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WATER METABOLISM IN THE NAMIB DESERT GOLDEN MOLE, *EREMITALPA GRANTI NAMIBENSIS* (CHRYSOCHLORIDAE)

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Abstract—1. Laboratory and field studies of energy and water metabolism employing isotopic dilution methods examined the ability of Namib Desert moles to survive on an insect diet without drinking water.
2. Water independence is achieved through efficient renal function while low rates of energy usage and torpor are further effective in reducing overall water requirements.

INTRODUCTION

Free water is usually absent in arid environments, thus the ability to exist without drinking water is a prerequisite for the survival of small desert mammals. The term 'water independent' applies primarily to granivorous rodents that can exist on dry seeds while water dependent species achieve water economy through utilization of moist food resources such as insects and/or green vegetation (Gettinger, 1984).

Morton (1980) argued that since water supply is a concomitant benefit of food intake in insect-eating mammals, it is energetically wasteful expending any physiological effort conserving it. Consequently water turnover rate in desert insectivores is likely to reflect rates of energy usage rather than an adaptation to environmental conditions *per se*, since turnover rates of energy and water in mammals are linked (Macfarlane and Howard, 1972; Macfarlane *et al.*, 1971; Maiga, 1984; Yousef *et al.*, 1974).

The present study examines the relationship between energy and water turnover and physiological adaptation in the Namib Desert golden mole, *Eremitalpa granti namibensis*, a small insectivore found in an energy sparse and arid sand dune habitat. Namib moles are nocturnally active on the dune surface while during the day they bury in loose shifting dune sand.

The objectives of this work were to examine (a) the ability of *E. g. namibensis* to survive on insects without drinking water, (b) the coupling of energy and water expenditure and the magnitude of energy and water requirements, and (c) the structure of the kidney and urine concentrating ability.

MATERIALS AND METHODS

Experimental animals

Adult moles were caught by hand in the Namib desert at Gobabeb (23°45′S. 15°30′E.) and kept in the laboratory for two to six months prior to experimentation. Moles were housed individually in glass terraria (60 × 30 × 30 cm) filled with Namib dune sand and were fed daily with mealworm larvae (*Tenebrio molitar*) and one day old mice (*Mus musculus*).

Gravimetric determinations of energy and water balance

Seven adult moles were maintained individually in glass terraria (30 × 24 × 24 cm) filled to a 15 cm depth with Namib dune sand. Terraria were kept in a constant environment cabinet at an ambient temperature of 29°C, 50% relative humidity and a 12 hr photoperiod with illumination from 07:00–19:00. A four day acclimation period preceded the ten day test period, during which the moles were weighed and fed daily at 17:00 with mealworms *ad lib*. Drinking water was not supplied. Food consumption was measured as the difference between the mass of larvae supplied in one day and those left unconsumed the following day.

Urine and faecal production were measured by placing moles in metabolic cages (19 × 12 × 12 cm) for 6 hr periods at different times during the 24 hr cycle. Urine was collected under mineral oil for each period and measured with a 0.5 ml graduated syringe. Osmolality of urine samples was measured with a cryoscopic osmometer. All faecal material collected was dried at 50°C to constant mass and weighed. The energy content of the food and faeces was measured by microbomb calorimetry. Each mole was subjected to eight collection periods spread evenly through the ten day experimental period. Since no significant differences were observed for urine or faecal production at different times of the 24 hr cycle, daily production per animal was calculated by using the average amount produced per 6 hr period times four.

Calculation of energy expenditure

Daily energy intake was calculated using the following equation (Grodzinski and Wunder, 1975):

$$DEI = GEI - (FE + UE)$$

where *DEI* is daily energy intake; *GEI* is gross energy intake (energy content of food × mass of food consumed per day); *FE* is energy lost in faeces (energy content of faeces × mass of faeces produced per day); *UE* is energy content of urine, and was not considered in these calculations as it constitutes a negligible fraction of energy exchange in small mammals (Grodzinski and Wunder, 1975). Since moles maintained relative stable mass (mass change <3.5%) during the experimental period, daily energy expenditure (*DEE*) was

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assumed to be equal to *DEI*, and representing only respiration required for body maintenance and activity (Drodz, 1975; Gessaman, 1973).

