Energetics and water relations of Namib desert rodents

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All the Namib rodents investigated, except *Petromus*, can survive without water on a diet of air-dried seed. Water turnover rates of these animals in the laboratory confirmed their low water requirements. Field water turnover rates were remarkably low, probably because *Petromyscus* and *Aethomys* aestivate and *Petromus* has a low daily energy expenditure (DEE). The rodents have an increased water turnover rate after advective fogs occur. Daily energy requirements for *Petromyscus* and *Aethomys* were similar to expected values in the laboratory, whereas *Gerbillurus* had a higher DEE, and *Petromus* and *Mus* had lower-than-predicted DEE's. Water turnover rate is coupled with energy turnover rate for the Namib rodents. These physiological attributes of the Namib rodents are consistent with the severity of their environment, are associated with their kidney structure, and reflect the evolutionary history and demography of the particular species.

S. Afr. J. Zool. 1980, 15: 131 - 137

Al die Namib knaagdiere wat ondersoek is, behalwe *Petromus*, kon sonder water op 'n dieët van lugdroë saad oorleef. Tempo van wateromset in hierdie diere in laboratorium toestande het hulle lae waterbenodighede bevestig. Tempo van wateromset onder veldtoestande was baie laag aangesien *Petromyscus* en *Aethomys* estiveer en as gevolg van die lae daaglikse energieverbruik (DEV) van *Petromus*. Die wateromset van die diere verhoog met voorkoms van seemis. Daaglikse energiebenodighede vir *Petromyscuc* en *Aethomys* is soortgelyk aan verwagte waardes in die laboratorium, terwyl *Gerbillurus* 'n hoër DEV, en *Petromus* en *Mus* 'n laer DEV getoon het as die voorspelde waardes. Wateromset is nou verwant aan energieomset. Hierdie fisiologiese eienskappe weerspieël die vyandige omgewing en die evolusionêre geskiedenis van hierdie besondere spesies in die Namibwoestyn en is gekorrelleer met niermorfologie en demografiese patrone.

S.-Afr. Tydskr. Dierk. 1980, 15: 131 - 137

Small mammals, and rodents in particular, are an important faunal element in deserts. The suite of physiological, behavioural and morphological attributes which enable small mammals to thrive in deserts has been intensively studied (Petter 1961; Kirmiz 1962; Schmidt-Nielsen 1964; Shkolnik & Borut 1967; MacMillen & Lee 1967, 1969; MacMillen, Baudinette & Lee 1972; MacMillen & Christopher 1975; Mares 1977 a, b; Meserve 1978). Small desert mammals typically avoid the extremes of temperature and humidity by being surface-active at night and remaining underground during the day. The capacity to highly concentrate urine and minimize respiratory water loss further contribute to the maintenance of positive water balance.

Namib rodents would be expected to have similar adaptations to other desert rodents, since the Namib is one of the oldest and harshest deserts. The Namib climate is unique, however, in that the climate is occasionally ameliorated by advective fogs which form over the cold, coastal Benguella current and move many kilometres inland. These advective fogs are an important source of water to many Namib invertebrates and vertebrates (Louw 1972; Seely & Hamilton 1976; Hamilton & Seely 1976), and appear to be of great significance to the breeding cycles of the small Namib mammals (Withers 1979).

The present study examines the energy and water balance of three Namib rodents which are found on the rocky outcrops (*Petromyscus collinus*, *Aethomys namaquensis*, *Petromus typicus*), and for *Mus minutoides*, *Gerbillurus paeba* and *Desmodillus auricularis*. We will examine the potential coupling of energy turnover and water turnover, and the possible effects of advective fog on the water balance of the Namib rodents.

Methods

The rodents were trapped in the Namib desert at Tumasberg (23° 10′S: 15° 32′E) and Kanaan (23° 53′S: 16° 07′E). *M. minutoides* were also captured in mesic environments (Cape Flats and Langebaan Lagoon). Animals were maintained in the laboratory for up to four months. *Petromus*, however, were extremely difficult to maintain in the laboratory.

