10.43
Food consumed (mg·g^{-1}·day^{-1})	78.48	7.50	69.51	10.30	73.65	10.16
Faecal production (mg·g^{-1}·day^{-1})	4.78	1.72	4.56	2.25	4.42	2.04
Mass change (mg·g^{-1}·day^{-1})	2.40	2.43	− 7.36	7.37	2.59	12.08
GEI[a] (kJ·g^{-1}·day^{-1})	1.64	0.16	1.45	0.22	1.54	0.21
FE[a] (kJ·g^{-1}·day^{-1})	0.09	0.03	0.09	0.04	0.08	0.04
ME[a] (kJ·g^{-1}·day^{-1})	− 0.08	0.08	0.18	0.17	− 0.08	0.28
DEI[a] (kJ·g^{-1}·day^{-1})	1.55	0.15	1.36	0.20	1.45	0.20
DEE[a] (kJ·g^{-1}·day^{-1})	1.46	0.13	1.55	0.12	1.53	0.17
AE[a] (%)	94.31	1.95	93.98	2.43	94.60	2.27
DEE[a] (%)	107.81	13.76	114.76	6.33	106.76	20.31
Gerbillurus paeba						
No. of animals	8		8		7	
Mean weight (g)	27.90	4.36	26.52	4.61	25.83	4.85
Food consumed (mg·g^{-1}·day^{-1})	124.58	14.22	115.56	18.90	129.67	15.79
Faecal production (mg·g^{-1}·day^{-1})	6.35	2.09	4.73	1.41	5.39	1.27
Mass change (mg·g^{-1}·day^{-1})	0.05	10.39	−17.98	11.90	3.14	5.11
GEI[a] (kJ·g^{-1}·day^{-1})	2.60	0.30	2.41	0.39	2.71	0.33
FE[a] (kJ·g^{-1}·day^{-1})	0.12	0.04	0.09	0.03	0.10	0.03
ME[a] (kJ·g^{-1}·day^{-1})	− 0.04	0.29	0.42	0.28	− 0.13	0.16
DEI[a] (kJ·g^{-1}·day^{-1})	2.48	0.26	2.32	0.40	2.60	0.31
DEE[a] (kJ·g^{-1}·day^{-1})	2.48	0.27	2.74	0.29	2.50	0.31
AE[a] (%)	95.53	1.12	96.15	1.34	96.21	0.72
DEE[a] (%)	134.92	7.92	145.46	9.20	130.97	15.76

[a] *GEI* gross energy intake; *FE* faecal energy; *ME* energy from mobilization or deposition of fat; *DEI* daily energy intake; *AE* assimilation efficiency; % *DEE* percentage of the predicted daily energy expenditure as calculated from Grodzinski and Wunder's (1975) allometric equation

Table 3. Influence of water availability on the energy balance of *Aethomys namaquensis* and *Gerbillurus paeba* on a high fibre diet (bran)

	Aethomys namaquensis				*Gerbillurus paeba*			
	$+H_2O$		$-H_2O$		$+H_2O$		$-H_2O$	
	$\bar{x}$ ±	SD	$\bar{x}$ ±	SD	$\bar{x}$ ±	SD	$\bar{x}$ ±	SD
No. of animals	8		7		7		5	
Mean weight (g)	55.45	11.72	39.58	11.64	26.65	3.99	18.99	2.05
Food consumed (mg·g^{-1}·day^{-1})	90.13	17.40	34.03	6.50	151.30	49.63	37.09	11.78
Faecal production (mg·g^{-1}·day^{-1})	35.72	10.10	11.60	2.16	56.29	18.63	13.31	6.03
Mass change (mg·g^{-1}·day^{-1})	−12.56	7.38	−47.27	7.38	−2.86	9.84	−25.80	7.16
GEI[a] (kJ·g^{-1}·day^{-1})	1.64	0.32	0.62	0.12	2.78	0.88	0.67	0.27
FE[a] (kJ·g^{-1}·day^{-1})	0.60	0.17	0.20	0.04	0.99	0.33	0.24	0.11
ME[a] (kJ·g^{-1}·day^{-1})	0.29	0.17	1.11	0.18	0.04	0.27	0.60	0.17
DEI[a] (kJ·g^{-1}·day^{-1})	1.04	0.25	0.42	0.11	1.79	0.56	0.39	0.11
DEE[a] (kJ·g^{-1}·day^{-1})	1.33	0.19	1.52	0.25	1.83	0.40	1.03	0.12
AE[a] (%)	63.31	8.69	66.82	6.10	64.45	2.10	64.58	7.02
DEE[a] (%)*	101.99	13.40	98.76	21.89	97.99	22.08	46.85	6.66