'Apparent assimilation efficiency' (*AE*) was calculated from *DEI* and *GEI* (Grodzinski and Wunder, 1975):

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

Calculation of water balance

Water balance measurements were based on the assumption that water intake (*WI*) equals water less (*WL*) for steady-state conditions (Buffenstein, 1984):

$$WI = D + P + M = WL = F + U + EWL.$$

Water intake. *D* is amount of water drunk, and was not considered since no water was supplied. *P* is preformed water in food, calculated as the difference in mass after oven-drying mealworms at 50°C to constant mass. *M* is metabolic water production from oxidation of food calculated by using conversion constants for protein, carbohydrate, and fat (Schmidt-Nielsen, 1979) (Table 1) and taking into consideration *AE* to account for metabolic water loss in egesta.

Water loss. *U* is daily urinary water loss. *F* is daily faecal water loss calculated from daily faecal production. Faeces were collected at 1 hr intervals from animals in metabolic chambers and water content calculated as the difference in mass after oven drying at 50°C to constant mass. *EWL* is pulmocutaneous water loss determined indirectly from the subtraction of daily faecal and urinary water loss from water intake.

Water turnover determinations using tritiated water (^{3}HHO)

The tritium dilution technique (Lifson and McClintock, 1966; Nagy, 1975) involves injecting a dose of tritiated water into the test subject. After equilibrating with body water, the specific activity of the isotope decreases with time due to the loss of labelled water from the animals via excretion and evaporative water loss and the input of unlabelled water via drinking, eating and oxidative metabolism of assimilated food. Measurements of the decline in specific activity of the isotope enables an assessment of the rate of water flux.

Validation trials

The precision of isotope measurement of water flux was assessed by comparing water influx measured gravimetrically with the isotopic mesaurement. During the experimental period, seven adult moles were maintained at 29°C, under similar conditions to those described previously for energy and water balance determinations. A three day acclimatization period was allowed prior to injecting moles intraperitoneally with ^{3}HHO (0.05 mCi in 0.5 ml sterile water). After a 3 hr equilibration period to allow isotopically-labelled water to come into equilibrium with body water (Mullen, 1970; Holleman and Dieterich, 1973), a blood sample was collected by toe clipping and a second sample taken ten days later. Blood samples (±0.1 ml) were stored at 4°C until further analysis. During the ten day test period, daily food consumption was monitored enabling simultaneous measurements of water flux by gravimetric and isotopic methods.

Table 1. Food values of *Tenebrio molitor* larvae

	Composition of mealworms (gg^{-1} dry mass)	Potential metabolic water yield (gg^{-1} dry mass of diet)
Fat	0.404	0.433
Protein	0.444	0.176
Carbohydrate	0.125	0.069
Ash	0.027	Total 0.678

Energy 25.02 kJ/g ash free dry mass
Preformed water 62.1%

Measurement of water turnover rates in the field

Field studies were conducted in the dunes near to Gobabeb during March 1987. Mean daily extremes of temperature and relative humidity were 31.9–13.8°C and 84.9–29.5%. No rainfall occurred but fog precipitation was 2.0 ml. Animals were caught by hand between 07:00 and 10:00 and weighted prior to intraperitoneal administration of 0.05 mCi ^{3}HHO in 0.5 ml sterile water. After a 3 hr equilibration period initial blood samples were collected and animals released at their exact site of capture. Of ten moles released, five (all females) were recaptured 9–15 days later, reweighed, and a second blood sample collected. All blood samples were stored at 4°C for three months.

Processing of blood samples

Vacuum sublimation in liquid nitrogen was used to extract water from blood (Vaughan and Boling, 1961). Extracted water was stored in tubes at 4°C until measurement of radioactivity on month later.

Radioactivity of extracted water was measured by diluting 20 μl amounts in 5 ml of Beckman Premixed-Ready-Soly HP/b scintillation fluid. Samples were counted for 2 min on a Beckman LS 3801 scintillation counter. Count accuracy was to 2% error and was corrected for background.

Water flux rates (gain and loss) were calculated with equation three of Nagy and Costa (1980), using gravimetric estimates for body water (see below).

Fat and water content determinations

Total body water content of moles (eight laboratory maintained individuals and 14 wild caught moles) was determined by oven drying fresh carcasses (with gut removed) to constant mass at 50°C. Total body water was calculated as difference in mass between dried and fresh carcasses. Tritium dilution procedures for estimating body water volumes were not used since these procedures may overestimate water content by as much a 10% (Gettinger, 1983; Green and Eberhard, 1983; Karasov, 1983; Nagy *et al.*, 1978).