Water relations

The tolerance of the various species to water deprivation was determined by maintaining individuals in the laboratory

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Received 21 November 1979; accepted 21 March 1980.

on a diet of air-dried seed (ambient r.h. 50%; temperature 20—22°C) with fresh apple or cucumber as a water source. Body mass was measured daily to ± 0,01 g, for three weeks of water deprivation or until death.

Per cent body water, and water turnover rate (WTR) were measured in the laboratory and in the field, using the isotopic dilution technique with tritiated water, TOH (Richmond, Langham & Trujillo 1962; Yousef, Johnson, Bradley & Sief 1974; Nagy 1975). Mice were injected intraperitoneally with 10 μCi of TOH (1 μCi per μl activity). A blood sample was collected from the suborbital eye sinus into a 100 μl heparinized hematocrit tube, three hours after injection. Equilibration time for the isotope was less than three hours. The blood samples were centrifuged for 4 min and the tube broken to separate a clear plasma sample. The volume of the plasma sample was calculated from the length it occupied in the hematocrit tube. The plasma samples were washed into 100 μl of 10% TCA in an Eppendorf vial, and stored for subsequent analysis. Distilled water and stock TOH samples were treated in the same manner as plasma samples. Blood samples were then removed from the mice at two to four day intervals, and treated in the above manner.

The WTR's of mice in the field were also measured during the dry season (November 1977). Essentially the same techniques were used as for the laboratory studies. Mice were live-trapped, injected with TOH, and a blood sample obtained after three hours. The animals were then released at the site of capture, and subsequently recaptured at two to four day intervals. Individual mice were recognized by toe-clipping (see Withers 1979).

The Eppendorf vials were then centrifuged in the laboratory to obtain protein-free supernatants, and a 50μl sample of the clear supernatant was thoroughly mixed with 10 ml of Packard Instagel scintillation cocktail. The counts per min, counting efficiency, and disintegrations per min were determined using a Beckman LS—250 or Packard 3385 Liquid Scintillation Counter. The initial per cent body water content, and water turnover rates were calculated using the equations of Yousef *et al.* (1974).

Energy expenditure

Daily energy expenditure (DEE) was determined for rodents in the laboratory, from their rates of food consumption and faecal production. The masses of seed consumed, and of faeces produced, were converted to energy equivalents using a bomb calorimeter (Gallenkamp). Assimilation efficiency was calculated as (energy ingested — energy excreted)/(energy ingested). Energy content of the urine was ignored, but is only about 1% of the total energy ingested (Grodzinsky & Wunder 1975). The preformed water intake of the animals (i.e. water present in the food) was determined from the mass of seed eaten, and the water content of the seed (typically 9% by weight). Metabolic water production was estimated from the DEE by assuming that 4,8 calories$=$1 ml $O_2$$=$0,64 ml H_2O (Schmidt–Nielsen 1964).

Demographic patterns for the rodent species were investigated by Withers (1979). The structures of the kidneys were investigated using standard histological techniques. Details of this study will be presented elsewhere (Withers MS).

All values are presented as mean ± standard error, with the number of observations (n). Statistical tests were either t-tests, paired t-tests where appropriate, and standard linear regressions; a probability of less than 0,05 was taken as the level of significance.

Results

Water relations

All Namib rodents, except for *Petromus*, survived for three weeks on a diet of air-dried seed, without exogenous water, and had stable or increasing body masses after that time (Fig. 1). *Gerbillurus paeba* also survived these conditions of water deprivation indefinitely (unpubl. obser., Buffenstein, 1977). The initial responses of the rodents to water deprivation varied markedly (Fig. 1). *Mus, Desmodillus* and *Petromyscus* (from Kanaan) generally showed no decline in body mass, whereas *Aethomys* initially had a pronounced decline in mass (except for a single individual) but mass subsequently stabilized and often increased. Only two *Petromus* were available for water deprivation experiments. One died after 23 days, having lost 35% of its original mass; the second died after losing 20% of its original mass. *Mus minutoides* from mesic habitats were unable to survive water deprivation, and died within 20 days after losing 20—30% of initial body mass.