[a] *GEI* gross energy intake; *FE* faecal energy; *ME* the energy from the mobilization or deposition of fat; *DEI* daily energy intake; *AE* assimilation efficiency; *DEE* %* the percentage of the predicted daily energy expenditure as calculated from Grodzinski and Wunder's (1975) allometric equation

Table 4. The effect of low fibre (millet) and high fibre (bran) on the drinking rates, urine production, faecal water loss and plasma and urine osmolality in *Aethomys namaquensis* and *Gerbillurus paeba*, kept both with and without drinking water

	Drinking rate (mg $H_2O \cdot g^{-1} \cdot day^{-1}$)		Urine production (mg $H_2O \cdot g^{-1} \cdot day^{-1}$)		Plasma conc. (mOsm·l^{-})		Urine conc. (mOsm·l^{-})		Faecal water content (%)		Faecal water loss (%)	
	$\bar{x}$	± SD	$\bar{x}$	± SD	$\bar{x}$	± SD	$\bar{x}$	± SD	$\bar{x}$	± SD	$\bar{x}$	± SD
Millet												
A. namaquensis												
$+H_2O$	95.2	30.4	20.9	6.0	332	36	1,762	914	53.08	2.98	3.97	2.04
$-H_2O$ 1 week	–		8.3	4.1	–		3,263	474	45.35	2.86	7.16	3.38
$-H_2O$ 2 weeks	–		8.1	3.2	396	52	3,732	610	45.70	2.96	6.97	2.69
G. paeba												
$+H_2O$	117.1	47.7	40.8	18.1	350	37	2,576	1,178	54.01	3.31	3.79	1.31
$-H_2O$ 1 week	–		5.8	2.3	–		3,956	499	44.52	2.57	4.11	1.14
$-H_2O$ 2 weeks	–		4.4	2.8	426	57	4,150	1,087	46.47	3.59	5.38	1.04
Bran												
A. namaquensis												
$+H_2O$	215.5	72.7	56.9	5.6	337	51	1,710	197	58.05	0.71	21.39	8.95
$-H_2O$	–		8.5	4.3	414	64	4,396	837	50.68	1.95	25.41	4.97
G. paeba												
$+H_2O$	283.9	58.2	109.6	37.3	362	49	1,679	313	60.97	1.47	28.81	12.32
$-H_2O$	–		4.6	2.9	471	68	5,615	816	49.99	1.20	41.07	20.54

Water balance

Drinking rates of the two species were not significantly ($P \geqq 0.10$) different (Table 4). Both species drank significantly more water ($P \leqq 0.001$) on the bran diet than when millet was the food source (Table 4). Species differences in total water intake, however, reflect mainly differences in the amount of water liberated from their different rates of metabolism (Table 5).

When water was deprived, urine production of both species declined markedly on both diets, although it was most pronounced when bran was the food source (Table 4). Urine concentration was inversely proportional to the quantity of urine produced and was highest when the rodents were on a diet of bran (Table 4).

Estimated EWL of both species were similar ($P \geqq 0.10$), irrespective of diet, when drinking water was freely available. EWL declined markedly with hydropenia, irrespective of diet, in both species. *Aethomys namaquensis* showed lower rates of EWL than *G. paeba* ($P \leqq 0.001$) when deprived of water on a millet diet. The converse was true on a bran diet, where EWL of *G. paeba* was significantly lower ($P \leqq 0.01$) than that of *A. namaquensis.*

Both species, irrespective of diet, produced faeces with similar water contents ($P \geqq 0.1$). When deprived of water, faecal water content declined (Table 4). Faecal water content was greater on the bran diet than on the millet diet. Consequently, when maintained on a bran diet, faecal water loss contributed significantly more to the total water flux (Table 5).