Dried carcasses were finely ground in a coffee grinder and extracted to constant mass with petroleum ether in a Soxhlet apparatus to determine fat content (Allen *et al.*, 1974; Sawicha-Kapusta, 1975).

Kidney morphology

Kidneys from two freshly-killed captive animals were fixed in Bouin's solution for 72 hr, embedded in paraffin wax, sectioned at 10 μm and stained using the masson trichrome staining method (Culling, 1974). Midsagittal sections were photographed under a binocular microscope (6–12 times magnification) the resulting photomicrograph enlarged to 20 × 16 cm and the area occupied by the cortex and the medulla measured with a planimeter. Relative medullary area (RMA) was calculated as medullary area/cortical area (Brownfield and Wunder, 1976).

For comparative purposes, RMA of kidneys from two *Amblysomus hottentotus* caught at Umdoni Park, Natal, was also determined.

RESULTS

Laboratory determinations of energy and water balance

A complete account of energy and water balance for *E. g. namibensis* is shown in Tables 2 and 3 respectively. The rate of fresh food consumption was low at about 14% of body mass each day, while daily energy expenditure was much less than that predicted by mass. The major avenue of water loss was pulmocutaneous accounting for 76% of the total loss.

Table 2. Energy budget of *E. g. namibensis* fed *Tenebrio molitor* larvae. Data expressed per gram dry mass

	Mean	±1 SD
No. of animals	7	
Mean weight (g)	27.29	6.93
Food consumption (g/day)	1.22	0.34
Faecal production (g/day)	0.48	0.12
Energy content of faeces (kJ/g)	10.35	1.62
GEI (kJ/day)	30.61	8.46
Faecal energy (kJ/day)	4.77	0.88
DEE (kJ/day)	25.84	8.25
% predicted *DEE**	54.10	14.47
Apparent assimilation efficiency (%)	83.34	5.38

*Calculated from Grodzinski and Wunder's (1975) equation for an insectivore and corrected for temperature according to Randolph (1980).

Faecal water loss was the second most important avenue (13%) and water loss in the urine the least (11%). Mean urine osmolality was 3.82 osmol/kg (SD ± 1.10). The ratio of energy to water turnover (WTR/DEE: ml H_2O/KJ) was 0.10 ml/kJ.

Kidney morphology

Both *A. hottentotus* and *E. g. namibensis* possess simple kidneys with a single papilla (Sperber, 1944). In *E. g. namibensis* the renal papilla was elongate extending well down into the ureter (Fig. 1). Relative medullary area was 1.64 for *E. g. namibensis* and 1.10 for *A. hottentotus*.

Body composition

Wild and laboratory moles showed no difference in percentage fat content but body water as a percentage of total body mass and lean body mass was significantly lower in captive individuals (Table 4). Since the disparity in body water did not reflect differences in fat stores, body water turnover comparison were made on the basis of total body mass assuming a mean water content of 49.61% for captive moles and 59.88% for wild moles.

Validation trials

Isotopic water flux showed a strong positive correlation with gravimetric determinations (Fig. 2), and in seven paired comparisons no significant difference was observed between the two measurements (paired t-test: $t = 1.17$; $P > 0.05$; df = 6). Although no consistent trend was apparent, mean turnover rates based on tritium dilution were 6.23 ml/kg day (6.7%) higher than gravimetric estimates (Table 5).

Table 3. Water budget of *E. g. namibensis* fed *Tenebrio molitor* larvae

	Mean	±1 SD
No. of animals	7	
Mass (g)	27.29	6.93
% Faecal water	43.14	14.66
Water intake		
Preformed water (ml/day)	2.00	0.52
Metabolic water (ml/day)	0.72	0.22
Total intake (ml/day)	2.70	0.74
Water loss		
Faecal (ml/day)	0.36	0.08
Urine (ml/day)	0.30	0.21
Pulmocutaneous (ml/day)	2.04	0.72
Total loss (ml/day)	2.70	0.74

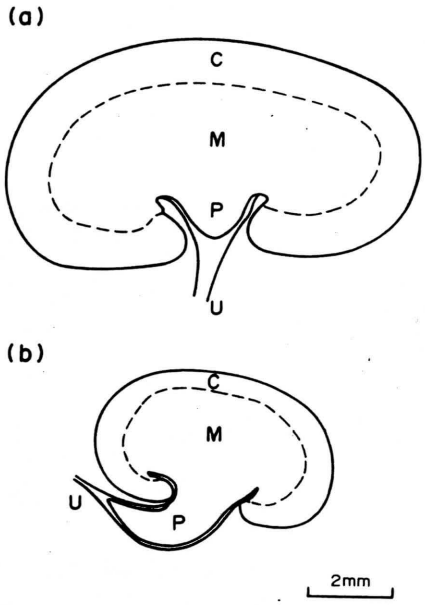

Fig. 1. Cross-section of the kidney showing the cortex (C), medulla (M), form of the papilla (P) and ureter (U): (a) *A. hottentotus*; (b) *E. g. namibensis*.