Water turnover rate of the laboratory animals was greater when provided with apple or cucumber (Table 1). The WTR's of water-deprived individuals were well-accounted for by estimates of preformed water and metabolic water gains. The WTR's of animals in the field were, surprisingly, lower than those measured for animals in the laboratory for *Petromyscus* ($P<0{,}001$) but not for *Aethomys* (P is NS). The WTR's of *Aethomys* and *Petromus* increased after the fog, but the differences were not significant because of the small sample sizes and variability in WTR for different individuals. The WTR of *Petromyscus* did increase after the fog (paired t-test, $P<0{,}05$); the difference was not significant with a normal t-test, because of individual variability in WTR. The additional amount of water which was turned-over by the rodents because of the advective fog was 3,1 ml for *Petromyscus* individuals, and 3,5 ml for *Aethomys* and 2,4 ml for *Petromus*.

The percent body water content of the rodents was generally between 60 and 70%. The values for *Petromyscus* (field) were 63,1 ± 1,3 (16), (laboratory) 72,2 ± 1,4 (5); *Aethomys* (field) 70,3 ± 2,5 (3), (laboratory) 68,4 (1); *Mus* (laboratory) 66,7 (1).

Energy expenditure

Daily rates of food consumption and faecal production are summarized in Table 2. The energy content of seed was 20—22 kJ g^{-1} and for the faeces was 18—22 kJ g^{-1} (all masses are air-dried). The rodents had a high assimilation efficiency, of 92—97% (ignoring the possible loss of 1% in the urine; Grodzinsky & Wunder 1975) except for *Petromus* which had an assimilation efficiency of 68—87%. The DEE's for *Petromyscus* and *Aethomys* were similar to expected values, whereas that for *Petromus* was much less than predicted; *Petromyscus* and *Aethomys* maintained constant body mass whereas the *Petromus* gained about 0,5 g day^{-1}. When water-deprived, the food consumption and DEE declined somewhat for *Petromyscus, Petromus* and *Aethomys* (although the differences were not

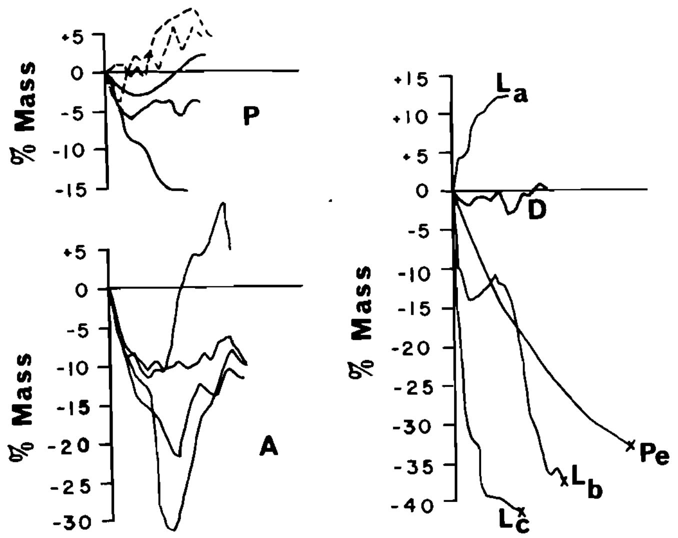

Fig. 1 Change in body mass, expressed as a % of initial mass for Namib rodents on a diet of air dried seed (see text). P: *Petromyscus* from Tumasberg (solid lines) and Kanaan (broken lines); A: *Aethomys* (Tumasberg); Pe: *Petromus* (Tumasberg); L: *Mus* from Tumasberg (a), and from mesic areas at the Cape Flats (b) and Langebaan Lagoon (c); D: *Desmondillus* (Tumasberg). Abscissa is 6 weeks.

significant). The DEE of *Mus* (3,1 kJ g^{-1} day $^{-1}$) and *Gerbillurus* (2,9 kJ g^{-1} day^{-1}) were different from the predicted values of 4,1 and 2,1 respectively.