Discussion

Millet

i) Water available: The DEE observed for both *G. paeba* and *A. namaquensis* fell within the range expected for rodents (Grodzinski and Wunder 1975; French et al. 1976). The DEE for *A. namaquensis* was similar to that expected (Withers et al. 1980), whereas that of *G. paeba* was far greater than predicted by mass for a granivorous rodent, indicating a greater propensity of *G. paeba* to supplement its seed diet with insects (Grodzinski and Wunder 1975). This is confirmed by stomach content data (unpublished observation, and Withers 1979). Both species maximally utilized their food source, having high assimilation efficiencies.

ii) Water deprived: Both *A. namaquensis* and *G. paeba* were able to survive on a millet diet without exogenous water for 10 weeks. This ability to survive indefinitely without water (Schmidt-Nielsen 1964; Chew 1965; Shkolnik and Borut 1969; Bradley and Yousef 1972; MacFarlane 1975) is due to

Table 5. Influence of diet and hydropenia on water balance in *Aethomys namaquensis* and *Gerbillurus paeba*. All values given are in mg $H_2O \cdot g^{-1} \cdot day^{-1}$

	Millet			Bran	
	$+H_2O$	$-H_2O$ 1 wk	$-H_2O$ 2 wk	$+H_2O$	$-H_2O$
A. namaquensis					
Intake					
Drunk	95.2	–	–	215.5	–
Preformed	7.1	6.3	6.6	4.6	1.8
MWP food[a]	46.5	40.8	43.5	31.4	12.4
MWP fat[b]	−2.4	5.4	−2.5	8.7	33.3
SW[c]	−2.4	7.4	−2.6	12.6	47.3
Min total[d]	146.4	52.5	47.6	260.2	47.5
Max total[d]	146.4	54.5	47.7	264.1	61.5
Loss					
Urine	20.9	8.3	8.1	56.9	8.5
Faeces	5.4	3.8	3.7	49.4	11.9
Min EWL[e]	120.1	40.4	35.8	153.9	27.1
Max EWL[e]	120.1	42.4	35.9	157.8	41.1
G. paeba					
Intake					
Drunk	117.1	–	–	283.9	–
Preformed	11.2	10.0	11.7	7.3	1.9
MWP food[a]	74.4	69.6	78.0	53.8	13.0
MWP fat[b]	−1.2	12.6	−3.9	1.2	18.0
SW[c]	−0.1	18.0	−3.1	2.9	25.8
Min total[d]	201.5	92.2	85.8	346.7	32.9
Max total[d]	202.6	97.6	86.6	348.4	40.7
Loss					
Urine	40.8	5.8	4.4	109.6	4.6
Faeces	7.5	3.8	4.7	102.4	13.3
Min EWL[e]	153.2	82.6	76.7	134.7	15.0
Max EWL[e]	154.3	88.0	77.5	136.4	22.8

[a] MWP is metabolic water production, assuming 0.03 ml of water are liberated per kJ metabolized

[b] Assuming all loss of mass is metabolic substrate

[c] Assuming all loss of mass is water

[d] Totals are determined by including either MWP fat or S in water intake

[e] EWL is evaporative water loss estimated from the water balance equation assuming water intake = water loss

reductions in evaporative, faecal and urinary water losses.

Gerbillurus paeba showed a greater weight loss in response to hydropenia (Fig. 1) which was reflected in the significant increase in DEE in the first week of water deprivation. This increase in DEE can be attributed to fat mobilization (assuming that all mass change is due to fat mobilization and not dehydration) and might therefore reflect increased initial metabolic stress or hyperactivity resulting from increased searching for a water supply. Thereafter, weight stabilized in this species and the DEE returned to predeprivational rates. *Aethomys namaquensis* showed a more gradual weight loss (Fig. 1). It continued to lose weight throughout the period when food consumption was monitored and in doing so, helped to maintain the DEE at approximately the same level as under ad lib. water conditions. The coefficient of digestive ability remained high with water deprivation which not only allows the maximum utilization of resources, but reduces the faecal output, thereby reducing the quantity of water lost through the faeces.

Weight-relative water requirements of the two species were found to be significantly different ($P \leq 0.05$). *Gerbillurus paeba*, having a higher DEE, liberated more metabolic water ($P < 0.001$). These estimates of daily water turnovers were within the range observed for most xerophilic rodents (MacFarlane et al. 1971; Holleman and Dietrich 1973; Yousef et al. 1974; Hewitt et al. 1981).