Tritiated water turnover in free-living and laboratory maintained animals

Isotopically-determined water turnover of free-living *E. g. namibensis* was significantly lower than that of laboratory maintained animals (Student's t-test: $t = 2.50$; $P < 0.05$; df = 10) (Table 6). The mean water flux of wild animals was 23% lower than that measured in the laboratory.

DISCUSSION

Interrelation of water turnover rate and daily energy expenditure

The turnover rates of energy and water are linked (Lifson and McClintock, 1966) and some correlation has been found between *ad lib.* water intake and resting energy expenditure of ruminants (MacFarlane and Howard, 1972), rodents (Mullen, 1970; Yousef *et al.*, 1974) and marsupials (Kennedy and MacFarlane, 1971). However, Withers *et al.* (1980) proposed that rates of water usage should be examined in relation to daily energy expenditure rather than

Table 4. Body composition of wild caught and laboratory maintained *E. g. namibensis*. Results expressed as the mean (±1 SD)

	Laboratory	Field	Sig.*
No. of animals	8	14	
Body mass (g)	18.69 (2.61)	20.17 (4.21)	—
Total body water (g)	9.17 (1.96)	12.18 (2.99)	—
% Water content†	49.61 (9.84)	59.88 (5.81)	$P < 0.01$
Total body fat (g)	2.94 (1.96)	2.00 (0.88)	—
% Fat content‡	28.28 (11.15)	23.71 (6.46)	$P < 0.05$
Lean body mass (g)	15.50 (1.84)	18.17 (3.61)	—
TBW/LBW§	58.07 (7.58)	66.39 (5.40)	$P < 0.02$

*Student's t-test (after arc–sin transformation).
†Expressed as percentage of total wet body mass.
‡Expressed as percentage of dry body mass.
§(Total body water/lean body mass) × 100.

Table 5. A comparison of gravimetric and isotopic water flux over a ten day period. Error (%) calculated as 100 (^{3}HHO value – gravimetric value/gravimetric value)

Animal No.	Mean body mass (g)	Water flux (ml H_2O/kg/day) ^{3}HHO	Gravimetric	% error
1	25.19	99.63	93.06	7.06
2	29.54	109.72	87.62	25.22
3	24.20	133.11	109.44	21.63
4	37.40	127.85	124.45	2.73
5	22.55	114.99	105.65	8.84
6	31.10	115.11	121.56	−5.31
7	23.66	96.67	111.71	−13.46
Mean (±1 SD)	27.66 (4.93)	113.87 (12.45)	107.64 (12.61)	6.67 (12.74)

resting rates of oxygen consumption. They added that for arid dwelling mammals which seldom drink, water turnover rate and daily energy expenditure must be coupled through diet and assimilation efficiency (since water turnover rate = preformed water + metabolic water = water intake = water loss for steady state conditions).

For granivorous desert rodents there is a low ratio of water to daily energy expenditure (WTR/DEE) of about 0.04 ml H_2O/kJ (Withers *et al.*, 1980), which is considerably less than the 0.10 ml H_2O/kJ calculated for *E. g. namibensis*.

This comparison of water exchange as a function of daily energy expenditure illustrates the major difference between mammalian insectivores and granivorous rodents in their physiological adaptation to aridity. Granivorous rodents obtain only small quantities of water from seeds and in the absence of drinking water must reduce water expenditure to a minimum by renal and permeability mechanisms (Haines *et al.*, 1974), while insectivores obtain larger amounts of water in their food.

Morton (1980) argued that in arid-dwelling insectivorous animals there is no need for adaptation to reduced water supply, since behavioural avoidance of stressful temperatures through nocturnalism and fossoriality, together with the high water content of an insect diet, effectively removes the physiological problem of water conservation. Consequently, the pattern of water usage is a direct reflection of energy turnover rate.