Discussion

The various mammals of the Namib desert include a high density and diversity of rodents (Coetzee 1969; Stuart 1975; Withers 1979) which are adapted to desert conditions. However, the degree of physiological adaptation to desert conditions might reflect their differing evolutionary histories, their various taxonomic affinities, and their contrasting demographic patterns (Roberts 1951; Meester 1966; Withers 1979).

The following discussion examines the water relations and energetics of the Namib rodents in relation to their evolutionary history, their ecology, and their demographic patterns.

Table 1 Water turnover rates (ml day^{-1}) of Namib desert rodents in the laboratory and in the field. Values are $\bar{x}$ ±s.e.(n)

	Petromyscus	*Aethomys*	*Petromus*
LABORATORY:			
Water-deprived	1,4±0,1 (4)	1,7±0,3 (5)	—
+ Apple	2,9±0,4 (4)	4,8±0,6 (5)	—
Metabolic water[1]	0,9	1,4	—
Preformed water	0,2	0,3	—
FIELD:			
Prefog[2]	0,8±0,1 (4)	2,2±0,2 (3)	4,4±0,6 (3)
Postfog[3]	1,4±0,2 (7)	3,2±0,2 (3)	5,1±0,8 (4)

[1] Assuming 4,8 cal per ml O_2 & 0,64 g H_2O per ml O_2.

[2] All of the period for determination of water flux was before the fog.

[3] Some, but not necessarily all of the period over which WTR was measured, occurred after the fog. Post-fog values are therefore minimum estimates of water gained from the fog.

Water relations

Independence of drinking water is a prerequisite for desert rodents, but the ability to survive indefinitely on a diet of air-dried seed is characteristic of only some desert species (Kirmiz 1962; Schmidt-Nielsen 1964; MacMillen & Lee 1967; Koford 1968). Many other desert rodents, such as those in the genera *Psammomys, Neotoma, Onychomys, Phyllotis* and *Eligmodontia,* require more preformed water than is found in air-dried seed (Schmidt-Nielsen 1964; MacMillen 1972; Mares 1977a, b; Meserve 1978).

Of the Namib rodents, all but *Petromus* survive on a diet of air-dried seed. The initial responses to water deprivation differed markedly. Some species (*Mus, Desmodillus, Petromyscus* from Kanaan) continued to gain mass even when water deprived; *Aethomys* rapidly lost mass when water deprived, but all individuals survived and often regained considerable mass. Other Namib rodents (*Gerbillurus paeba, G. tytonis* and *Rhabdomys pumillio*) also survive on a dry-seed diet (Buffenstein 1977; pers. observ.).

Table 2 Energy balance of Namib desert rodents in the laboratory on a diet of air-dried bird seed and with, and with, *ad lib* water. Values are $\bar{x}$ ±s.e.(n)

		Water consumption (ml day^{-1})[1]	Food consumption (g day^{-1})	Faecal production (g day^{-1})	Assimilation efficiency (%)	Daily expenditure	
						Actual (kJg^{-1} day^{-1})	Predicted[2]
Petromyscus	(n=4)	2,0	1,85±0,075	0,11±0,03	95±0,5	2,1±0,1	2,2
(19 g)	(n=3)	—	1,61	0,12	92	1,8	2,2
Aethomys	(n=4)	4,1	3,01±0,08	0,18±0,07	95±0,8	1,4±0,1	1,4
(46 g)	(n=2)	—	2,25	0,11	94	1,2	1,4
Petromus	(n=1)	8,0	4,5	1,7	67	0,55	1,0
(130 g)	(n=3)[3]	—	2,4±0,11	0,6	76	0,38	1,0

[1] Drinking from water bottles, except *Petromus* were provided with cucumber (95,9% water)

[2] Grodzinsky and Wunder, 1975

[3] Individuals did not maintain body mass and died.

The response to water deprivation of different geographic populations of *Petromyscus* and *Mus* indicate that local populations from low rainfall regions (Kanaan *Petromyscus*, Tumasberg *Mus*) are less dependent upon exogenous water than are populations from more mesic regions (Tumasberg *Petromyscus;* Langebaan and Cape Flats *Mus*). Reaka and Armitage (1976) report similar subspecific variation in exogenous water requirements for deer mice (*Peromyscus maniculatus*) from North America.