Gerbillurus paeba was initially more stressed by water deprivation. However after six days without free water, mass stabilized. Because *G. paeba* has a smaller body size than *A. namaquensis* its surface-area/volume ratio and weight specific metabolic rates are higher, causing a higher rate of evaporative water loss and greater water stress. As with other desert rodents (Haines and Shield 1971; Christian et al. 1978), evaporative water loss declined with hydropenia in both species. Reduced urinary water loss in *G. paeba* was facilitated through an approximate two-fold increase in urine concentration and the excretion of some nitrogenous wastes as a solid precipitate of allantoin (Buffenstein et al., in preparation).

Aethomys namaquensis gradually lost weight over a longer period. Total metabolic water liberated exceeded water lost through pulmocutaneous evaporation ensuring virtual independence of exogenous water. Although *G. paeba* reduced urinary water loss while *A. namaquensis* reduced evaporative water loss (Table 5), both species were able to maintain a positive water balance on millet.

Bran

i) When millet was replaced with a more fibrous diet, neither species was able to maintain a positive water balance. The digestive ability coefficient on this diet was much lower than that of millet. Digestive ability varies inversely with fibre content in *Microtus pennsylvanicus* (Shenk et al. 1970). Digestive ability on a bran diet was lower than recorded for rodents on a natural diet (Johnson and Schreiber 1979) and would therefore be more stressful. Whilst 30% of bran is indigestible fibre, the low assimilation efficiency suggests that less of the potentially digestible food was digested. This probably resulted from faster rate of passage through the gut. A concomitant increase in faecal production and decrease in DEI accompanied this low digestive ability in both species. The GEI was not significantly different ($P \geqq 0.10$) to that on a millet diet in either species. Both species attempted to adjust intake to meet the requirements for nutrition. The low digestive ability and finite capacity of their stomachs, however, prevented the achievement of a constant DEI. The deficit in energy intake was rectified by mobilizing fat reserves even under ad lib. water conditions. *Gerbillurus paeba* showed a greater weight specific GEI and related faecal output than *A. namaquensis*, accounting for its higher DEE.

ii) Water deprived: When water deprived, GEI in both species was markedly reduced. This seems to be maladaptive for less water of metabolism would be liberated: Assuming GEI when hydropenic was the same as that when water was supplied ad lib., both species would show a negative water balance only when the percentage faecal water content of hydropenic animals was the same as that of rodents supplied with drinking water (Tables 4 and 5). Therefore, the only way increasing or maintaining GEI could be disadvantageous, would be if the animals could not control the hydration of the faeces. If a low water content of faeces comes about only by having a slow rate of passage (enabling more absorption of water) and a low rate of passage can only occur by eating less bran, then a high GEI and a low faecal water content are mutually exclusive. Even with the decline in food consumption, faecal water loss during hydropenia was 3–4 times greater than on the millet diet.

Aethomys namaquensis maintained similar levels of DEE on both diets, by balancing the energy intake deficit with energy stored as fat. In addition, the apparent assimilation efficiency increased with hydropenia, although it was still much lower than on a millet diet. This is a common occurrence when food intake is reduced. Reduced food intake probably allowed for a slower rate of passage and hence the opportunity for more absorption of both water and nutrients. It is not known whether *A. namaquensis* uses coprophagy, but it has been seen licking faeces in the laboratory. Under stressful conditions coprophagy would be advantageous.

Gerbillurus paeba showed a marked decrease in DEE accompanied by declines in evaporative water loss and in apparent assimilation efficiency, suggesting that it employs torpor under these circumstances. Similar declines have been observed in *Gerbillus pusillus* in torpor (Buffenstein 1984).

Neither species survived more than eight days without free water. Their inability to survive may be attributed to their low assimilation efficiency and the resulting increase in faecal water loss. Although *A. namaquensis* consumes proportionately more fibrous food than *G. paeba* in its natural diet (unpublished data) and its gastro-intestinal tract is morphologically better adapted to handle fibrous food, through caecal fermentation (unpublished data), it too could not survive dry high fibre diets. The significance of faecal water loss to water balance is seen in Tables 4 and 5. Because of the marked decline in mass, it is extremely difficult to estimate accurately the energy budget during hydropenia. Mass decline has little effect on water balance (Table 5) in that the quantity of water liberated by the catabolism of fat ($1.1\ \mathrm{g\ H_2O \cdot g^{-1}}$) is approximately equal to the amount of water assuming all mass changes are due to dehydration.