A major problem facing *E. g. namibensis* is a sparse and patchily distributed food resource (Fielden Perrin and Hickman, 1990), thus a low daily energy expenditure is viewed primarily as of adaptive significance to survival in an energy sparse environment. Considering the coupling between energy and water usage, low rates of energy turnover in the Namib mole results in a concomitant reduction in water requirements. Indeed, water turnover rate of *E. g. namibensis* is amongst the lowest recorded for insectivorous species measured under similar experimental conditions (Table 7).

Table 6. A comparison of tritiated water turnover in free-living and laboratory maintained *E. g. namibensis*. Results expressed as the mean (±1 SD)

	Free-living	Laboratory
No. of animals	5	7
Period of measurement (days)	9–15	10
Body mass (g)	19.76 (2.68)	27.66 (4.93)
Water turnover (ml/kg/day)	87.64 (20.07)	113.87 (12.45)

Water independance in relation to kidney function

The present study has shown that *E. g. namibensis* is independent of drinking water when fed on mealworms containing 62% water content. Free-living Namib moles feed predominantly on termites and insect larvae which have water contents ranging from 63% to 80% (Fielden, Perrin and Hickman, 1990; Redford and Dorea, 1984). It is probable, therefore, that *E. g. namibensis* can always obtain sufficient water with its food especially since excess water expenditure on heat dissipation is avoided through nocturnal and burrowing habits.

Although an insect diet has a high moisture content the high protein intake involves the liability of considerable nitrogenous wastes (Schmidt-Nielsen and Newsome, 1962). In mammals, nitrogenous wastes from protein catabolism must be excreted in urine primarily as urea. Consequently urinary water losses from an insect diet exceed those of a seed diet (Lindstedt, 1980). In some instances the additional water in an insect diet does not compensate for the increased urinary water loss. Certain species of insectivorous desert bats cannot achieve water balance on an insect diet alone and require drinking water to maintain circulation and excretion (Carpenter, 1969; Geluso, 1978). The success of these animals in deserts is because they can fly long distances to free water sources.

Thus contrary to Morton's (1980) arguments, a physiological factor limiting survival of insectivorous

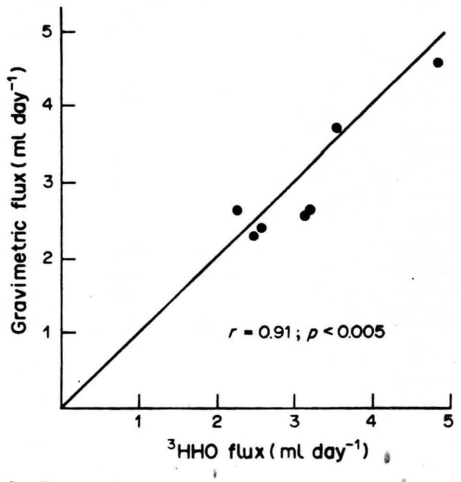

Fig. 2. Comparison of gravimetric and isotopic water turnover in *E. g. namibensis*. Solid line represents a 1:1 relationships.

Table 7. Water turnover in insectivorous mammals in the laboratory with minimum water requirements

Species	Mass (g)	Water flux ml/day	Water flux ml $kg^{-0.82}$†/day	Source
Macrotus lagotis	1081	36.6	33.2	Hulbert and Dawson, 1974
Isodon macrourus	1469	40.9	35.7	Hulbert and Dawson, 1974
Perameles nasuta	972	38.9	45.0	Hulbert and Dawson, 1974
*Eremitalpa granti namibensis**	27	2.7	51.7	This study
*Dasyurides byrnei**	127	10.0	57.8	Haines *et al.*, 1974
Antechinus stuarti	26	7.6	153.0	Nagy *et al.*, 1978
*Sminthopsis crassicaudata**	14	5.0	164.7	Morton, 1980
Blarina brevicauda	23	9.4	247.8	Deavers and Hudson, 1979

*Arid dwelling.
†Water turnover rates standardised to correct for differences in body mass using the exponent 0.82 (MacFarlane and Howard, 1972).

mammals in deserts is the capacity to excrete large quantities of urea in small volumes of urine. An examination of urinary concentrating abilities of small insectivorous mammals during water deprivation supports this conclusion (Table 8). Although there is some overlap, desert species including *E. g. namibensis* produce a more concentrated urine (2300–4300 mosmol/kg, than mesic inhabiting species (1800–3000 mosmol/kg). In the Namib mole, production of a concentrated urine reduced water loss via this avenue to only 11% of the total. In contrast, urination in the mesic dwelling shrew, *Blarina brevicauda* (Deavers and Hudson, 1979) and the dasyurid marsupial, *Antechinus stuartii* (Nagy *et al.*, 1978) accounts for 34% and 20% respectively of the total water loss on a water restricted diet.