The inability of *Petromus* to survive water-deprivation on an air-dried seed diet seems paradoxical, since it has a lower mass-specific WTR and DEE than the other Namib rodents (Tables 1 & 2) and its kidney appears to be more specialized for urine concentration (Withers MS). Further study of *Petromus* is needed to resolve this paradox.

The WTR's of the rodents varied markedly, both intra-specifically and inter-specifically, depending upon water availability. For example, *Petromyscus, Aethomys* and *Gerbillurus* would drink large amounts of water (2,0; 4,1; and 2,0 ml day^{-1} respectively) compared to their minimum water requirements (1,4; 1,7 and 1,5 ml day^{-1}) eating air-dried seed. Other desert rodents also invariably drink if given the opportunity. Non-desert rodents generally require more water than desert rodents (Richmond *et al.*1962; Holleman & Dieterich 1973). The WTR of rodents is, consequently, poorly predicted from body mass (WTR; ml day^{-1}; M, grams) as:

$$\log_{10}\text{WTR} = -0{,}83\ (\pm\ 0{,}20) + 0{,}84\ (\pm 0{,}07)\cdot\log_{10} \text{M}$$

with $r^2 = 0{,}65$ (n = 39; data from Richmond *et al.* 1062; Holleman & Dieterich 1973; Mullen 1970, 1971; McFarlane & Howard 1972; MacFarlane 1975; Yousef *et al.* 1974; MacMillen & Christopher 1975; present study).

However, desert rodents can sustain lower WTR's than mesic species, and the minimum WTR's of desert species are relatively well predicted as:

$$\log_{10}\text{WTR}_{\text{min}} = -1{,}26\ (\pm 0{,}12) + 0{,}88\ (\pm 0{,}07)\cdot\log_{10} \text{M}$$

with $r^2 = 0{,}98$ (n = 6; data from Richmond *et al.* 1962; Mullen 1970, 1971; present study).

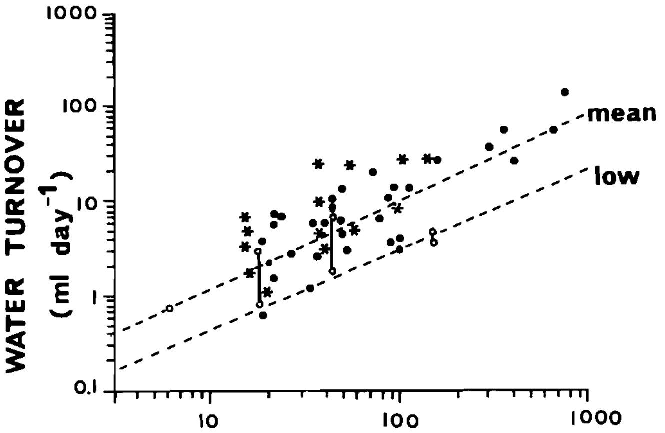

Fig. 2 Water turnover rates for rodents in the field (•) and in the laboratory (•) under a variety of conditions. Data from Namib rodents (present study) are hollow circles, and the variability depending upon water regime is shown. Regression lines are for all species (mean) and for six desert species (low); see text. See text for sources of other data.

There are relatively few WTR measurements for free-living desert rodents (Mullen 1970, 1971; MacMillen & Christopher 1975; Grenot & Serrano 1979), and free-living WTR's are typically higher than minimum WTR's in the laboratory (Fig. 2). However, *Petromyscus* had a significantly lower WTR in the field than did laboratory animals. *Aethomys* had the same WTR in the field as laboratory individuals. The field WTR for *Petromus* is lower than that predicted for the minimum WTR of desert rodents in the laboratory. These low field WTR's of the Namib rodents, measured in a typical dry season, indicate that the physiological adaptations of these species which restrict water turnover are of adaptive value to extant field populations each year. The low field WTR's further suggest that energy turnover is low (see below).