It does appear that when on a bran diet, water was mobilised from various compartments and that these rodents had become dehydrated. This was shown by elevated haematocrits and increased plasma osmolality in both species. Similar haemoconcentration has been observed in other arid-dwelling rodents e.g. *Dipodomys* (Kenagy 1973; Scelza and Knoll 1982), *Gerbillus, Jaculus* (Haggag and El Husseini 1974), *Rattus* (Baverstock 1976) and *Meriones* (Donaldson and Edwards 1981).

Urine volumes on a bran diet declined to 60% of those in animals deprived of water on a millet diet. Maximum urine concentration on a bran diet was higher than in rodents on a protein-loaded diet (unpublished data) and were also greater than that predicted by relative medullary area; $3850\ \mathrm{mOsm \cdot kg^{-1}}$ for *A. namaquensis* and $4606\ \mathrm{mOsm \cdot kg^{-1}}$ for *G. paeba* (unpublished data). Concentrations higher than those predicted by relative medullary area measurements (Brownfield and Wunder 1976) have also been observed in *Dipodomys*, *Notomys* and *Jaculus* (Deavers and Hudson 1979; Hewitt 1981).

It is evident that increased faecal water loss (Table 5), as a result of the high fibre content of the bran diet, was primarily responsible for the negative water balance obtained during hydropenia. Faecal water loss is normally overlooked, as most water balance studies provide rodents with a seed diet where digestive ability approaches a physiological maximum. Faecal water loss under these circumstances is proportionately low (<8%). It is obvious, then, that diet selection against high fibre foods in the wild would be critical during the periods when water is severely limiting.

Acknowledgements. Professor JUM Jarvis is sincerely thanked for reviewing this manuscript. Dr E Joubert, M Griffin and the SWA Department of Nature Conservation are thanked for their encouragement and for permission to work in the Namib Desert Park. Dr CG Coetzee of the State Museum, Windhoek, kindly lent Sherman traps. D Gianakouros is also thanked for her help with the microbomb calorimetry. This work was partially funded by a CSIR bursary.

References

Baverstock PR (1976) Water balance and kidney function in four species of *Rattus* from ecologically diverse environments. Aust J Zool 24:7–17

Bradley WG, Yousef MK (1972) Small mammals in the desert. In: Yousef MK, Horvath SM, Bullard RW (eds) Physiological adaptations: desert and mountain. Academic Press, New York, pp 127–142

Brownfield MS, Wunder BA (1976) Relative medullary area: a new structural index for estimating urinary concentrating capacity of mammals. Comp Biochem Physiol 55A:69–75

Buffenstein R (1984) Energy and water balance during torpor and hydropenia in the pigmy gerbil, *Gerbillus pusillus*. J Comp Physiol B 154:535–544

Chew RM (1965) Water metabolism of mammals. In: Mayer WV, van Gelder RG (eds) Physiological mammalogy, vol 2. Academic Press, New York, pp 44–178

Christian D, Matson JO, Rosenberg SG (1978) Comparative water balance in two species of *Liomys* (Rodentia: Heteromyidae). Comp Biochem Physiol 61A:589–594

Deavers DR, Hudson JW (1979) Water metabolism and estimated field budgets in two rodents (*Clethrionomys gapperi* and *Peromyscus leucopus*) and in an insectivore (*Blarina brevicauda*) inhabiting the same mesic environment. Physiol Zool 52:137–152

Donaldson K, Edwards BA (1981) A comparison of the effects of saline imbibition and water deprivation on the composition of blood, urine and pituitary neural lobe of the gerbil (*Meriones unguiculatus*). Comp Biochem Physiol 64A:31–35

French NR, Grant WE, Grodzinski W, Swift DM (1976) Small mammal energetics in grassland ecosystems. Ecol Monographs 46:201–220