As no information on the water metabolism of the African golden moles exists it is difficult to establish whether efficient kidney function in *E. g. namibensis* represents an adaptation to an arid environment, or whether this physiological attribute is a general characteristic of the family.

Gross kidney morphology is a reliable indicator of urinary concentrating capacity (Sperber, 1944; Schmidt-Nielsen and O'Dell, 1961). Mammals with greater kidney concentrating ability often have elongate renal papillae and more prominent medullae than animals with lesser abilities. Renal indices involving medullary areas are more strongly correlated with and thus better estimators of renal performance than ones utilizing medullary thickness (see Brownfield and Wunder, 1976, for review). The data of Brownfield and Wunder (1976) yielded the following predictive equation:

Maximum urine concentration (mosmol/kg) = 837 + 2106 RMA where RMA is relative medullary area. Using this equation the predicted maximum concentration of the urine of the Namib mole is 4300 mosmol/kg and for the Hottentot golden mole, 3200 mosmol/kg. These findings are consistent with the ecological distribution of these two species with *E. g. namibensis* having kidneys better adapted for water conservation than the mesic zone *A. hottentotus*.

The smaller size of *E. g. namibensis* (±25 g) in comparison to *A. hottentotus* (±70 g) may also account for more efficient renal function since Lawler and Geluso (1986) found renal indices to be highly and negatively correlated with body mass in sympatric heteromyid rodents of similar dietary habits. Higher concentrating abilities in smaller species were suggested as a compensatory mechanism for greater rates of evaporative water loss due to a larger surface area to volume ratio.

Validation of the ^{3}HHO *technique*

Use of the ^{3}HHO method to measure water turnover is based on several assumptions (Nagy and Costa, 1980) which under almost any conditions are violated (Lifson and McClintock, 1966; Mullen, 1971; Nagy and Costa, 1980) resulting in either over or under estimates of water flux. In burrowing and fossorial animals, violation of the assumption that no water (labelled or unlabelled) enters the body with inspired air or through the skin, is especially troublesome (Gettinger, 1983; Mullen, 1971). Burrows are often humid (Kennerly, 1964) hence animals inhabiting such environments will receive a considerable

Table 8. Mean osmotic concentration of the urine of insectivorous mammals in the laboratory during water restriction

Species	Urine osmolarity (mosmol/kg)	Source
Arid zone		
Pipistrellus hesperus	4340	Geluso, 1978
Hemiechinus auritus	4010	Yaakobi and Sholkni, 1974
Antrozous pallidus	3980	Geluso, 1975
Eremitalpa granti namibensis	3820	This study
Paraechinus aethiopicus	3634	Yaakobi and Sholknik, 1974
Macrotis lagotis	3566	Hulbert and Dawson, 1974
Onychomys torridus	3180	Schmidt-Nielsen and Haines, 1964
Sminthopsis crassicaudata	2322	Morton, 1980
Mesic zone		
Erinaceus europaeus	3062	Yaakobi and Shkolnik, 1974
Isoodon macrourus	2942	Hulbert and Dawson, 1974
Myotis volans	2910	Geluso, 1978
Planigale maculata	2317	Morton, 1980
Blarina brevicauda	1820	Deavers and Hudson, 1979

input of water vapour. Similarly, within the confined microenvironment of a mole submerged in sand, accumulation of water vapour from respiratory surfaces and excreta may reach near saturation levels.

Nagy and Costa (1980), concluded that water flux measurements in burrowing and fossorial mammals are more likely to include overestimates due to unlabelled vapour influx than underestimates resulting from labelled vapour influx. In Kangaroo rats (*Dipodomys merriami*), these authors found overestimates due to unlabelled influx resulting in errors of up to 52% and 20% in moist and dry burrows respectively.