Many invertebrates and vertebrates of the Namib desert are able to drink condensed fog water (Louw 1972; Seely & Hamilton 1976; Hamilton & Seely 1976). *Petromyscus*, and most likely *Aethomys* and *Petromus*, assimilate water from advective fogs, since their WTR's increased after a fog. Water uptake could occur by drinking, or by eating hydrated vegetation or insects.

Energetics

The daily energy expenditure (DEE) of *Petromyscus* and *Aethomys* in the laboratory were similar to predicted values for rodents (Grodzinsky & Wunder 1975). The DEE of *Gerbillurus* was higher than predicted, probably because these gerbils are hyperactive in captivity. *Mus* and *Petromus*, although the data are few, clearly have much lower DEE's than predicted. Perhaps a low DEE is of adaptive value to small desert mammals (with high mass-specific metabolic rates) or herbivorous desert rodents (with less digestible diets).

Granivorous desert rodents typically have high assimilation efficiencies, of 85—90% (Grodzinsky & Wunder 1975; Schreiber 1979). The Namib rodents, except for *Petromus*, have somewhat higher assimilation efficiencies of 92—97%. The low assimilation efficiency of *Petromus* may result from its having a large caecum for post-gastric fermentation of grass. Faeces reflecting a previous high-fibre diet might have been produced during the experimental period, thereby causing assimilation efficiency to be underestimated. Nevertheless, the DEE of *Petromus* is still at least 25% less than predicted even if its assimilation efficiency for seed was 95%.

Interrelation of WTR and DEE

It has been suggested that water turnover and energy turnover are 'linked' (MacFarlane, Howard, Haines, Kennedy & Sharp 1971; MacFarlane 1975; Yousef *et al.* 1974). In fact, WTR and DEE must be coupled through diet and assimilation efficiency (in the absence of drinking) since WTR = preformed water + metabolic water = water intake = water loss for steady-state conditions. Drinking, of course, would obscure any coupling of WTR and DEE.

Petromyscus and *Aethomys*, in the laboratory, had identical diets (air-dried seed) and assimilation efficiencies, and indeed had the same ratio of WTR/DEE of 0,040 to 0,042 ml H_2O kJ^{-1}. Water-deprived *Mus* also had a WTR/DEE of 0,04 ml kJ^{-1}. As expected, drinking obscured this coupling of WTR and DEE. When apple was given as a water supplement, the WTR/DEE of *Petromyscus*

Table 3 Water turnover rates (WTR: ml day^{-1}), daily energy expenditure (DEE, kJ day^{-1}) and ratio of water to energy turnover (WTR/DEE: ml H_2O kJ^{-1}) for foodstuffs and for various desert mammals under a variety of conditions

	WTR	DEE	WTR/DEE	Comments
Protein metabolism	—	—	0,024	calculated from Peters and Van Slyke, 1946
Fat metabolism	—	—	0,029	calculated from Peters and Van Slyke, 1946
Carbohydrate metabolism	—	—	0,034	calculated from Peters and Van Slyke, 1946
Perognathus formosus	0,62	24,4	0,027	laboratory, food deprived; Mullen 1970
	1,5–2,6	33,3–63,9	0,033–0,051	field, Mullen 1970
Dipodomys merriami	2,1–4,1	44,4–76,2	0,068–0,183	field, non-hibernating; Mullen 1971
	3,9–14,4	26,0–109,6	0,031–0,063	field, hibernating?; Mullen 1971
Dipodomys microps	5,8–20,5	11,5–154,3	0,053–0,571	field; Mullen 1971
Petromyscus collinus	2,9	39,9	0,073	laboratory, + apple; present study
	1,4	34,2	0,041	laboratory, water deprived; present study
	0,8	≤20[1]	≥0,04[1]	field, before fog; present study
	1,4	—	—	field, after fog; present study
Aethomys	4,8	64,4	0,098	laboratory, + apple; present study
namaquensis	1,7	45,2	0,040	laboratory, water deprived; present study
	2,2	≤55[1]	≥0,04	field, before fog; present study
	3,2	—	—	field, after fog; present study
Petromus typicus	4,4	100	0,44	laboratory + field data; present study
Hereford steer	—	—	0,396	laboratory, minimum drinking requirements, Taylor, 1968[2]
Eland	—	—	0,396	laboratory, minimum drinking requirements, Taylor, 1968
Zebu steer	—	—	0,241	laboratory, minimum drinking requirements, Taylor, 1968
African Buffalo	—	—	0,229	laboratory, minimum drinking requirements, Taylor, 1968
Wildebeest	—	—	0,168	laboratory, minimum drinking requirements, Taylor, 1968
Oryx	—	—	0,142	laboratory, minimum drinking requirements, Taylor, 1968
Grant's gazelle	—	—	0,102	laboratory, minimum drinking requirements, Taylor, 1968
Thompson's gazelle	—	—	0,092	laboratory, minimum drinking requirements, Taylor, 1968