Grodzinski W, Wunder BA (1975) Ecological bioenergetics of small mammals. In: Golley FB, Pettrusewicz K, Ryskowski L (eds) Small mammals; their productivity and population dynamics. Cambridge University Press, London, pp 173–204

Haggag G, El-Husseini M (1974) The adrenal cortex and water conservation in desert rodents. Comp Biochem Physiol 47A:351–359

Haines H, Shield CF (III) (1971) Reduced evaporation in house mice (*Mus musculus*) acclimated to water restriction. Comp Biochem Physiol 39A:53–61

Halpern BH, Pacaud A (1951) Technique de prélevèment d'echantillons de sang chez les petits animaux de laboratoire par fonction du plexus ophthalmique. CR Séanc Soc Biol 145:1465–1466

Hewitt S (1981) Plasticity of renal function in the Australian desert rodent, *Notomys alexis*. Comp Biochem Physiol 68A:297–304

Hewitt S, Wheldrake JF, Baudinette RV (1981) Water balance and renal function in the Australian desert rodent, *Notomys alexis*: the effect of diet on water turnover rate, glomerular filtration rate, renal plasma flow and renal blood flow. Comp Biochem Physiol 68A:405–410

Holleman DF, Dietrich DF (1973) Body water content and turnover of several species of rodents as evaluated by the tritiated water method. J Mamm 54:456–465

Jagosz J, Gorecki A, Possi-Cabaj M (1979) The bioenergetics of deposit and utilization of stored energy in the common vole. Acta Theriol 28:391–397

Johnson DR, Schreiber RK (1979) Assimilation, respiration and production. b) Vertebrates. In: Goodall DW, Perry RA (eds) Arid-land ecosystems: structure, functioning and management, vol 1. Cambridge University Press, Cambridge, pp 731–741

Kenagy GJ (1973) Adaptations for leaf eating in the Great Basin Kangaroo rat, *Dipodomys microps*. Oecologia 12:383–412

Louw GN, Seely MK (1982) Ecology of desert organisms. Longmans, London

Leung WTW, Rao MN (1972) Food composition table for use in East Asia. Food and Agricultural Organisation of the United Nations: Rome, and US Department of Health, Education and Welfare, Georgia

MacFarlane WV (1975) Ecophysiology of water and energy in desert marsupials and rodents. In: Prakash I, Ghosh PK (eds) Rodents in desert environments. The Hague, Junk, pp 389–369

MacFarlane WV, Howard B, Haines H, Kennedy PJ, Sharp CM (1971) The hierarchy of water and energy turnover of desert mammals. Nature 234:483–485

MacMillen RE, Hinds DS (1983) Water regulatory efficiency in heteromyid rodents. A model and its application. Ecology 1964:152–164

Scelza J, Knoll J (1982) Seasonal variation in various blood indices of the kangaroo rat, *Dipodomys panamintinus*. Comp Biochem Physiol 71A:237–241

Schmidt-Nielsen K (1964) Terrestrial animals in dry heat: desert rodents. In: Dill DB, Adolph EF, Wilber CG (eds) Handbook of physiology, vol. 4: Environmental physiology. American Physiological Society, Washington, pp 493–507

Schmidt-Nielsen K (1975) Animal physiology, adaptation and environment. Cambridge University Press, Cambridge

Schmidt-Nielsen K (1979) Desert animals. Physiological problems of heat and water, 2nd edn. Oxford University Press, Oxford

Shenk JS, Elliot FC, Thomas TW (1970) Meadow vole nutrition studies with semisynthetic diets. J Nutrition 100:1437–1446

Shkolnik A, Borut A (1969) Temperature and water relations in two species of spiny mouse (*Acomys*). J Mamm 50:245–255

Withers PC (1979) Ecology of a small mammal community on a rocky outcrop in the Namib desert. Madoqua 2:229–246

Withers PC (1982) Effect of diet and assimilation efficiency on water balance for two desert rodents. J Arid Environ 5:375–384

Withers PC, Louw GN, Henschel J (1980) Energetics and water relations in Namib desert rodents. S Afr J Zool 15:131–137

Yousef MK, Johnson HD, Bradley WG, Seif SM (1974) Tritiated water turnover in rodents: desert and mountain. Physiol Zool 47:153–162

Zar JH (1974) Biostatistical analysis. Prentice Hall, Englewood Cliffs, New Jersey