In validation trails for *E. g. namibensis* tritiated water turnover was strongly correlated with, and did not differ significantly from, gravimetric water turnover. Nevertheless, five of seven isotopic measurements overestimated actual water flux (error 3–25%) indicating that unlabelled water vapour influx introduced some error into calculations of turnover rates. Similar overestimations can be expected for free living animals which spend much of the day buried in dune sand. Since water flux rates were not consistently overestimated by isotope turnover, a second source of error may have arisen from the assumption that all test animals had a total body water content of 49.6%. Underestimates of body water would result in underestimates of water flux and vice versa. Thus tritiated water turnover, as it was measured here, appears useful as an index but does not measure water turnover *per se*.

For free-living animals, a constant body water content of 59.9% was assumed. The reason for higher water contents in wild moles is not known since no significant difference in fat content was noted between wild and captive individuals. In other studies higher water contents in wild animals in comparison to captive individuals have been attributed to the accumulation of excess fat in captivity (Churchfield, 1981; Holleman *et al.*, 1982; Richmond *et al.*, 1960).

Water and energy flux in the field

Water fluxes of free-living desert insectivores are typically higher than minimum water turnover rates measured in the laboratory (Hulbert and Dawson, 1974; Hulbert and Gordon, 1972; Morton, 1980). Higher rates in the field reflected the extra metabolic demands of a free life and sometimes the intake of free water (Morton, 1980). In contrast *E. g. namibensis* had a significantly lower water turnover rate in the field than in the laboratory.

Whether the relative contributions of the different avenues of water intake were the same in the wild as in the laboratory is not known. Condensed fog provides a source of drinking water for many Namib dune animals (Hamilton and Seely, 1976; Louw, 1974) and fog precipitation did occur during the study period. However, it is significant that the distribution of *E. g. namibensis* is not confined to the Namib fog belt as for *Bittis perinqueyi* and *Aporosaura anchietae*, two reptiles which make regular use of condensing fog water (Louw, 1972). Furthermore, water provided to captive animals in a shallow Petri dish was always ignored, whereas other golden moles and talpid moles drink freely in captivity (Kuyper, 1979; Mellanby, 1967). These observations suggest that Namib moles seldom drink but rely solely on dietary water intake.

For animals that obtain moisture exclusively from their food, estimates of energy expenditure can be derived from measurements of water flux (Gettinger, 1984; Green and Eberhard, 1983; Sapsford and Mendelsohn, 1984; Withers *et al.*, 1980). Since $WTR/DEE = 0.10$ for *E. g. namibensis* it follows that $DEE = WTR/0.10$ (Withers *et al.*, 1980). Assuming the same WTR/DEE ratio for free-living moles as captive moles, field metabolic rate was calculated as field water turnover rate (ml/day)/ $0.10 = 17.8$ kJ/day.

Estimates of daily energy expenditure for free-living moles were less than measurements on laboratory animals (25.84 kJ/day) which were not involved in searching for food, mates and predator avoidance. Such low field metabolic rates reflect energy conservation. Fielden, Waggoner, Perrin and Hickman (in press) postulated employment of diurnal torpor by Namib moles as a means of reducing energy expenditure in an environment where food availability is limited. The results of this present investigation support these previous conclusions. Since a lowered rate of metabolism results in a reduction of water loss in respiration and in the excretion of metabolites, torpor is also as an effective water conserving mechanism (Bradford, 1974; Buffenstein, 1984).

In caution, the precision of the relationship between water turnover and metabolisable energy depends largely on the accuracy of water turnover measurements and on the predictability of the water and energy content of the prey (Sapsford and Mendelsohn, 1983). It has been shown that isotopic water flux in *E. g. namibensis* is subject to some error. Furthermore, energy and water content of the Namib mole's major prey resource, the dune termite (Fielden, Perrin and Hickman, 1990) may differ from that of mealworms resulting in a different WTR/DEE ratio to that measured in the laboratory. Thus estimates of field energy expenditure in *E. g. namibensis* must remain tentative until other experimental techniques are applied. Procedures anticipitated include employment of doubly labelled water ($D^{18}O$ or $^{3}HH^{18}O$), a technique which has been used frequently and successfully on vertebrates (see Nagy, 1987, for review).

SUMMARY

While nocturnal and burrowing habits may enable Namib moles to avoid excess water expenditure on heat dissipation, it does not provide an escape from the usual surface conditions of water scarcity. Exploitation of an insect food resource does not remove the physiological problem of water conservation and for *E. g. namibensis* to survive without drinking necessitates an efficient kidney function. Low rates of energy usage and employment of torpor are further effective in reducing overall water requirements.

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