[1] Calculated assuming WTR/DEE≥0,04 (see text)

[2] Calculated from Taylor (1968) assuming 1kJ = 0,03 ml H_2O

increased to 0,073 ml kJ^{-1} and that for *Aethomys* was 0,098 ml kJ^{-1}. There are few comparable data for other mammals (Table 4) despite the potential of feeding trial experiments and D_2O^{18} studies to simultaneously measure WTR and DEE. Previous studies which correlated water and energy turnover (MacFarlane and co-workers; Yousef *et al.* 1974) are misleading since they use resting rates of oxygen consumption (not DEE) for comparison with daily water turnover rates. Nevertheless, their data also indicate some correlation between energy and water turnover.

Table 4 Body temperatures for euthermic and aestivating Namib rodents (°C). Ambient temperature for aestivating rodents was 18-22 °C. All values are $\bar{x} \pm$ s.e.(n.) Temperatures were measured with a WESCOR quick-responding mercury thermometer

	Euthermic (laboratory)	Aestivating (field)
Petromus	34,9±0,5 (6)	—
Aethomys	34,9±0,6 (6)	19,8
Petromyscus	33,6±0,5 (6)	18,0; 18,8; 23,6
Desert rodents[1]	36,6±0,2 (23)	
Non-desert[1]	37,6±0,2 (19)	

[1] Hart, 1971

The available data indicate that there is a similar, low ratio for WTR/DEE of about 0,04 ml H_2O kJ^{-1} for desert rodents. This ratio corresponds to almost exactly one molecule of H_2O per molecule of oxygen. This ratio of 0,04 ml kJ^{-1} is considerably less than that of desert ungulates (Table 3). The lowest value of WTR/DEE possible for an animal is determined by the stoichiometry of metabolic water production to O_2 consumption; i.e. for protein, it is 0,024 ml kJ^{-1} and is 0,029 for fat and 0,034 for carbohydrate (calculated from Peters & Van Slyke 1946). The WTR/DEE of a starved, water-deprived animal should be between 0,024 and 0,034 ml kJ^{-1}, depending upon the metabolic substrate. Significantly, the WTR/DEE of a starved, water deprived pocket mouse is 0,027 ml kJ^{-1} (calculated from data of Mullen 1970).

The ratio of WTR/DEE has heuristic value, apart from being an index to water economy. It should be possible to obtain maximum estimates of energy turnover from estimates of water turnover since WTR/DEE≥0,04 and DEE≤WTR/0,04. Maximal estimates of DEE for the Namib rodents at Tumasberg obtained in this manner (Table 3) are less than the predicted minimal values for laboratory animals, which do not have to seek out food, defend territories, and partake in other energy-consuming activities (Grodzinsky & Wunder 1975). A low field DEE for *Petromus* is consistent with its low laboratory DEE, but *Petromyscus* and *Aethomys* had normal laboratory DEE's. A low field DEE reflects energy conservation, and perhaps aestivation. In fact, both *Petromyscus* and *Aethomys* individuals were found to undergo torpor in the field during the hot, dry summer months but not during the remainder of the year. Three *Petromyscus* individuals and one *Aethomys* were found in live-traps with body temperatures similar to ambient temperature (Table 4) and all individuals were released (still torpid) and were subsequently recaptured. These species are, therefore, able to survive moderate hypothermia (about 20 °C) and can regain their normal body temperature in nature. This is clear evidence for aestivation, particularly in conjunction with the independent measure of low energy turnovers. No animals were observed to aestivate in the laboratory when water deprived, but air-dried seed is clearly not an incapacitating water stress to these animals. Individuals in the laboratory did, however, have low body temperatures compared to many other mammals, as do desert rodents in general (Table 4; Hart 1971).

The results of this physiological study, together with ecological, demographic and distributional studies, indicate that the degree of physiological adaptation to desert conditions is associated with kidney morphology, distribution within the Namib desert, and certain demographic variables such as mortality and reproductive potential (Table 5). *Aethomys*, the most recent invader of the Namib (Meester 1965), has a relatively unspecialized kidney (Withers MS), is restricted to the eastern Namib which is relatively more mesic than the western portion (Stuart 1975; personal observations), has a low annual survival rate and has a high reproductive potential (Withers 1979). *Petromus* is a highly specialized herbivorous, diurnal desert rodent with low water and energy requirements, a kidney highly adapted for urine concentrating ability, is found throughout the Namib including the most xeric rocky areas, has a very high annual survival rate and has a relatively low reproductive potential. *Petromus* is, significantly, the oldest rodent inhabitant of the Namib (Meester 1965). *Petromyscus* tends to be intermediate in almost all of these respects. Christian (1979) also reports similar associations between water metabolism of laboratory animals and demographic patterns, for other Namib rodents (*Desmodillus auricularis, Gerbillurus paeba* and *Rhabdomys pumillio*).

It is gratifying to find such associations between physiological and population parameters which we would suspect had adaptive significance to desert species. However, caution must be exercized in interpreting such associations between physiology and population dynamics. In fact, demographic patterns of rodents clearly reflect their taxonomic affinities (French, Stoddard, Robek 1975). Murid rodents in general, and also the Namib murids (*Aethomys, Rhabdomys*), tend to have unstable population cycles associated with high mortality and high reproductive potential. Cricetid rodents in general, and also the Namib cricetids (*Petromyscus*) have more stable populations, associated with higher survival rates and lower reproductive potentials. If a high survival-rate, low reproductive-potential demographic pattern confers a selective advantage to desert rodents, then cricetids are pre-adapted to occupy desert rodent niches, compared to murids. Nevertheless, we might still expect all desert rodents, and other desert mammals, to minimize the water and energy costs of reproductive effort and maximize the survival of the adult individuals. It will be of considerable interest to examine the water balance, energetics and demographic patterns of other desert rodents in this light.

Table 5 Minimal water and energy requirements (i.e. animals in the laboratory with a diet of air-dried seed), renal index to urine-concentrating ability (percent medullary area) and demographic parameters (mean annual survival rate and ♀ reproductive potential) for the Namib desert rodents

	Petromus	*Petromyscus*	*Aethomys*
Minimum WTR (ml g^{-1} day^{-1})	0,029	0,04	0,049
Minimum DEE (kJ g^{-1} day^{-1})	0,55	1,8	1,2
Kidney[1] per cent medullary area	71	65	61
annual[2] survival rate	0,67	0,286	≈0
annual[2] reproductive potential (#young/year/♀)	2—3	2—3	4—6

[1] Withers, MS. [2] Withers, 1979

Acknowledgements

We gratefully acknowledge financial support from the University of Cape Town primarily through a UCT Bursary to P.C.W. We thank Dr E. Joubert and the SWA Department of Nature Conservation for encouragement and permission to work in the Namib Desert Park. We are particularly grateful to those who assisted with arduous field work; M. Lucas, A. Linley, A. Guillot, M. Delafonteine, P. O'Neill, J. Jarvis and R. Buffenstein. We also gratefully acknowledge the hospitality and cooperation of the DERU staff at Gobabeb and Ganab. I. Parker kindly assisted with scintillation counting.

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